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MORPHOLOGY AND DISTRIBUTION OF *HETEROTHECA CAMPORUM* VAR. *GLANDULISSIMA* AND ITS OCCURRENCE ON SHALE SUBSTRATES IN NORTHEASTERN TENNESSEE

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ABSTRACT

The geographical range of *Heterotheca camporum* var. *glandulissima* is expanded to include four counties in northeastern Tennessee. Most of the newly reported occurrences are found in the Booher Knobs region, an area of shale knobs overlain with Montevallo soils. Large populations occur at several localities, often associated with quarries and roadsides but occasionally in more natural sites. In this region, there appears to be high fidelity to the shale substrate. The morphology of the northeastern Tennessee plants was similar to prior descriptions of *H. camporum* var. *glandulissima* except on some plants peduncle and phyllary glands were sparse or absent. There is evidence of population differentiation for the density of phyllary glands. The species appears to have undergone relatively recent proliferation in the shale belt but the time of initial colonization of the region and the shale knobs remains questionable.

The genus *Heterotheca* (Asteraceae) is restricted to North America and Mexico with a center of diversity in the Great Plains and southwestern U.S. (Harms 1963; Semple 1996, 2006; Nesom 2020). *Heterotheca camporum* (Greene) Shinners is the easternmost representative of the *H. villosa* species group of sect. *Phyllotheca* (Harms 1963; Semple 2006; Nesom 2020). Although H. *camporum* is uniformly tetraploid (2n = 36) throughout its range, observations of geographically based morphological variation have been noted for plant height, leaf width, leaf margin teeth, and leaf and phyllary pubescence and glandularity (Harms 1963; Semple 1983). There are indications that plants from northern parts of the geographical range have narrower leaves and are more densely glandular on upper stem leaves and phyllaries. However, Harms (1963) concluded that an absence of correlations among these characters and range-wide variability in most characters argue against recognition of subspecific taxa. Further, an environmental influence on the variable characters was detected in two common garden experiments, one based on seedlings and the other on transplants (Harms 1963; Nesom 2020) but in an experimental transplant of rootstocks, the dense glandularity remained fixed (Semple 1983).

While acknowledging range-wide variation in most morphological characters, Semple (1983) nevertheless, showed that plants from the eastern part of the geographical range (Alabama, Kentucky, North Carolina, Tennessee) tend to be taller in stature with more glandular but less pubescent upper stems, peduncles, and phyllaries. On the basis of this geographically based morphological differentiation, Semple recognized *Heterotheca camporum* var. *glandulissima* Semple. Moreover, an examination of herbarium specimens showed that var. *glandulissima* had recently colonized the eastern portion of its current range, having been absent prior to 1925 (Semple 1983). From 1925 to 1949 the species became widespread in central Tennessee and reached one county each in northern Alabama and central Kentucky. Further range expansion, south to Mississippi, north to Virginia, and east to eastern North Carolina occurred from 1950–1983 (Semple 1983). The range of var. *glandulissima* was subsequently updated to include western Arkansas and western Missouri (Semple 1996).

Under Semple's varietal delineation, *Heterotheca camporum* var. *camporum* is "endemic to limestone bluffs, cedar glades, and sandy prairie in the Prairie Peninsula region of the midwestern U.S." extending south to eastern Missouri and northern Arkansas at elevations of 100–300 meters. East of the Mississippi River, the distribution of var. *glandulissima* is allopatric with var. *camporum*, with locations in central Tennessee east to the Ridge and Valley physiographic province of Tennessee and Virginia, where it is found on "limestone bluffs and glades, roadsides, fields, and disturbed areas" and up to more upland elevations (30–760 m) (Cronquist 1980; Semple 1983, 1996). Nesom (2020) updated the distribution of var. *glandulissima* by adding sites throughout the Southeast as well as expanding the region of parapatry to var. *camporum* in northern Arkansas and southern Missouri.

The goal of this study was to further update the geographic range of *Heterotheca camporum* var. *glandulissima* with an emphasis on fine-scale analysis of occurrences in northeastern Tennessee and to conduct a comparison of diagnostic morphology of specimens from the new locations to literature descriptions. The relationship of var. *glandulissima* to shale and shale-derived soils was examined for southeastern specimens. In addition, a locality for *H. subaxillaris* (Britton & Rusby) that was located in 2015 was examined to determine whether the species has established in the region. These goals were accomplished by field work in northeastern Tennessee and an examination of herbarium specimens using the SERNEC online database (SERNEC 2020).

METHODS

Study site

Localities were most intensively searched from 2017–2020 in the three-county area of Carter, Sullivan, and Washington cos., Tennessee, with an emphasis on the region referred to (on some topographic maps) as the Booher Knobs (Figs. 1, 2). These knobs trend southwest to northeast with a long axis represented in the southwest as two fingers in Johnson City (Washington Co.) extending northeast to Bluff City (Sullivan Co.), and ranging on the short axis from Watauga (Carter Co.) on the southeast, north to Piney Flats (Sullivan Co.). The knobs are easily recognized as highly dissected, steep, low hills (elevation 460–580 m) (Fig. 2B). The area is underlain by rocks of the Sevier Shale (Middle Ordovician), comprised in northeastern Tennessee a series of light blue calcareous shales that weather to yellowish-brown channery loam soils (Keith 1895; Prouty 1946; Hardman et al. 1966; Nandi et al. 2009) (Figs. 1C, 2, 3). Montevallo soils dominate the uplands of the Booher Knobs. On moderate to steep slopes, these soils are acid, well-drained, low in organic matter and therefore subject to drought (Davis 1994).

Exploration of the knobs of northeastern Tennessee was part of a larger floristic study of the knobs. A characteristic flora, composed of species not common elsewhere in the region, is associated with the Montevallo soil of the knobs. The shale has been mined at several quarries in the region, some currently in operation and many that were small, abandoned, and not reclaimed, leaving a substrate devoid of topsoil but a surface dominated by exposed loose shale with fragments approximately 1–8 cm^2 in size (Figs. 1, 4). The study of *Heterotheca camporum* was initiated particularly because it appeared to have some fidelity to this geographically distinct area, i.e., the species was widespread and abundant there but relatively scarce elsewhere in the region.

Geographic distribution and habitat

The SERNEC (2020) database was searched for specimens in states of the southeastern USA, i.e., the hypothesized recently colonized region, to update the geographic distribution and to use specimen label data to assess associations with substrate and soil. Particular emphasis was placed on whether there were prior reports of the species in knob-like topography or on shale-derived soil. For the northeastern Tennessee region, field collections from the knobs region were made during the 2017–2020 growing seasons.

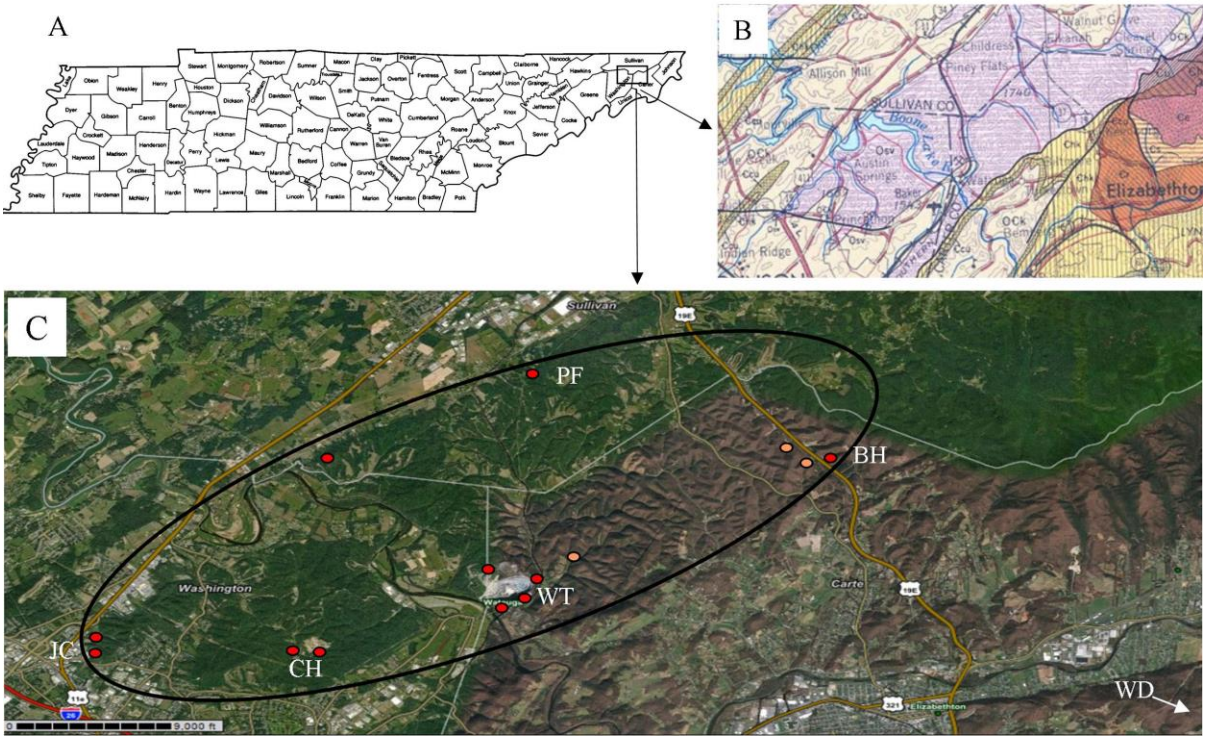

Figure 1. Location of the Booher Knobs in northeastern Tennessee. A. Map of Tennessee with ellipse highlighting study location encompassing parts of Carter, Sullivan, and Washington County. B. Portion of geological map showing the Sevier Shale (pink) northwest of Elizabethton and northeastern of Johnson City (map from Hardman et al. 1966). C. Air photo of the study location showing collection sites for *Heterotheca camporum* var. *glandulissima* specimens used in the morphological analysis (red dots) and other sites with abundant populations (pink dots). The large quarry visible due south of the three-county boundary is located in the town of Watauga. Population acronyms; BH = Bunker Hill, CH = Cash Hollow, JC = Johnson City, PF = Piney Flats, WD = Watauga Dam, WT = Watauga Town

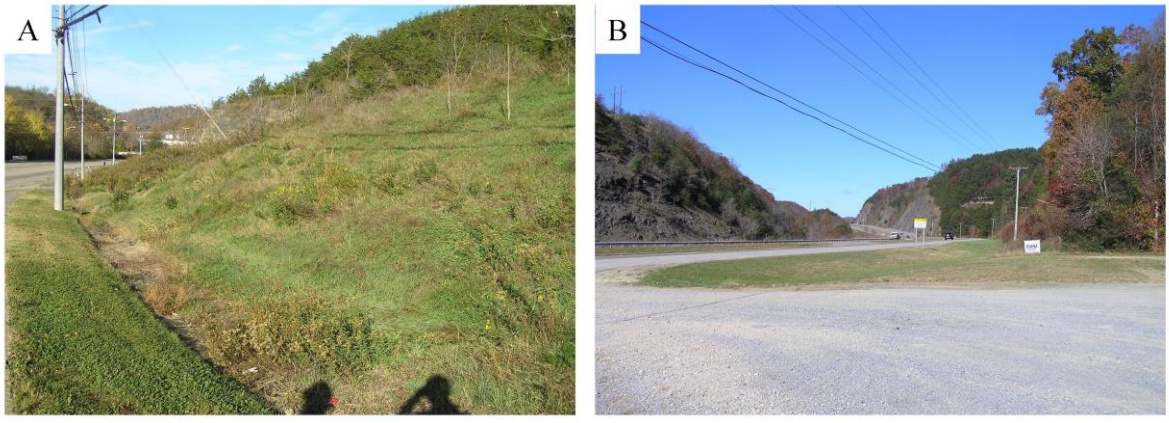

Figure 2. The Booher Knobs region of northeastern Tennessee. A. Disturbed area at the southern finger of the region in Johnson City with scattered plants of *Heterotheca camporum* var. *glandulissima*. B. Road cuts through the shale knobs looking north along Rt. 19E towards Bunker Hill. Plants are abundant in some areas of these road cuts and roadsides.

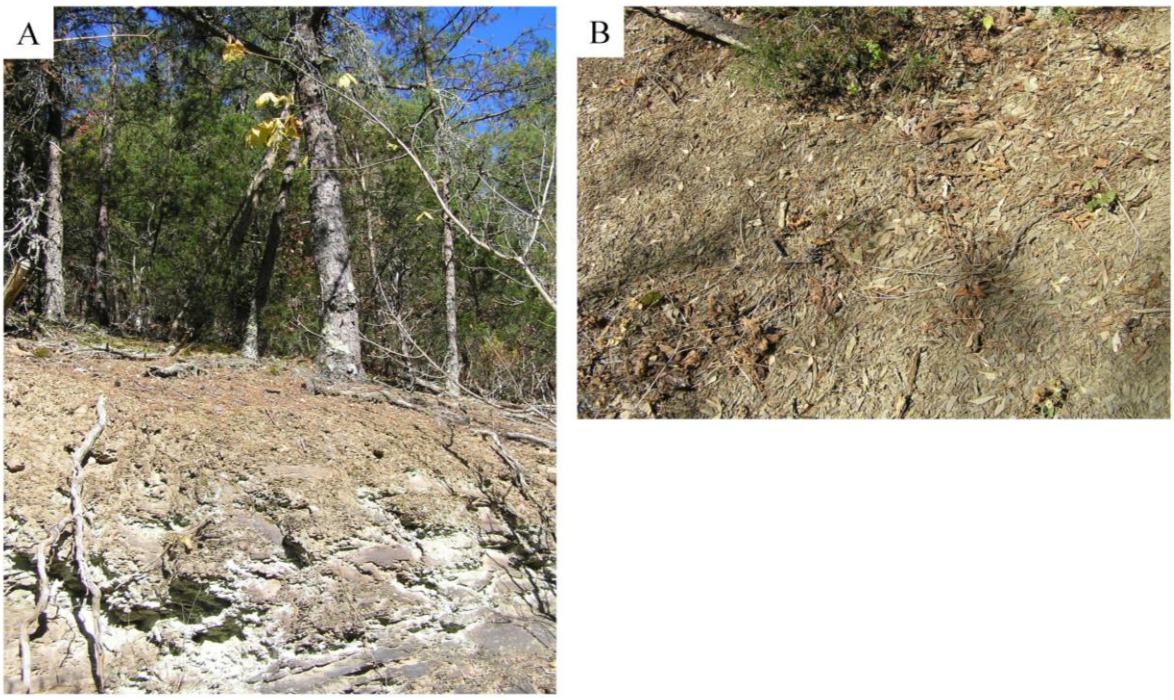

Figure 3. A. Natural outcropping of the Sevier Shale on a south-facing slope with *Pinus virginiana* in the background. B. Yellowish-brown channery loam of the Montevallo soil.

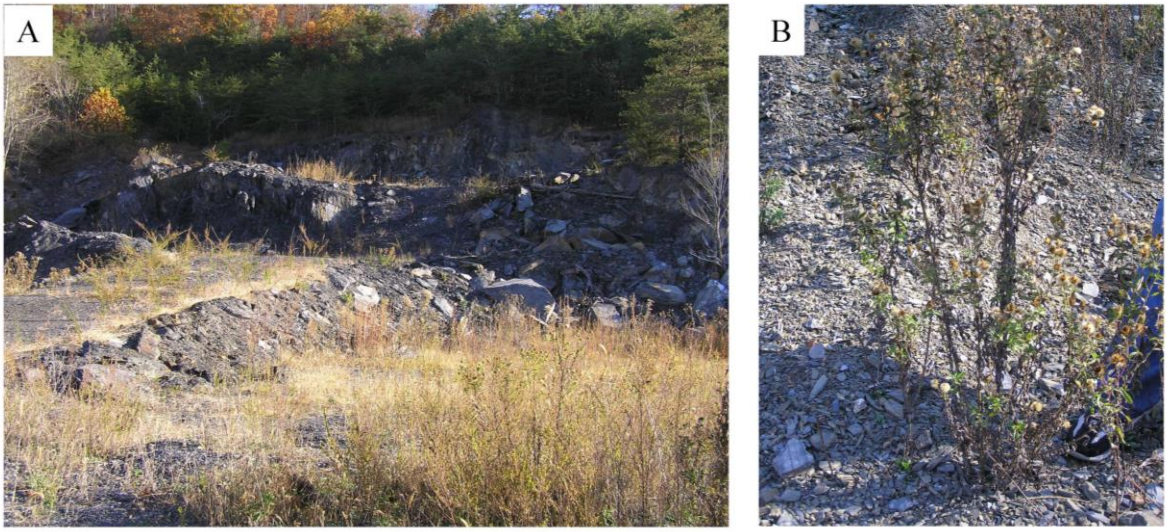

Figure 4. A. Abandoned quarry with *Heterotheca camporum* var. *glandulissima* in the foreground and *Pinus virginiana* in the background. B. Tall plant (~110 cm) of *H. camporum* var. *glandulissima* growing directly in the shale debris of former quarry.

Morphology

A morphological analysis was carried out to quantify the density of glands and hairs on diagnostic tissues, determine if plants from the shale region were similar to those in the remainder of the range of *Heterotheca camporum* var. *glandulissima*, and determine whether there were differences among populations within the shale region. The sample consisted of 27 plants from six populations, five in the Booher Knobs and one at Watauga Dam, with 3–6 plants per population. All plants were collected within a 5-day span to minimize potential seasonal influences on morphology. Nine characters were measured, all except leaf length and width chosen because they were diagnostic for *H. camporum* var. *glandulissima* (Table 1). A correlation analysis was carried out with significance based on the Pearson correlation coefficient, and an analysis of variance was conducted for each character to determine if populations differed. Analyses were carried out using SAS v. 9.4 (SAS Institute Inc. 2016).

RESULTS

Heterotheca camporum var. *glandulissima* was collected from seven northeastern Tennessee localities within the tri-county Booher Knobs area (Fig. 5), one locality at Watauga Dam (Carter Co.), and one locality at the Holston Army Ammunition Plant (Greene Co.). All of the Booher Knobs localities were from shale substrates including four in proximity to quarries and the remainder from roadsides and adjoining open areas. Distinctions between "populations" at some locations was relatively subjective because plants were exceedingly abundant and occurred in more or less continuous distributions along roadsides or in quarries and adjoining areas. The species was often the dominant one where it occurred or was intermixed with exotics such as *Lespedeza sericea* and natives such as *Solidago speciosa*, *Symphyotrichum pilosum* var. *pilosum* and *Vernonia gigantea*.

In the ETSU herbarium, older specimens of *Heterotheca camporum* var. *glandulissima* (collection dates ranged from 1976–1995) from beyond the knobs region include one sheet from the Watauga Dam locality, one from Warrior's Path State Park (Sullivan Co., probably a dolomite substrate), and two from indefinite locations in Johnson City (Washington Co.). There were also five sheets from the shale knobs collected in 2018.

A persistent (> 5 years) population of *Heterotheca subaxillaris* was found in proximity to the railroad yard at Erwin (Unicoi Co.). The species is common along the margins of the railroad tracks, in the yard area, and along the periphery of the adjacent roadside for a distance of about 0.5 km. Traveling east, this railroad yard is located in the final town prior to entering the Nolichucky River gorge, a major artery for transport of coal from Kentucky and West Virginia to the Piedmont of North Carolina. Similarly, in Tennessee, *H. subaxillaris* has been reported in proximity to railroads in Davidson, Knox, Marshall, and Sumner cos., Tenn (SERNEC 2020).

The morphology of *Heterotheca camporum* var. *glandulissima* from northeastern Tennessee is largely consistent with the original literature description in having sparse phyllary pubescence but abundant glands and peduncles and upper stems that were more glandular and less pubescent (Table 1, Fig. 6). Plant height was exceptionally variable — plants less than 20 cm on debris-strewn rocky quarry sites may flower but in deeper substrates some plants attained the reported tall stature (> 120 cm). Leaf length and width were the only variables with a significant correlation ($r = 0.78$, $P < 0.0001$). There were significant differences among populations only for the density of phyllary glands (fig. 6). An a posteriori test showed plants from Cash Hollow (CH) tended toward a higher density of glands compared to Piney Flats (PF), Bunker Hill (BH), and Watauga Dam (WD) but not significantly more than Johnson City (JC) or Watauga Town (WT) (ANOVA: $F_{5,21} = 4.78$; $P = 0.005$; means: CH = 14.6,WT = 11.0, JC = 10.8, WD = 5.3, PF = 5.0, BH = 4.0).

Table 1. Characters measured and their means and ranges for the morphological analysis of *Heterotheca camporum* var. *glandulissima* from northeastern Tennessee. Measurements from Semple (1983) are shown for comparison. Sample size = 22–27 per character, densities expressed as number per 1.0 x 0.2 mm rectangle, s.d. = standard deviation of the mean, n.d. = not done

Character	Description	Mean (s.d.)	Range	Semple (1983) Mean (Range)
Height (cm)	stem base to top of highest head	67.3 (13.8)	46–103	95.7 (35–140)
Upper leaf length (mm)	leaf 10 cm from bottom of lowest inflorescence branch	47.5 (11.6)	26–74	35.3 (15–70)
Upper leaf width (mm)	leaf 10 cm from bottom of lowest inflorescence branch	10.5 (3.4)	4–16	7.2 (2–16)
Upper stem glands	number of glands per 1.0 x 0.2 mm rectangle; 3 cm from lowest inflorescence branch	13.5 (7.1)	3–32	few/many
Upper stem hairs	number of hairs per 1.0 x 0.2 mm rectangle; 3 cm from lowest inflorescence branch	1.4 (1.1)	0–4	n.d.
Peduncle glands	number of glands per 1.0 x 0.2 mm rectangle; 1 cm below uppermost head	13.3 (9.3)	2–42	many
Peduncle hairs	number of hairs per 1.0 x 0.2 mm rectangle; 1.0 cm below uppermost head	2.5 (2.3)	0–8	n.d.
Phyllary glands	number of glands per 1.0 x 0.2 mm rectangle; from phyllary upward curve of the second phyllary series from outside	8.9 (5.5)	0–22	many
Phyllary hairs	number of glands per 1.0 x 0.2 mm rectangle; from phyllary upward curve of the second phyllary series from outside	0.6 (0.9)	0–3	sparse

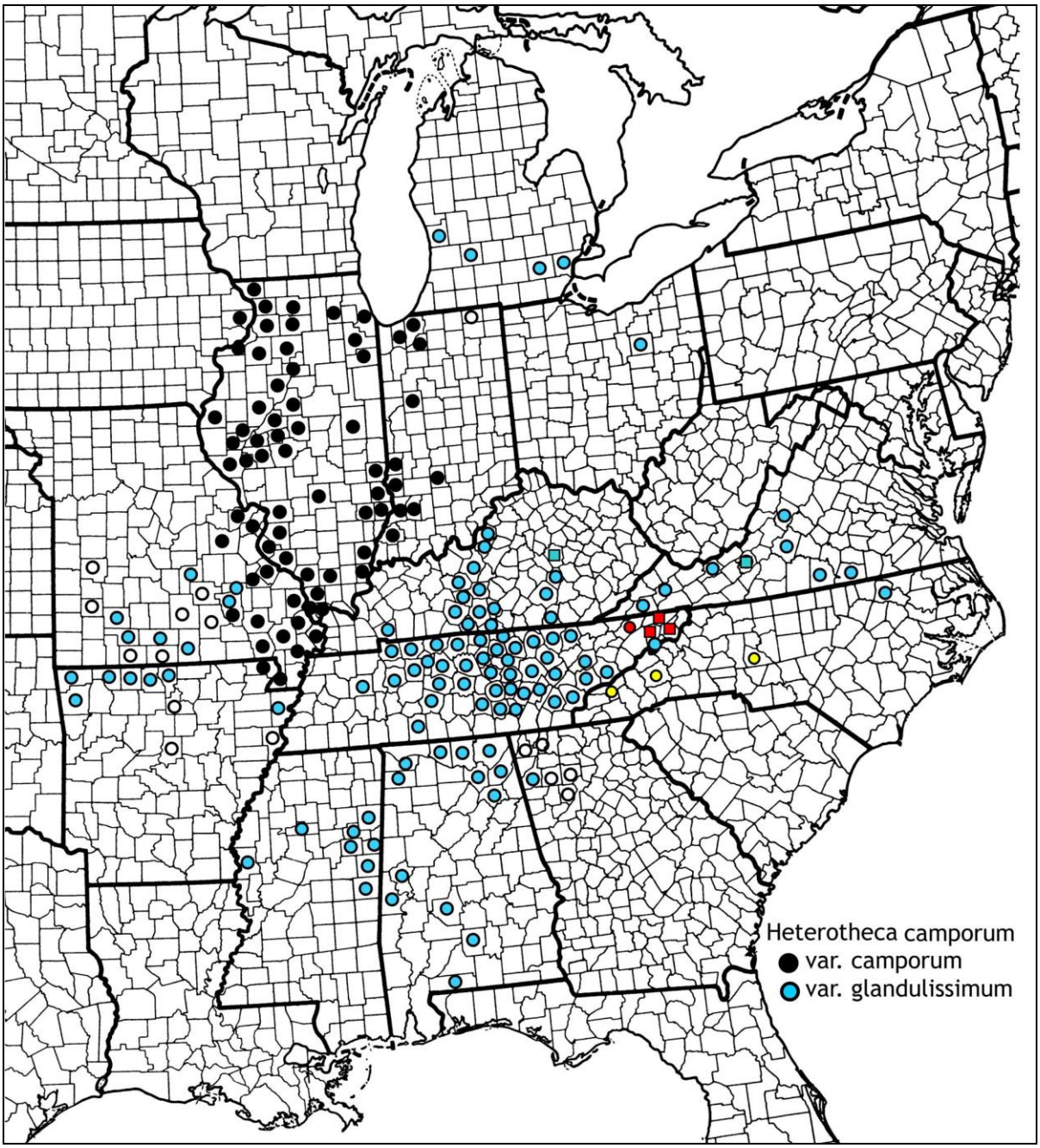

Figure 5. County distribution map of *Heterotheca camporum* var. *camporum* (black) and var. *glandulissima* (blue) (based on Nesom 2020, used by permission) (unfilled dots were specimens not seen by Nesom), showing newly added counties in northeastern Tennessee from current field work (red), and newly added counties in North Carolina from database records (yellow). Squares (three in northeastern Tennessee, one each in Kentucky and Virginia) represent collections from shale substrates.

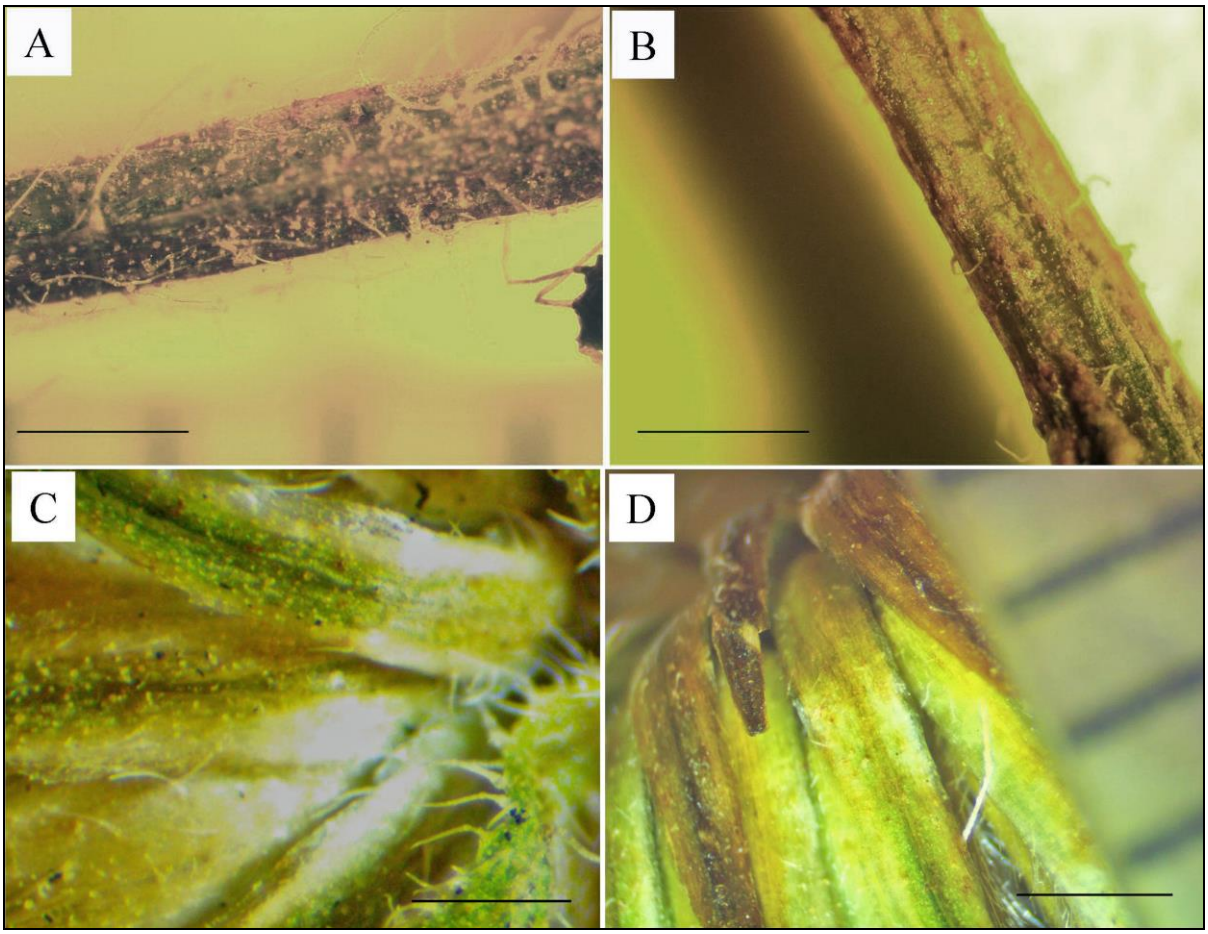

Figure 6. Peduncles with dense (A) or sparse (B) glands and phyllaries with dense (C) or sparse (D) glands. All specimens from northeastern Tennessee, deposited at ETSU and collected by Levy and Walker (A = *20463c*, B = *20466*, C = *20456b*, D = *20466*). Scale bar = 1mm.

Distribution and habitat

Montevallo soils extend far beyond the Booher Knobs region, ranging from Alabama north to Virginia in the Ridge and Valley physiographic province (Soil Web 2020). Although *Heterotheca camporum* var. *glandulissima* has high fidelity to this soil series in the Booher Knobs region and Montevallo soils extend north with little interruption, var. *glandulissima* is regionally rare outside the core knobs area. Similarly, some of the other characteristic Booher Knobs species (*Brickellia eupatorioides* var. *eupatorioides*, *Opuntia humifusa*, *Penstemon brevisepalis*) are largely restricted to the core tri-county area. If these species can be considered bioindicators, there must be a sufficient change in habitat that is not readily apparent from an examination of physiography, soils, and dominant flora. Regardless of the reason for restriction to the Booher Knobs, the rarity of other sites in the region and the scarcity of shale-associated specimens elsewhere suggests an experimental test for of ecotypic differentiation would be worthwhile.

The occurrence of *Heterotheca camporum* var. *glandulissima* at the Holston Army Ammunition Plant in Hawkins County represents a location that would more closely link northeastern Tennessee to the more common locales further south and west and would require less of a long-distance dispersal to reach the knobs. In Virginia, the species has been reported from 8 counties (SERNEC 2020; Virginia Botanical Associates 2020) and has apparently spread rapidly over limestone, dolomite, and disturbed areas in recent decades, especially along the median of I-81 in the Ridge and Valley physiographic region (G. Fleming, pers. comm.). Two specimens from

Montgomery County were associated with shale, one of which is from a "channery soil on hillside" north of Ironto. Ironto is the southern limit of the shale barrens associated with the Brallier shale formation (Wherry 1930; Platt 1951). Based on the label location, this specimen was likely collected from the Berks soil, a channery loam derived from shale. Of the 16 counties in Kentucky with specimens of var. *glandulissima*, the only specimen citing a shale substrate was from Madison County. Although many herbarium specimens lack substrate data, none of the specimens from Alabama, Georgia, North Carolina, and Tennessee (south and west of the study region) listed shale as a substrate but limestone, dolomite, chalk (Alabama), and roadsides were frequently cited.

Nesom (2020) questioned the hypothesis of recent colonization of the eastern part of the range of *Heterotheca camporum* var. *glandulissima*. In a list of habitats in the native geographical range, Nesom (2020) also included shale outcrops along with the more commonly cited limestone, chalk, and roadside occurrences. Moreover, Nesom also noted specimens of eglandular plants collected in Alabama. At Shell Hollow in the knobs, the species was found directly on a naturally-occurring shale outcrop. More information on such potentially natural occurrences is difficult to obtain because there is little public land in the knobs region and undisturbed sites are rare. In the knobs, *Heterotheca camporum* var. *glandulissima* can be abundant over large areas (> 1 ha), but it appears to have very low tolerance of shade or competition. At sites that are more vegetated than rock outcrops or channery shale debris, plants are smaller, less floriferous, and populations are sparser. Therefore the species may be easily eliminated from more fertile and stable sites.

Nesom further suggested that the destruction of the UKT Herbarium by fire in 1934 may explain the absence of Tennessee specimens prior to 1925. However, A. Gattinger, a prolific explorer and collector of the Tennessee flora, especially in the Nashville Basin, left no duplicates of *H. camporum* among the 1407 Tennessee specimens listed on SERNEC and did not include H. *camporum* in his floras (Gattinger 1897, 1901). Albeit negative evidence, this suggests the species was either absent in Tennessee or much rarer compared to modern times.

Morphology

Based on an absence of significant character correlations, the densities of hairs and glands appear independent of each other and the density of each varies independently among plant tissues (stems, peduncles, phyllaries). Further, the densities of glands and hairs were not inversely correlated as might be expected if they were differential responses to different environmental cues. A consequence of this character independence was the observation of population differentiation for phyllary glands, but not for other pubescence or gland characters. Population differentiation suggests there has been sufficient time and isolation among populations for differences to arise; alternatively, there may have been differences among founding propagules of populations or the observation of population differentiation may have been a sampling artifact. The relative degree of uniformity within individuals and within populations argues against the sampling artifact hypothesis.

Morphological character values for stem height, leaf length, and leaf width were congruent with those reported by Semple (1983) (Table 1). For the gland and hair traits that were reported qualitatively by Semple, the density of upper stem glands and phyllary pubescence agreed with Semple's descriptions of "few/many," and "sparse," respectively. However, Semple described peduncle and phyllary glands as "many" but the observations here ranged from few or zero, respectively, to many for each (Fig. 6). Nesom (2020) also noted specimens from Alabama and Mississippi chalk outcrops that were eglandular.

The observations of *Heterotheca camporum* var. *glandulissima* from northeastern Tennessee expand the diversity of preferred habitats and demonstrate a greater degree of morphological variation than previously reported. In northeastern Tennessee, the species appears to have undergone relatively

recent proliferation in the shale belt but with uncertainty surrounding the extent of habitation of natural sites, the time of initial colonization of the region and the shale knobs remains questionable.

Specimens examined (all at ETSU and collected by *Levy and Walker*; * = specimens used in the morphometric analysis). *Heterotheca camporum* var. *glandulissima*. Tennessee. Carter Co.: Rte 19E, E side, ~2 mi S Bunker Hill Rd, Sevier Shale, abundant in open areas, 9 Nov 2020, *20463a–e**; Watauga Dam, N side, 10 Nov 2020, *20465a–c**; Watauga Dam, S side, 10 Nov 2020, *20466**; near upper end of Watauga Dam, on bluffs alongside dam, 8 Oct 2015, *15755*. Hawkins Co.: Holston Army Ammunition Plant, one plant in field in sun; 1/4 mi E main gate, 1/4 mi S Rte 11W, 7 Sep 2019, *19845*; Holston Army Ammunition Plant, ~0.1 mi E of E boundary of HAAP, 0.2 mi NE of water trmnt plant, colony in field with gravel, 29 Sep 2019, *191043*. Sullivan Co.: Piney Flats, Piney Flats Rd, just S of RR crossing, Sevier Shale, abundant around periphery of quarry, 9 Nov 2020 *20463a–c**; Piney Flats Rd just S of RR crossing, 1/2 mi S of Piney Flats Center, old quarry of Sevier Shale, this species has complete fidelity to the Sevier Shale, 30 Aug. 2018, *18355*. Washington Co.: N side East Oakland Ave across from Springbrook Dr, Johnson City, Sevier Shale, old quarry and adjacent area, abundant, 7 Nov 2020, *20456a–d**; N side East Oakland Ave across from Springbrook Dr, Johnson City, Sevier Shale, old quarry and adjacent area, abundant, 8 Nov 2020, *20456a–b**; Cash Hollow, ~1 mi N East Lakeview Dr, Johnson City, Sevier Shale, abundant at old quarry, 8 Nov 2020, *20458a-c**; Cash Hollow, ~1 mi N East Lakeview Dr, Johnson City, Sevier Shale, around landfill, 8 Nov 2020, *20459a-b**; Watauga town, near jct Piney Flats Rd, along RR tracks, 9 Nov 2020, *20460**; Watauga town, 1/4 mi N jct Piney Flats Rd, Sevier Shale, abundant around periphery of quarry, 9 Nov 2020, *20461**; Watauga town, near jct Piney Flats Rd., Sevier Shale, abundant around periphery of quarry, 9 Nov 2020, *20462a–b**; Sevier Shale, above General Shale and Brick near intersect. of Princeton Rd and Oakland Ave, abundant over shale, 26 July 2018, *18263*; near intersect. of Princeton Rd and Oakland Ave, above Toyota dealership, ubiquitous on eroded black shale of Sevier Shale, in sun, 14 Sep 2018, *18377*; Persinger Rd, Sevier Shale belt, disturbed area on shale in sun, absolute fidelity to the shale, 18 Sep 2018, *18383*; Herb Hodge Rd along Watauga River just S of Sullivan Co. line, over shale, plants 4-5' tall, 25 Oct 2018, *18463*.

***Heterotheca subaxillaris*. Tennessee.** Unicoi Co.: Erwin, along RR across from animal shelter near water treatment plant, in sun, many plants, 29 Sep 2015, *15691*; Erwin, W side of RR yard, W side of N Industrial Dr., common at roadside and in RR area, 7 Nov 2020, *20467, 20468, 20469*.

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