**The *Heterotheca villosa* group in the Great Plains**

Taxonomic arrangements of the Great Plains heterothecas have varied and identifications have been inconsistent. For the most part, generally recognized entities ("angustifolia," "ballardii," "hispida," "villosa") are tetraploid, which facilitates hybridization and introgression, but ideas of their sympatry and interaction have been obscure and the frequency and abundance of such genetic mixing remains speculative. Diploids occur in *Heterotheca canescens* and *H. stenophylla* and these, too, appear to interact with tetraploids. The treatment here attempts to provide a morphological and evolutionary overview and at least a pragmatic basis for further study.

Harms (1963) included *Heterotheca hirsutissima* (identified as *H. horrida*) as part of this group, but with its consistent diploidy and lack of capitular bracts, it appears to be less immediately related. It does not hybridize or intergrade extensively with any of the "Great Plains villosa group."

**Key to Great Plains species of the *Heterotheca villosa* group**

1. Leaves linear to narrowly oblanceolate, rigid, margins narrowly revolute; trichome bases strongly multicellular-pustulate.
   2. Involucres 9–17 mm wide (pressed); leaves 1–6 mm wide; leaf and bract margins long-ciliate along at least the proximal 1/2 ..... 15. **Heterotheca stenophylla**
   2. Involucres 5–8 mm wide (pressed); leaves 0.5–2(–4) mm wide; leaf and bract margins eciliate or short-ciliate along proximal 1/5–1/4.
      3. Leaf surfaces short-strigose; phyllaries eglandular and sparsely strigose, or glabrous except minutely glandular proximally, or sparsely sessile-glandular ..... 14. **Heterotheca angustifolia**
      3. Leaf surfaces hispidulous to hispid-hirsute; phyllaries densely sessile-glandular and without other hairs or sessile-glandular and sparsely strigose ..... 16. **Heterotheca scabrifolia**

1. Leaves of various shapes, including linear in *H. canescens*, not rigid, margins not revolute; trichome bases usually wider than the extended portion above but not strongly multicellular-pustulate.
   4. Stems strigose to strigose-sericeous or strigose-villous, hairs antrorsely oriented, sometimes with antrorsely oriented understory and spreading overstory.
      5. Leaf surfaces and phyllary apices eglandular; involucres 11–15 mm wide; rays 20–26 ..... 11. **Heterotheca villosa**
      5. Leaf surfaces and phyllary apices (distal 1/4) sessile-glandular; involucres 7–10 mm wide; rays 12–22 ..... 13. **Heterotheca canescens**
   4. Stems hirsutulous to hirsute, hirsute-pilose to hirsute-villous, or hispid-pilose, hairs spreading to spreading-deflexed in both the understory and overstory.
      6. Stems and leaves densely and conspicuously sessile-glandular; involucres 7–10 mm wide ..... 17. **Heterotheca wisconsinensis**
      6. Stems and leaves eglandular; involucres 8–13 mm wide or (12–)14–20 mm wide.
         7. Heads mostly relatively short-peduncled in a compactly corymboid arrangment; involucres 8–13 mm wide; ray flowers 13–24 ..... 10. **Heterotheca hispida**
         7. Heads mostly long-peduncled and solitary; involucres (12–)14–20 mm wide; ray flowers (25–)30–55 ..... 12. **Heterotheca ballardii**

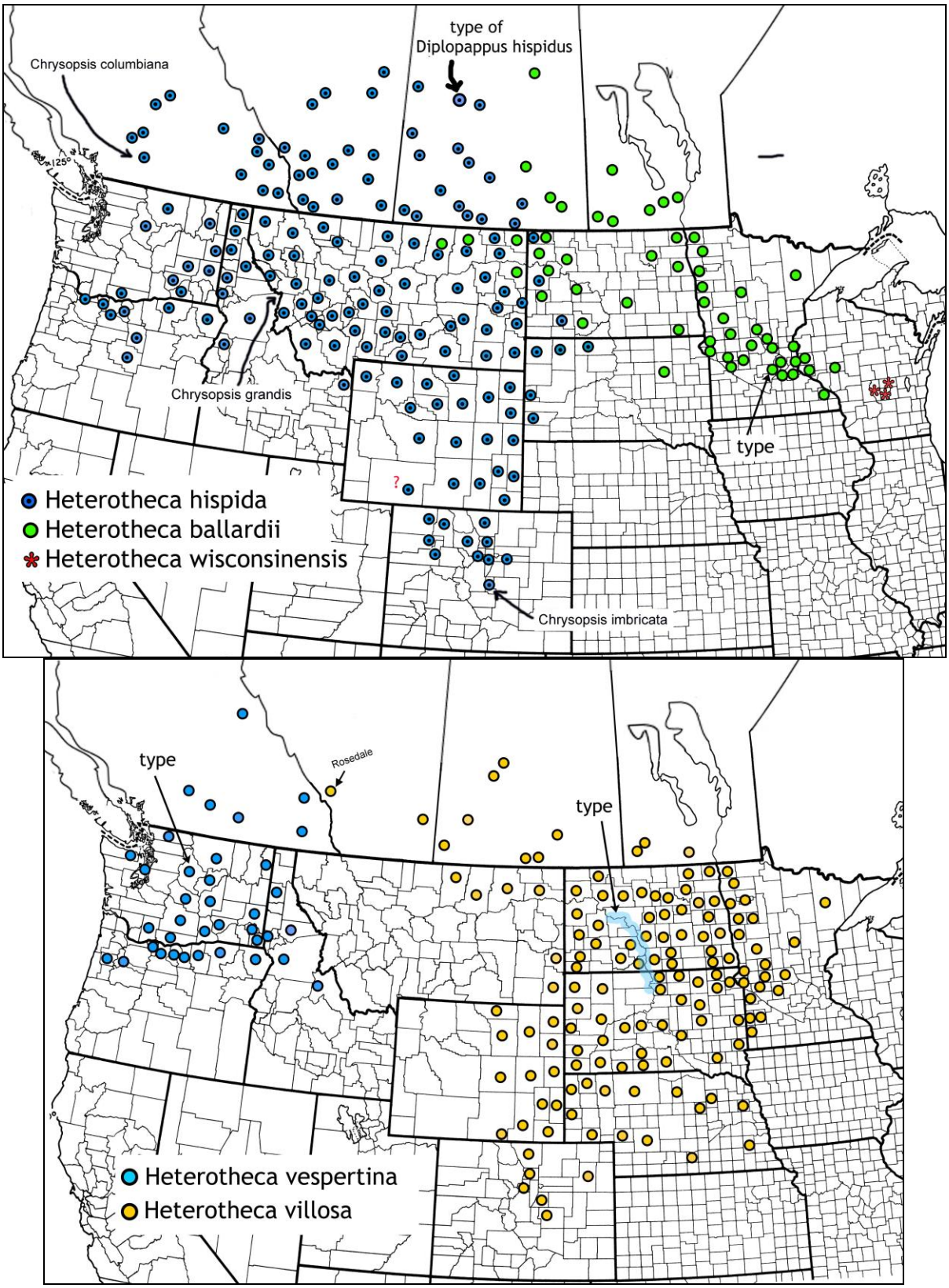


Figure 38. Upper: Distribution of *Heterotheca hispida*, *H. ballardii*, and *H. wisconsinensis*. Lower: Distribution of *H. vespertina* and *H. villosa*. For discussion of the type locality of *H. villosa*, along the stretch of blue-highlighted Missouri River, see Nesom 2020 (Phytoneuron 2020-66: 1–9).

**10. HETEROTHECA HISPIDA** (Hook.) Nesom, **comb. nov.** *Diplopappus hispidus* Hook., Fl. Bor.-Amer. 2(7): 22. 1834. *Chrysopsis hispida* (Hook.) DC., Prodr. 7: 279. 1838. *Chrysopsis villosa* var. *hispida* (Hook.) A. Gray, Synopt. Fl. N. Amer. 1, 2: 123. 1884. *Heterotheca villosa* var. *hispida* (Hook.) Harms, Brittonia 26: 61. 1974. **TYPE**: **CANADA**. **Saskatchewan**. Carlton House, 1827, *Richardson s.n.* (holotype: BM 1026321 image!).

The BM sheet (upper half, the Richardson collection) includes three separate stems — Semple annotated shoot no. 1 as the "holotype" in 1988 (Fig. 26); he later noted (1990, p. 226) that "The middle shoot No. 1 is designated herein the lectotype" but in 1994 and in 1996 (p. 126) he indicated that "shoot no. 2" (on the left) is the lectotype. All three stems have similar vestiture, leaf shape, and involucre size and all can be construed to be of the same gathering, a single population, thus all are considered here to be part of the type. The stem vestiture is sparsely hirsute-pilose or hispid-pilose, of relatively long, spreading to slightly deflexed hairs in a single story.

Protologue: "totus pilis patentibus hispidus, foliis oblongo-spathulatis basi angustatis subpetiolatis, ramis subcorymbosis, involucri foliolis angustatis acutis glabriusculis. Hab. Carlton-House Fort. *Dr. Richardson*." Semple (1990, p. 226) noted that "Obvious features of the shoot are its glands and relatively few hispid hairs."

*Chrysopsis villosa* (Pursh) Nutt. var. *discoidea* A. Gray, Synopt. Fl. N. Amer. (ed. 2) 1, 2: 123. 1884. *Diplogon villosum* var. *discoidea* (A. Gray) Kuntze, Rev. Gen. Pl. 1: 334. 1891. **TYPE**: **USA**. **Montana**. [Ravalli Co.]: Cañon from Ross's Hole to Bitterroot Valley, 26 Jul 1880, *S. Watson 141* (holotype: GH image!).

The morphology/vestiture is very similar to that of *Chrysopsis columbiana*. Gray described the heads as "destitute of rays," but as noted by Semple in annotation of the holotype, "rays are present on immature heads, eaten away on mature ones."

*Chrysopsis columbiana* Greene, Erythea 2: 95. 1894. **TYPE**: **CANADA**. **British Columbia**. protologue: Spencer's Bridge, 1881; label: Spences Bridge, 3 May 1889; *J. Macoun s.n.* (probable holotype: NDG 53892 image!; isotype [as cited by Semple 1990]: CAN).

The NDG specimen does not have an annotation by Greene but it is the only one in his herbarium that closely matches the protologue. The collection date is different and the type locality is Spences Bridge (not "Spencer's," as in the protologue), a long-established community on the Thompson River in south-central British Columbia. Macoun's handwritten label data say "Spences" Bridge, 3 May 1889.

As described by Greene: "Leaves few, scattered, spreading or deflexed: pubescence of both stem and foliage white, spreading and hispidulous." Semple (1990) noted that these plants have a "very dense indument of hairs compared to the type of var. *hispida*." Stems are densely hirsute to hirsute-villous with slightly deflexed hairs in a single story, all medium long, shorter distally.

*Chrysopsis imbricata* A. Nels., Bot. Gaz. 37: 263. 1904. *Chrysopsis foliosa* var. *imbricata* (A. Nels.) A. Nels. in Coult. & Nels., New Man. Bot. Centr. Rocky Mts., 493. 1909. **TYPE**: **USA**. **Colorado**. [El Paso or Teller Co.]: Pike's Peak, open slopes, 1 Sep 1901, *A. Nelson 8618* (holotype: RM! image!).

The stem vestiture is hirsute-villous with deflexed hairs; leaf surfaces are hirsute-villous. These plants have similarities to *Heterothca pumila* in vestiture, but the heads are in a closely corymboid arrangement and the capitular bracts are linear, at most slightly longer than the involucre.

*Chrysopsis grandis* Rydb., Bull. Torrey Bot. Club 37: 129. 1910. **TYPE**: **USA**. **Montana**. [Missoula Co.]: Jocko Creek, 1000 m, 16 Jun 1901, *D.T. McDougal 275* (holotype: NY image!).

The morphology/vestiture is very similar to that of *Chrysopsis columbiana* except for slightly larger involucres.

*Chrysopsis butleri* Rydb., Bull. Torrey Bot. Club 37: 129. 1910. **TYPE**: **USA**. **Montana**. Gallatin Co.: Gateway, 17 Aug 1908, *B.T. Butler 620* (holotype: NY image!).

The stem vestiture is densely and evenly hirsutulous with slightly deflexed hairs in a single story — very similar to that of *Chrysopsis columbiana* but with slightly shorter hairs.

Stems densely hirsutulous to hirsute, hirsute-pilose to hirsute-villous, or hispid-pilose with spreading to spreading-deflexed hairs, usually in a single story but sometimes with an upper story of distinctly longer hairs. Leaf and bract surfaces loosely ascending-strigose to hirsute, margins ciliate. Heads short-peduncled in a corymboid arrangment (sometimes with longer peduncles and toward solitary), usually with narrow but clearly evident capitular bracts. Chromosome numbers, 2n=18, 36.

Semple has made chromosome counts from many populations of *Heterotheca hispida* in Canada (British Columbia, Alberta, Saskatchewan) and in the USA (Oregon, Montana, Wyoming) — diploids occur in each of these states, tetraploids in Alberta, Montana, and Wyoming. I am unable to find a morphological or geographical pattern to the occurrence of the tetraploids, but variation in the species (as recognized here) is complex and it seems likely that further study of chromosome numbers could be helpful toward a better understanding of evolutionary patterns.

Stem vestiture of *Heterotheca hispida* is consistently spreading but variable in length and density. Particularly in Montana, stems are densely hirsutulous (exemplified by the type of *Chrysopsis butleri*; also Fig. 40) with stiff, sharp-pointed, distinctly deflexed hairs. Variants in Montana and elsewhere, especially in Canada, have less dense vestiture of longer hairs; the type of *Diplopappus hispidus* is an extreme example of this (Fig. 39), with vestiture suggestive of *H. hirsuta* but lacking the glandularity of the latter. As interpreted here, the geographic coherence of this variable system of plants suggests that a single entity is represented (with at least one significant caveat, as in the following paragraph).

In Carbon Co., Wyoming, and adjacent areas of the Albany, Fremont, and Natrona counties (the Platte/Laramie River Drainage area), there appears to be a "race" within what is identified here as *Heterotheca hispida* of relatively small-statured plants with mostly 1-headed stems, short, spreading stem vestiture, and evident sessile-glandular leaf surfaces seen through the non-glandular hairs. These plants were abundantly collected by Univ. of Wyoming student Amy Roderick in 1997 and 1998. It does not appear to be an early-season growth form, as collections have been made through early September. More characteristic *H. hispida* occurs in the same area but not as abundantly. A plausible speculation is that this population system originated as a hybrid between *H. hispida* and *H. hirsuta*, which are sympatric in the area. Plants of similar aspect occur sporadically elsewhere (in the RM collections, they are common in Park Co., Wyoming), but they lack the distinctive glandularity of those in the Platte/Laramie area. The type of *Chrysopsis mollis* Nutt. (see *H. villosa* synonymy) may be a plant of this population system — it was collected by Nuttall apparently in close proximity to the type of *C. foliosa* Nutt., which is identified here as *H. villosa*. Field study may be able to provide a more definitive perspective.

**Representative records examined for *Heterotheca hispida* in South Dakota**. Corson Co.: 5 mi NW of Wakpala, prairie hilltop pasture, 12 Sep 1968, *Stephens 29166* (> *H. villosa*?; KANU image!). Lawrence Co.: Spearfish, Lookout Mtn Park, at the end of Pony Express Lane, ridge line, 1358 m, 1 Sep 2013, *Halse 8954* (BRY, CAS). Perkins Co.: 1 mi S, 10 mi E of Bison, upland shortgrass prairie, 26 Jul 1966, *Stephens 8000* (KANU image!).

**Records examined for North Dakota**. Divide Co.: *Harms 18512* (KANU image!). Hettinger Co.: *Stephens 50083* (KANU image!). McKenzie Co.: Little Missouri National Grassland, 6 mi S, 2 mi W of Cartwright, NW-facing prairie slope, 24 Jul 1981, *Rohde 3051* (MO).

**Utah**: Salt Lake City, Aug 1879, *M.E. Jones s.n.* (POM) – the ID is unambiguous but the collection was far out of range, possibly a waif, more likely an aberrant form of *Heterotheca utahensis*. Not mapped as *H. hispida*.


Figure 39. *Heterotheca hispida*. Upper: BM holotype of *Diplopappus hispidus*. Lower: Details from middle stem of holotype.

Figure 40. *Heterotheca hispida*, common and abundant expression. Bozeman, Montana. Photo by Matt Lavin, 27 June 2003.


Figure 41. *Heterotheca hispida*. Representative collection, Sheridan Co., Montana, *Stephens 13194* (KANU).

**11. HETEROTHECA VILLOSA** (Pursh) Shinners, Field & Lab. 19: 71. 1951. *Amellus villosus* Pursh, Fl. Amer. Sept. 2: 564. 1814 [1813]. *Inula villosa* (Pursh) Nutt., Gen. N. Amer. Pl. 2: 151. 1818. *Diplopappus villosus* (Pursh) Hook., Fl. Bor.-Amer. 2: 22. 1834. *Chrysopsis villosa* (Pursh) Nutt. ex DC., Prodr. 5: 327. 1836. *Diplogon villosum* (Pursh) Kuntze , Revis. Gen. Pl. 1: 334. 1891. **TYPE**: [**South Dakota** or **North Dakota**]. Protologue: "On the Missouri," June or early July, *J. Bradbury s.n.* (holotype: apparently lost or destroyed, fide Semple 1990). **NEOTYPE** (Nesom 2019, p. 4): Label: "Missouri, Nuttall." As deduced: Along the Missouri River in South Dakota or North Dakota, July or August 1811, *T. Nuttall s.n.* (PH-001726/00002717, stem no. 2, image!). **Superceded neotype** (Semple 1990, p. 225): ["UNITED STATES. Missouri, [in 1811], *Nuttall s.n.* (PH-001726, shoot no. 1, image!)." Locality as deduced (see Nesom 2019): Along the Missouri River in South Dakota or North Dakota, July or August, 1811.

*Heterotheca foliosa* (Nutt.) Shinners, Field & Lab. 29: 71. 1951. *Chrysopsis foliosa* Nutt., Trans. Amer. Philos. Soc. n.s., 7: 316. 1841. *Chrysopsis villosa* var. *foliosa* (Nutt.) Cronq., Bull. Torrey Bot. Club 74: 150. 1947. *Heterotheca villosa* var. *foliosa* (Nutt.) Harms, Wrightia 4: 15. 1968. **TYPE**: [**Wyoming**. Probably Natrona Co.]: Protologue: "In the Rocky Mountain plains, near the banks of the Platte. Flowering in August," [early Jun 1834], *T. Nuttall s.n.* (holotype: BM image!, 3 stems, probably from 2 or 3 different plants, but reasonably from the same population; isotype: GH 55855 image!, stem on right side of sheet).

The BM collection has Nuttall's annotation as "Chrysopsis * foliosa, R. Mts." The right-hand stem of GH 55855 is essentially identical in morphology to those on the BM sheet; the label in Nuttall's script says "Chrysopsis foliosa Nutt., E side of Rocky Mts." The left-hand plant (GH 5585) has spreading reflexed stem vestiture and is identified here as *Heterotheca hispida*.

Nuttall, with Wyeth's expedition, traveled along the North Platte River in central Wyoming in early June (ca. 6-12 June) 1834, probably in Natrona County (see Wyeth 1834). If the collection of *Chrysopsis foliosa* were made in June, the nature of his reference to "Flowering in August" is not clear (the Wyeth expedition was already west of Fort Hall, Idaho, by August), but perhaps he observed that full flowering of the population would be reached by that month (the stems of the holotype are in full flower). Nuttall's description of *C. foliosa*, especially features of the leaves, puts it close to the present concept of *H. villosa*: "About foot high, sending up many hairy stems from the same root. Nearly allied to *C. villosa* but far more pubescent and hoary, with the leaves widest at the base ... sericeously villous, and more or less canescent ... flowers fastigiate, corymbose; leaves entire, oblong or oblong-ovate, subamplexicaule .... A very showy species." Neither overstory nor understory is clearly antrorsely appressed, however, but rather all stem vestiture of Nuttall's collection is spreading with a slight but distinct antrorse orientation — these plants perhaps are introgressants between *H. villosa* and *H. hispida*.

*Chrysopsis mollis* Nutt., Trans. Philos. Soc. n.s., 7: 316. 1841. **TYPE**: [**Wyoming**. Probably Natrona Co.]: Protologue: "In the Rocky Mountain plains, near the banks of the Platte, [early Jun 1834]." Label: "R. Mts." *T. Nuttall s.n.* (holotype: BM image!; isotype: PH 25429 image!).

Labels on both the BM and PH specimens have "Chrysopsis * mollis" handwritten by Nuttall.

*Heterotheca villosa* in the strict sense is characterized by heads in a closely corymboid capitulescence, involucres 11–15 mm wide and subtended by capitular bracts, and loosely strigose-villous leaves and stems with eglandular surfaces. Stem vestiture is 2-storied — the understory is antrorsely oriented while the overstory comprises much longer, spreading hairs. Chromosome number, 2*n*=36 (Semple 2008).


Figure 42. *Heterotheca villosa*, Lawrence Co., South Dakota. *Stephens 16844* (KANU).


Figure 43. *Heterotheca villosa*, Harding Co., South Dakota. *Stephens 7929* (KANU). On proximal half of stem, all hairs spreading; on distal third, understory antrorse with spreading overstory.


Figure 44. *Heterotheca villosa*, Butte Co., South Dakota. *Stephens 24506* (KANU). Numerous lateral branches have arisen below damage to the primary axis. Strigose vestiture of relatively short, coarse hairs and stiffly spreading marginal cilia suggest an influence from *H. angustifolia*.

The types of *Chrysopsis mollis* and *C. foliosa* were apparently collected by Nuttall at the same locality and were described simultaneously (in sequence, both on page 316). For *C. mollis*, he noted "HAB. With the above, which it much resembles, but the leaves are more oblong, not in the least scabrous nor any where ciliate; the stem, also, softly villous." The capitular bracts of *C. mollis* are nearly filiform and give the plant a distinct appearance, which obviously Nuttall saw, but there is no other species besides *H. villosa* in this region with close, densely strigose-villous stem vestiture and 'softly villous' leaf vestiture — *C. mollis* is interpreted here to be a variant of *C. villosa*, possibly genetically influenced by some other species, perhaps even a distinct but previously unrecognized species (see further comments under *H. hispida* regarding a population system in Albany, Carbon, Fremont, and Natrona counties, Wyoming).

Where *Heterotheca villosa* and *H. hispida* occur in sympatry — a relatively small part of the geographic range of each species (e.g., in eastern Wyoming and adjacent areas) — putative intermediates are commonly encountered but most plants can usually be placed in one or the other species, indicating that gene flow is occurring but that some degree of isolation is in effect. This taxonomy can be seen as somewhat arbitrary but it serves a pragmatic purpose and if the evolutionary interpretation is correct, it also reflects the biological situation of two distinct entities with hybridization and introgression in their area of sympatry. The taxonomic distinction is essentially based on orientation of stem vestiture — spreading to slightly deflexed in *H. hispida* vs. at least the understory distinctly antrorse in *H. villosa*. As noted above, the type of *Chrysopsis foliosa* perhaps is an introgressant; it seems to be a morphological intermediate.

The situation between *Heterotheca villosa* and *H. ballardii* is similar, although *H. ballardii* (vs. *H. hispida*) is sympatric over a greater part of its total range with *H. villosa*. Both taxa apparently are at least primarily tetraploid where sympatric and putative intermediates or introgressants are frequently encountered but the distinction between *H. villosa* and *H. ballardii* in typical form is more pronounced than between *H. villosa* and *H. hispida*. *Heterotheca ballardii* (compared to *H. villosa*) has longer peduncles and spreading stem vestiture in understory and overstory (see Nesom 2020 for further discussion and comparison).

**Westernmost record**. **Montana**. Blaine Co.: 0.25 mi W of Ft. Belknap, brushy, weedy floodplain of Milk River, dry sandy soil, 20 Jul 1973, 20 Jul 1973, *Stephens 68271* (KANU image!).

**12. HETEROTHECA BALLARDII** (Rydb.) Nesom, **comb. nov.** *Chrysopsis ballardii* Rydb., Brittonia 1: 100. 1931. *Heterotheca villosa* var. *ballardii* (Rydb.) Semple, Novon 4: 53. 1994. **TYPE**: **Minnesota**. [Carver Co.]: Chaska, Jul 1891, *C.A. Ballard 640* (holotype: MIN image!).

*Heterotheca ballardii* is characterized by its relatively large heads solitary or loosely clustered on long peduncles, the heads with narrow, coarsely ciliate capitular or subcapitular bracts. Stems hirsute with spreading to slightly deflexed hairs, sometimes loosely antrorsely oriented (influence of *H. villosa* ?); leaves oblong to oblanceolate, epetiolate, not clasping; stems, leaves, and phyllaries eglandular; involucres (12–)14–20 mm wide (pressed); ray flowers (25–)30–55. See Nesom (2020) for photos of the type and representative specimens. Chromosome number, 2*n*=36 (Semple 2008).

The concept here of *Heterotheca ballardii* is generally similar to Semple's (as *H. villosa* var. *ballardii*). He noted (1994, p. 53) that it "is the generally robust, larger-headed, many-rayed, eglandular, oblong-leaved race of the species occurring on the northeastern prairies of Canada and the United States. Typical variety *villosa* has oblanceolate leaves and smaller heads with fewer rays."


Figure 45. *Chrysopsis ballardii*, Carver Co., Minnesota. Holotype (MIN).

*Heterotheca ballardii* is sympatric over nearly its entire range with *H. villosa* — intermediates are encountered but each can be recognized in fairly typical form. *Heterotheca ballardii* and *H. hispida* slightly overlap in range but I have not seen obvious morphological intermediates between them — *H. hispida*-like plants (with a more congested inflorescence, especially) are scattered through the range of *H. ballardii* but this probably is parallelism or genetic influence of *H. villosa*.

Collections of each of the three species noted above have been made in McKenzie County in western North Dakota:

***Heterotheca ballardii***. 5 mi N, 10 mi E of Watford City, roadside ditch, 8 Jul 1980, *Rohde 1338* (MO).

***Heterotheca hispida***. 6 mi S, 2 mi W of Cartwright, Little Missouri Natl Grassland, NW-facing prairie slope, 24 Jul 1981, *Rohde 3051* (MO).

***Heterotheca villosa***. 14 mi S, 3 mi W of Watford City, North Unit, Theodore Roosevelt Natl Park, Squaw Creek Campground, road edge, 9 Jul 1980, *Rohde 1370* (MO).

**Montana records (representative) for *Heterotheca ballardii***. Richland Co.: 19 mi N of Sidney, upland prairie pasture hillside, 28 Jun 1968, *Stephens & Brooks 23581* (KANU image!). Sheridan Co.: 4 mi W of Westby, upland prairie pasture, 5 Jul 1967, *Stephens & Brooks 13194* (KANU image!). In Valley and Phillips counties, many collections of *H. ballardii* were made by J.M. Charboneau in 2010 and 2011 (all at RM) — in these counties, typical *H. ballardii*, typical *H. hispida*, and intermediates occur.

**13. HETEROTHECA CANESCENS** (DC.) Shinners, Field & Lab. 19: 68. 1951. *Haplopappus canescens* DC., Prodr. 5: 349. 1836. *Chrysopsis canescens* (DC.) Torr. & A. Gray Fl. N. Amer. 2(2): 256. 1842 [nom. illeg.], not *Chrysopsis canescens* DC., Prodr. 5: 328. 1836. *Chrysopsis villosa* var. *canescens* (DC.) A. Gray, Synopt. Fl. N. Amer. 1(2): 123. 1884. *Chrysopsis berlandieri* Greene [nom. nov.], Erythea 2: 96. 1894. **TYPE: Texas**. Protologue: "4 in Mexicanae prov. Texas districtibus orientalibus nov. et dec. flor. legit cl. Berlandier (pl. exs. n. 1877)" — GH label: "Comancheries orientales des Texas, Nov. et Dec. 1828," No. 502 [ex 10] = 1877 (holotype: G-DC; isotypes: GH, HAL, NY, US, WIS). Images! of all types.

The trip made by Berlandier in November and December 1828 began in San Antonio (Bexar Co.) and looped through Kendall, Kerr, Bandera, Uvalde, and Medina counties (see Figure 46). *Heterotheca canescens* is known from each of these counties except Medina.

Flowering May–Aug(–Sep). Sandy clay, clay loam, black clay, limestone and igneous soils, sandy gypseous soils, rocky and gravelly soils, sandstone outcrops, dunes, prairies, open hills, alluvium, roadsides, fencerows; 100–2600 ft.

*Heterotheca canescens* is characterized by "(1) the dense canescent, sericeous pubescence of its phyllaries, leaves, and stems, (2) small, short-rayed heads, (3) narrow, upper and middle leaves and deciduous lower leaves, (4) numerous sivery-canescent axillary shoots, and (5) a highly rhizomatous habit" (Harms 1963, p. 30). The vestiture is densely strigose and silvery gray-green but plants of some collections may dry with a darker color and "there is usually some variation in the degree of canescence in larger colonies, with separate clones frequently distinguishable by slight differences in color aspect" (Harms, p. 37). Leaf surfaces are prominently sessile-glandular beneath the strigose vestiture. Its characterization as "rhizomatous" alludes to the production of caudex branches or offsets that become long and node-rooting like rhizomes — these are not a consistent feature in herbarium specimens, but in the field, *H. canescens* usually shows a distinctly colonial aspect.

The description of *Heterotheca canescens* by Harms referred only to diploid populations, but it essentially characterizes tetraploids as well (see Fig. 32 and coFmments below). He noted (p. 35) that the species represents a consistently diploid and "rather uniform species ... stretched along a

relatively narrow corridor" from southern Texas north to central Kansas and that (p. 37) "The primary taxonomic problem involving *H. canescens* results from the close approach to it of various segregants of the Texas populations of *H. villosa* [referring to *H. angustifolia*, as identified here]."

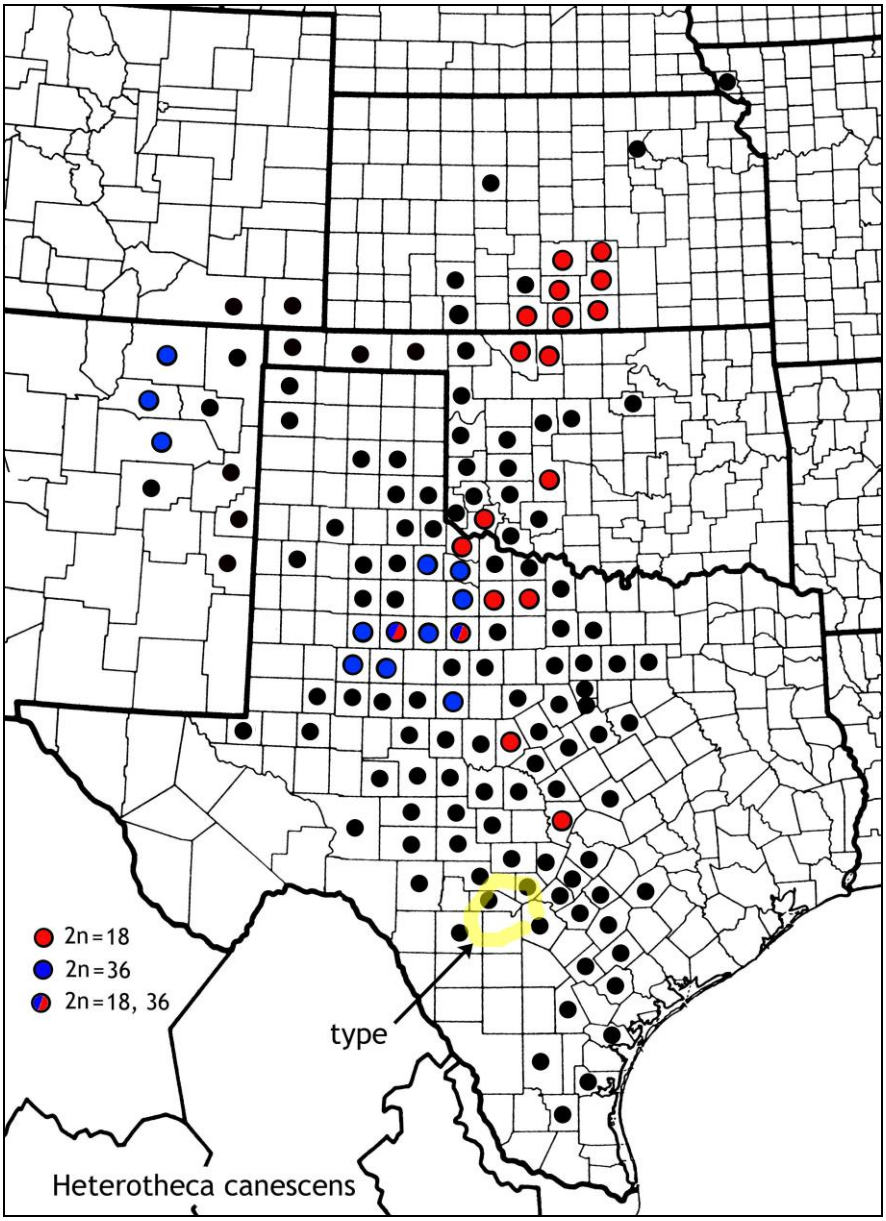


Figure 46. Distribution of *Heterotheca canescens*. Chromosome numbers mapped mostly from data of Harms and Semple. Yellow highlight outlines the route of Berlandier's 1828 trip (see note under type summary, above) — the type collection was made somewhere along his route.

Harms (1963) identified all tetraploid *Heterotheca* in New Mexico and northwestern Texas as part of *Heterotheca villosa* var. *angustifolia*, but differences in vestiture and habit distinguish *H. canescens* (key couplet below). In some places, the two species are distinct in close proximity (e.g., Fig. 56, Crosby Co., Texas); intermediates occur through their area of sympatry, where both are tetraploid (Figs. 57 and 58). New Mexico plants of *H. canescens* outside of the range of *H. angustifolia* (west of it, in Colfax, San Miguel, and Mora counties) and apparently without its genetic

influence, have a colonial habit and silvery, silky-sericeous vestiture. Similar plants are found in other New Mexico counties, where typical *H. angustifolia* also occurs.

In the range of diploid (typical) *Heterotheca canescens*, leaves are mostly linear to linear-oblanceolate, and Harms (1963) identified only these plants as *H. canescens*. In its tetraploid range, *H. canescens* (including colonial forms with sericeous vestiture) produces more distinctly oblanceolate leaves, more like *H. angustifolia*. Correlation between ploidy level and leaf shape in *H. canescens* seems strong enough that taxonomic recognition of two entities might be justified.

Figure 47. *Heterotheca canescens*, Bandera Co., Texas, area of type locality. *Miller 5825* (TEX).


Figure 48. *Heterotheca canescens*, Uvalde Co., Texas, area of type locality. *Correll & Johnston 18135* (LL).

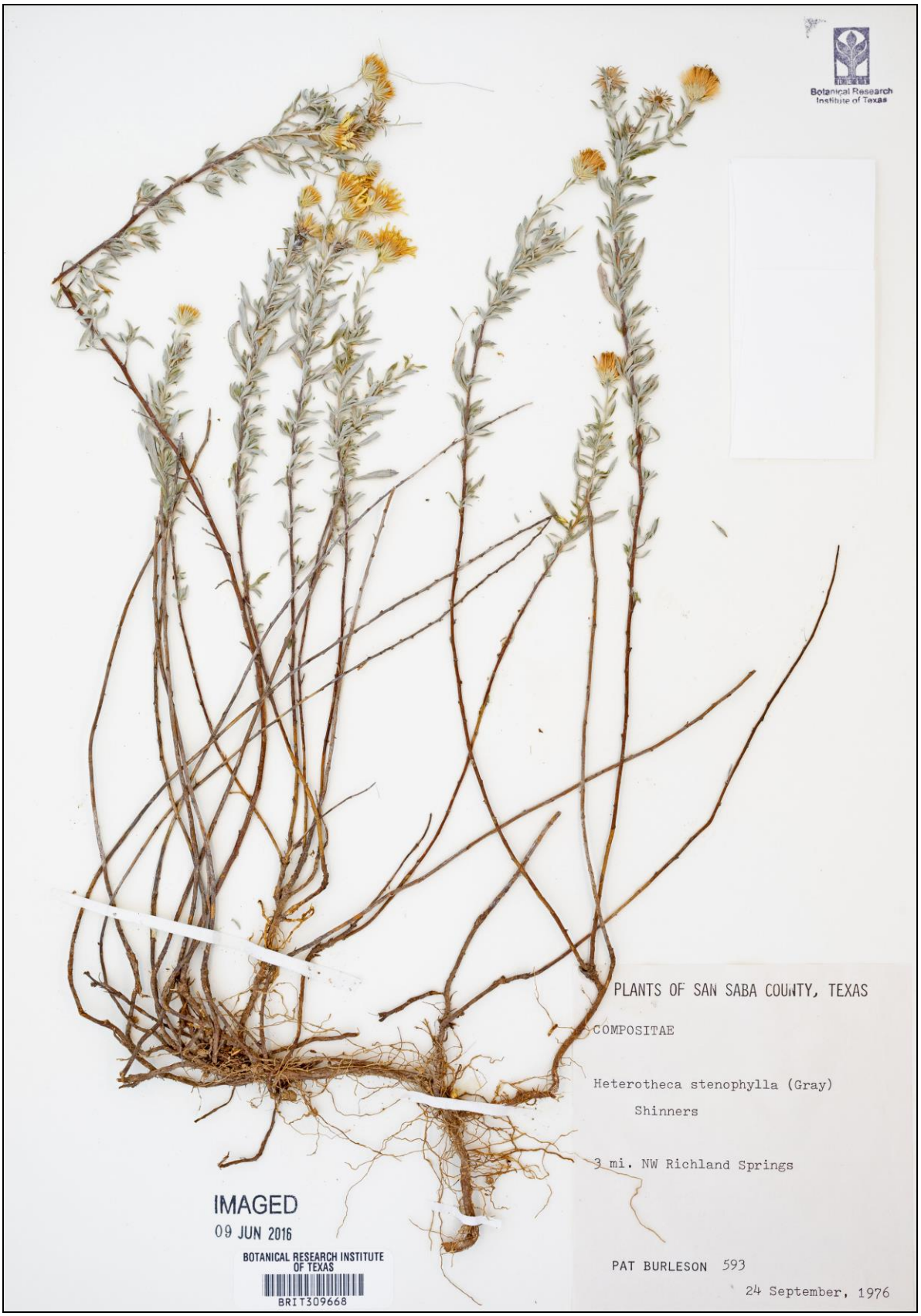


Figure 49. *Heterotheca canescens*, San Saba Co., Texas. Strongly colonial habit. *Burleson 593* (BRIT).


Figure 50. *Heterotheca canescens*, Colfax Co., New Mexico. *Harms 19113* (KANU). The northwestern, tetraploid population system (see map in Fig. 46) tends to have vestiture less dense than typical and relatively broad leaves.


Figure 51. *Heterotheca canescens*, Union Co., New Mexico. *Harms 19110* (KANU). Perhaps influenced by *H. angustifolia*. Leaves are silvery-sericeous but narrower than in the plant in Figure 50.


Figure 52. *Heterotheca canescens*, probably with influence of *H. angustifolia*, Lamb Co., Texas. *Turner & Melchert 4828* (TEX).

Plants of *Heterotheca canescens* from Holt Co., Missouri (Mound City, on the mounds, 29 Sep 1931, *Kellogg s.n.*, MO), apparently are disjunct and represent the northernmost extension of the species — they perhaps are influenced by genes of *H. angustifolia*.

Plants from trans-Pecos Texas with a vestiture similar to *Heterotheca canescens* (closely strigose, silvery-sericeous), identified by Harms (1963) as "the Davis Mt. variant" and by Semple (2006) as disjunct populations of *H. canescens*, are identified here as *H. zionensis* at the southeastern end of it range. Plants of *H. zionensis* produce stems thicker, taller, more sparingly branched, more sparsely leafy and without prominent axillary tufts of small leaves, they are more erect from the base, strictly caespitose, without rhizomes, and the heads lack capitular bracts.

The ranges of *Heterotheca pedunculata* and *H. canescens* appear to be contiguous or nearly so in north-central New Mexico, but the two apparently do not intergrade. Both have relatively dense and closely strigose vestiture of thin-based hairs, but *H. canescens* has longer, thicker, and more densely leafy stems, axillary buds and axillary tufts of leaves, prominent marginal leaf cilia, and larger heads with narrower phyllaries. *Legler 10441* and *10813* from Vermejo Park Ranch in Colfax County are *H. canescens*; *Legler 10327* (COLO image!, RM, UNM image!) is *H. pedunculata*.

**14. HETEROTHECA ANGUSTIFOLIA** (Rydb.) Nesom, **comb. nov.** *Chrysopsis angustifolia* Rydb., Bull. Torrey Bot. Club 37: 128. 1910. *Heterotheca villosa* var. *angustifolia* (Rydb.) Harms, Wrightia 4: 16. 1968. *Chrysopsis villosa* var. *angustifolia* (Rydb.) Cronq., Bull. Torrey Bot. Club 74: 150. 1947. *Heterotheca stenophylla* var. *angustifolia* (Rydb.) Semple, Novon 4: 53. 1994. **LECTOTYPE** (Semple 1990): **Nebraska**. Hooker Co.: Near Mullen, Middle Loup River, on sandhills, 14 Sep 1893, *P.A. Rydberg 1766* (NY; isolectotypes: GH, NEB [typo as *Rydberg* "*1716*"], NY, US). Images! of all types.

Perennial, caespitose from a thick, woody taproot, without rhizomes. Vestiture of leaves and stems loosely strigose with stiff, thick-based hairs not obscuring the green surfaces. Leaves rigid, oblanceolate to narrowly oblanceolate, ascending, margins narrowly revolute. Heads mostly short-pedunculate in a closely clustered capitulescence, with closely subtending linear to linear-lanceolate capitular bracts; involucres 5–8 mm wide.

*Heterotheca angustifolia* has been treated as a variety of *H. stenophylla* (by Semple) and a variety of *H. villosa* (by Harms), and it might also plausibly be taxonomically linked with *H. canescens*, in view of their intergradation (analogous to that between *H. angustifolia* and *H. villosa*). It is consistently tetraploid (2n=36, many counts) and apparently hybridizes and intergrades with *H. villosa* and with *H. canescens* in areas of sympatry. On the other hand, *H. angustifolia* in its characteristic (typical) form occurs throughout its range, from South Dakota to Texas, and it is reasonably regarded as a distinct species. Intemediates with *H. stenophylla* are encountered rarely.

a1. Leaves rigid, margins narrowly revolute; trichomes rigid with pustulate bases; involucres 5–8 mm wide ..... 14. **Heterotheca angustifolia**

a1. Leaves not rigid, margins flat; trichomes usually loose with bases usually wider than the extended portion above but not strongly pustulate-based; involucres 11–15 mm wide ..... 11. **Heterotheca villosa**

a2. Leaves oblanceolate, rigid, margins narrowly revolute; axillary tufts of small leaves absent or not dense and prominent; vestiture sparse to moderately dense and not obscuring the green epidermis, trichome bases strongly pustulate; leaf surfaces and phyllary apices eglandular; plants caespitose, not rhizomatous ..... 14. **Heterotheca angustifolia**

a2. Leaves linear to narrowly oblanceolate, not rigid, margins flat; axillary tufts of small leaves abundant and prominent; vestiture dense and silvery-sericeous, trichome bases usually wider than the extended portion above but not strongly pustulate; leaf surfaces and phyllary apices sessile-glandular; plants colonial, rhizomatous ..... 13. **Heterotheca canescens**

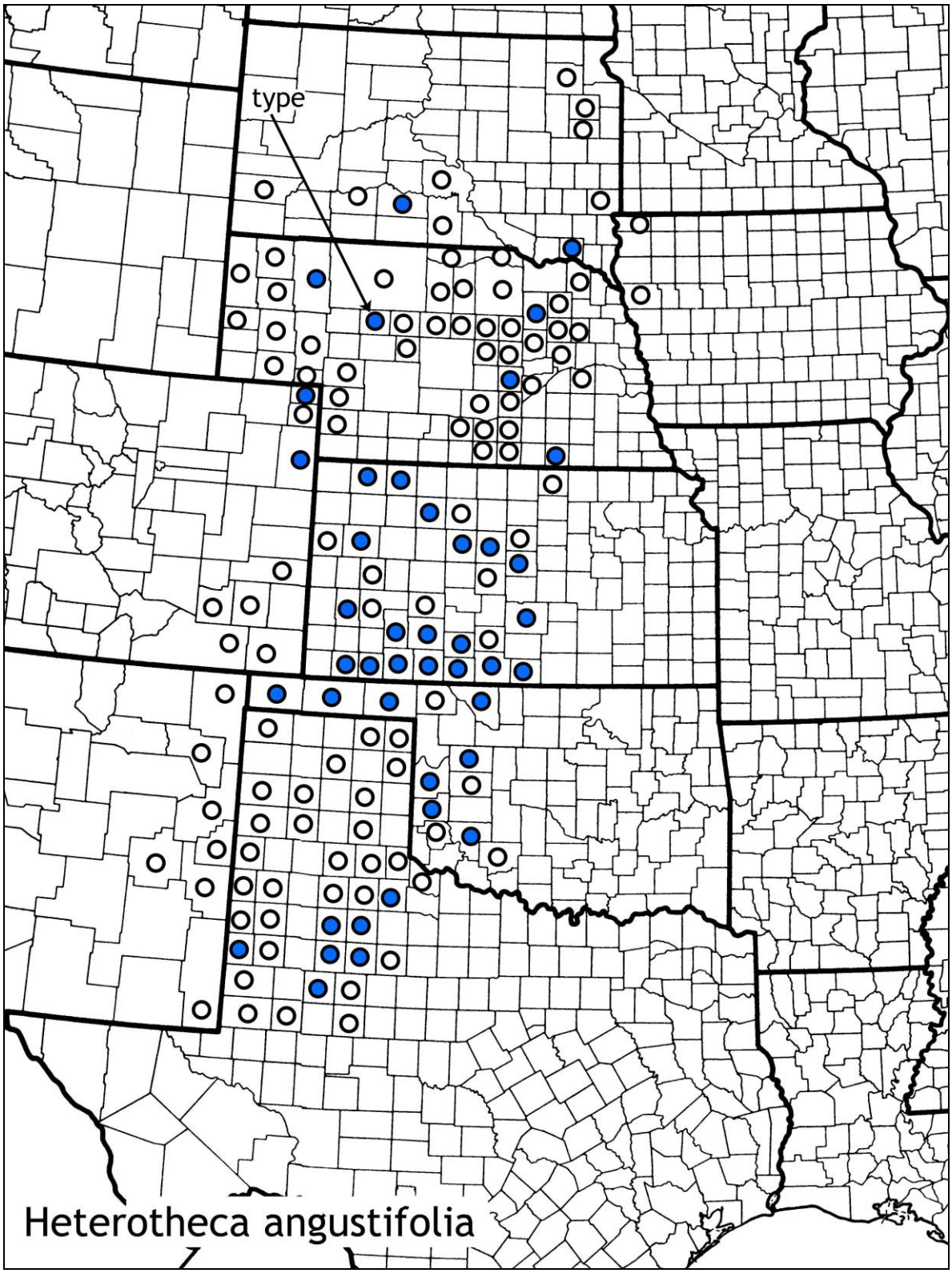


Figure 53. Distribution of *Heterotheca angustifolia*. Blue symbols are tetraploid chromosome counts, data mostly from Harms and Semple.


Figure 54. Typical *Heterotheca angustifolia*, Rawlins Co., Kansas, where sympatric with neither *H. villosa* nor *H. canescens*. *Harms 1255* (KANU).


Figure 55. *Heterotheca angustifolia*, typical form, Hemphill Co., Texas. *Rowell 4071* (TEX).


Figure 56. *Heterotheca* from Crosby Co., Texas, apparently representing a mixed collection of two sympatric species — *H. angustifolia* (dark green) and *H. canescens* (silver-gray). *Tharp 4536* (TEX).


Figure 57. *Heterotheca angustifolia*, Texas Co., Oklahoma. *Harms 1974-B* (KANU). Nearly typical morphology and vestiture, although annotated by Harms as possibly intermediate with *H. canescens*. See Fig. 58 from Texas County.


Figure 58. *Heterotheca angustifolia*, Texas Co., Oklahoma. *Harms 1974* (KANU). Vestiture of this plant, with thin-based hairs, is more like *H. canescens*.

The ranges of *Heterotheca pedunculata* and *H. canescens* appear to be contiguous or nearly so in north-central New Mexico, but the two apparently do not intergrade. Both have relatively dense and closely strigose vestiture of thin-based hairs, but *H. canescens* has longer, thicker, and more densely leafy stems, axillary buds and axillary tufts of leaves, prominent marginal leaf cilia, and larger heads with narrower phyllaries. *Legler 10441* and *10813* from Vermejo Park Ranch in Colfax County are *H. canescens*; *Legler 10327* (COLO image!, RM, UNM image!) is *H. pedunculata*.

**15. HETEROTHECA STENOPHYLLA** (A. Gray) Shinners, Field & Lab. 19: 68. 1951. *Chrysopsis hispida* var. *stenophylla* A. Gray, Boston J. Nat. Hist. 6 (Pl. Lindh.): 223. 1850. *Chrysopsis villosa* var. *stenophylla* (A. Gray) A. Gray, Synopt. Fl. N. Amer. (ed. 2) 1(2): 123. 1884. *Chrysopsis stenophylla* (A. Gray) Greene, Erythea 2: 96. 1894. **TYPE**: **Texas**. [Llano Co.]: Protologue: "On the Llano, from strong ligneous roots in crevices of smooth granite rocks, Nov," 1847, *F.J. Lindheimer 631* (holotype: GH 55862 image!; isotypes: BRIT!, CAN, DS image!, GH 55861 image!, K, MO!, ND-G, NY-4 sheets images!, P-2 sheets images!, US image!, YU image!).

*Heterotheca stenophylla* occurs on granite and limestone in the Edwards Plateau of central Texas (the type from a granite habitat) — it is characterized by large, solitary heads and rigid, linear to narrowly oblanceolate leaves and capitular bracts with narrowly revolute, long-ciliate margins. The hispid trichomes have distinctly pustulate bases. Leaves and bracts sometimes are glandular. Ray flowers 12–27. Chromosome number, 2*n*=18 (Burnet Co.: *R. Johnson 1907-a*, KANU; *McGregor 16792*, KANU; both vouchers were cited by Harms 1974 and Semple 2008, but they are not in the KANU database; *Semple 2198*, as cited below).

Flowering (Apr–)Jun–Oct(–Nov). Cracks, crevices, and ledges and shallow soil pockets in granite and limestone; 900-1900 m. The species in the concept here is endemic to the Edwards Plateau of central Texas.

*Heterotheca stenophylla*, regarded here as an uncommon Edwards Plateau endemic, differs in morphology, geography, and ecology from plants previously identified as typical *H. stenophylla* from prairie habitats further north and northwest in Texas and from Oklahoma to Nebraska. The prairie population system is identified here as *Heterotheca scabrifolia*. The diploid chromosome count for typical (large-headed) *H. stenophylla* suggests that the size difference in heads between species cannot be attributed to a ploidal difference.

1. Heads 9–17 mm wide (pressed), solitary at ends of long branches or loosely clustered on leafy-bracteate peduncles 2–7 cm long; leaves 1–6 mm wide, leaf and bract margins long-ciliate usually along at least the proximal 1/2; phyllaries eglandular and sparsely strigose, glabrous or sometimes minutely glandular proximally, or sparsely sessile-glandular ..... 15. **Heterotheca stenophylla**

1. Heads 5–8 mm wide (pressed), usually in cymiform to subcymiform clusters on leafy-bracteate peduncles (0.5–)1–2.5 cm long, rarely solitary; leaves 0.5–2(–4) mm wide, leaf and bract margins eciliate or short-ciliate along proximal 1/5–1/4; phyllaries densely sessile-glandular and without other hairs or sessile-glandular and sparsely strigose ..... 16. **Heterotheca scabrifolia**

**Additional collections, typical *Heterotheca stenophylla*. Texas**. Burnet Co.: Inks Lake State Park, ca. 0.5 mi SE of SE end of Inks Dam, ca. 960 ft, occasional, with two *Cheilanthes* spp., rooted in fractures of dry boulders of Valley Spring Gneiss exposed on sparsely vegetated hills along powerlines, 13 Jun 1995, *Carr 14692* (TEX); 1.8 mi S of Inks Park Headqtrs, crest of hill just S of park on P-4, a few scattered plants growing among rocks, 18 Jun 1976, *Semple 2198* (BRIT, TEX). Hays Co.: Wimberly, 22 Jul 1946, *Correll 13398* (BRIT); 7 mi. ENE of jct with Co. Road 32 in Fischer (Comal Co.) on county road toward Woodcreek, at crossing of Blanco river in west-central part of Hays Co., area of oak woods in rolling hills, on steep, rocky bank along river, branches

somewhat pendent, 13 Oct 1990, *Nesom 7230* (TEX, UTEP); ca. 0.75 mi NNW of Wimberley, near jct of Cypress Creek and Blanco River, 9 Aug 1961, *Walker 8* (BRIT, TEX). Kimble Co.: Exit ramp to Hwy 290 from IH-10, road to Fredericksburg, S side of Hwy 290, 13 Jun 1999, *Turner 99-378* (TEX). Llano Co.: Llano, arid rocks, 15 May 1899, *Bray 331* (TEX); near summit of Turkey Peak just east of Enchanted Rock, locally abundant in crevices of granitic boulders, 24 Jul 1976, *Butterwick 2996* (TEX); S bank of Llano River ca. 15-50 ft E of State Hwy 16 bridge in Llano, locally common on granite boulders on unshaded steep slope, 7 Jun 1988, *Carr 8932* (BRIT); 7.5 mi E of Llano on Texas 29, granite rock deposits, 1 Jul 1983, *Keeney 3555* (BRIT); between Llano and San Saba, along Hwy 16, on upper slopes of granite ridge, 29 Apr 1946, *Lundell 14576* (LL); Llano, 11 Jun 1930, *Tharp 7356* (LL). McCulloch Co.: S of Brady, along Hwy 87, 7.2 mi S of jct with Hwy 71, roadside park along the banks of the San Saba River, low stony hill range site, limestone ledge immediately above the river, 28 Aug 2013, *Hansen 7562* (TEX). Mason Co.: SW of Mason along Farm Road 1871, 9.1 mi SW of junction with Hwy 87, at Llano River crossing, loamy bottomland range site, limestone ledge above the river, 12 Sep 2013, *Hansen 7683* (TEX); Mason Mt. Wildlife Management Area, 5 air mi NNW of Mason, 2.1 mi N of jct of Hwy 29 and Hwy 398 then 2.4 mi NW on dirt road, 24 Sep 1999, *Singhurst et al. 8203* (TEX); W of Mason, among granite rocks, 23 Jul 1946, *Wolff s.n.* (TEX). Menard Co.: NE of Hext, near the San Saba River crossing along Ranch Rd 1311, 3.15 mi N of its jct with Texas Hwy 29, roadside, 8 Jul 1989, *Lievens 4095* (LSU). Travis Co.: Streambed crossing between Hamilton Pool turnoff and Pedernales River on Hamilton Pool road (FM 3238), shallow soil pockets on bare limestone, bordered by *Platanus*, *Fraxinus*, etc., in oak and cedar woodland, ca. 900 ft, 18 Sep 1983, *Ertter 5146* (TEX); on boulder of Hamilton Creek, below Hamilton Pool, one population found on one large boulder, 1 Nov 1979, *Johnston s.n.* (TEX).

**16. HETEROTHECA SCABRIFOLIA** (A. Nels.) Nesom, **comb. nov.** *Chrysopsis scabrifolia* A. Nels., Bot. Gaz. 37: 264. 1904. **TYPE**: **Oklahoma**. Woods Co.: [no other locality data,] 29 Jun 1900, *P.J. White s.n.* (holotype: RM! digital image!).

*Heterotheca scabrifolia* previously has been identified as *H. stenophylla* (as *H. stenophylla* var. *stenophylla* by Semple), with which it shares rigid, linear to narrowly oblanceolate leaves, capitular bracts with revolute, ciliate margins, and vestiture not obscuring surfaces, the trichomes with distinctly multicellular-pustulate bases — but *H. scabrifolia* is distinct in its relatively small, distally clustered heads, more consistently glandular herbage, and shorter marginal cilia (see key couplet, p. 72). Ray flowers 14–20. Chromosome numbers, 2*n*=18, 36.

Flowering Jun-Oct. Plains and open hills, sandstone outcrops, dunes and sandhill prairies, gypsum outcrops and hills, red, gravelly soil, gypsiferous sandy loam, calcareous roadbanks, creek terraces; 1500–2700 ft.

Differences in head size and arrangement between *Heterotheca scabrifolia* and *H. stenophylla* are consistent. Plants from Taylor Co. and Eastland Co., Texas (Figs. 73 and 74; mapped in Fig. 59), slightly north of the range of *H. stenophylla*, have small, clustered heads characteristic of *H. scabrifolia* but the densely long-ciliate leaf and bract margins of typical *H. stenophylla*, not seen elsewhere in *H. scabrifolia*. These are the only collections observed that suggest incomplete differentiation or some past episode of gene flow.

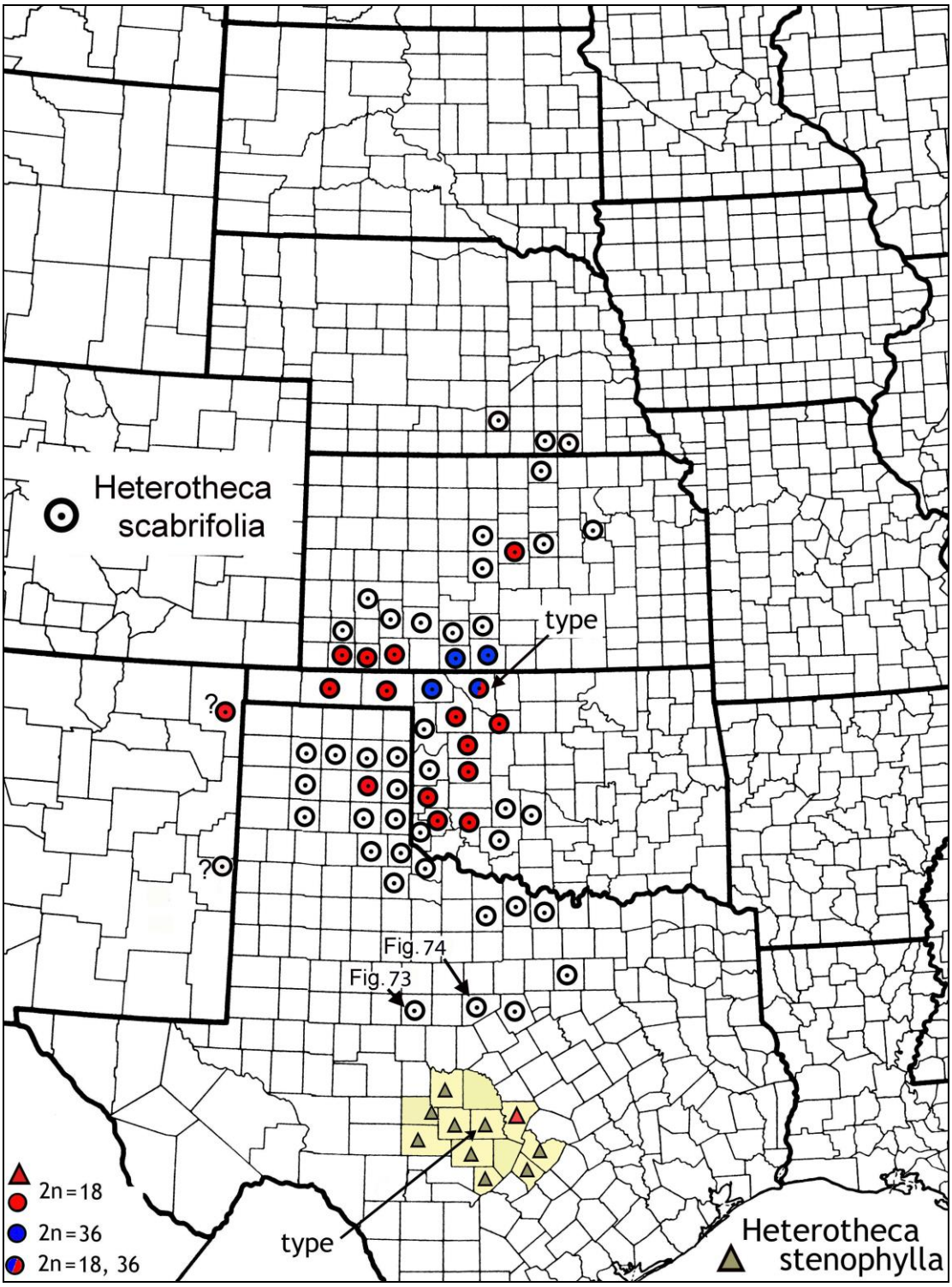


Figure 59. Distribution of *Heterotheca stenophylla* and *H. scabrifolia*, showing locations of diploid and tetraploid chromosome counts. Chromosome data mostly from Harms and Semple. Vouchers for *H. stenophylla* in Kendall and Gillespie counties seen but not recorded/cited. Records for Union Co. and Roosevelt Co., New Mexico, are cited by Harms and Semple but have not been seen in the present study (see text comments). Some Nebraska records added from Kaul et al. (2011, ed. 2). Yellow highlight emphasizes the geography of typical *H. stenophylla*. Collections from Taylor and Eastland counties (see Figs. 73 and 74) apparently are intermediate between the two species.

Figure 60. *Heterotheca stenophylla*, McCulloch Co., Texas, on exposed limestone beside the San Saba River at crossing of Hwy 87 south of Brady (site of *Hansen 7562*, TEX). PhotoS by Nesom, 7 August 2015.

Figure 61. *Heterotheca stenophylla*, McCulloch Co., Texas, same population as in Fig. 45. Large, solitary heads, eglandular phyllaries, densely long-ciliate leaves and capitular bracts. Photo by Nesom, 7 August 2015.


Figure 62. *Heterophylla stenophylla*, from GH isotype, Llano Co., Texas.


Figure 63. *Heterotheca stenophylla*, Travis Co., Texas. *Ertter 5136* (TEX).


Figure 64. *Heterotheca stenophylla*, Burnet Co., Texas, with broad leaves but typical vestiture. *Root 366* (KHD). Similarly broad-leaved forms also have been collected in Hays and Llano counties.


Figure 65. *Heterotheca stenophylla*, Mason Co., Texas. *Hansen 7683* (TEX).

Harms (1963, 1974) cited a single collection of *Heterotheca scabrifolia* (as *H. stenophylla*) from New Mexico and reported it as diploid — Union Co.: 14.5 mi WSW Clayton, *Harms 1862*, **2n=18** (KANU); Semple (1996, 2008) also cited *Harms 1862* as *H. stenophylla*. This specimen is not in the KANU online database nor can it be located at KANU. Semple also cited a collection from Roosevelt Co. as *H. stenophylla* (SW of Clovis, *Harrison s.n.*, GH). I have not seen a collection of typical *H. stenophylla* from New Mexico — it is indicated here (map, Fig. 46), tentatively, as a member of the New Mexico flora.

*Heterotheca scabrifolia* sometimes grows in close sympatry with *H. canescens* without apparent gene flow. Typical forms of both species were collected at the same locality in Comanche Co., Oklahoma (where both apparently are diploid): Wichita Mts, 3 mi N of Meers, xeric pasture with outcrops of Arbuckle limestone, 21 Oct 1944, *Hopkins & Nelson 812* (WTU, *H. scabrifolia*, stems and leaves glandular and hispid with short, pustulate-based hairs), *814* (WTU, *H. canescens*, stems and leaves densely strigose with long, thin-based hairs).

Harms (1963) found evidence suggesting that tetraploidy in *Heterotheca scabrifolia* in Oklahoma/Kansas may be correlated with slightly larger heads. Offspring of progeny tests from Oklahoma/Kansas *H. scabrifolia* tetraploids produced variants ranging from typical *H. scabrifolia* to typical *H. angustifolia*. *Heterotheca angustifolia* (consistently tetraploid) in the same area shows influence of *H. scabrifolia*.

Similar variability in *Heterotheca angustifolia* of northern Nebraska and adjacent South Dakota (see map, Fig. 40) and Iowa (Lyon Co., e.g., see Figs. 62, 63, 64), fide Harms, suggests that the whole population system in that area is tetraploid and intergrading with *H. angustifolia* (tetraploid counts made from Yankton Co., South Dakota, and Antelope Co., Nebraska). In a 4x Yankton Co. population, Harms found that most plants (89%) were typical *H. angustifolia*; 3% were *H. scabrifolia*. Most plants in Lyon Co., Iowa, have a reduced vestiture similar to *H. scabrifolia* but, following annotations by Harms and Semple, they are identified here as *H. angustifolia*. They have linear-lanceolate leaves with revolute margins and sharply acute apices, sparsely hirsute-strigose to hispid-hirsute with short, pustulate-based hairs, the proximal margins (and bract margins) coarsely ciliate; stems sparsely strigose-hirsute with loose ascending hairs; heads mostly solitary; phyllaries sparsely short-strigose. Plants of the Iowa collections by Gleason and Shimek are glandular, but on plants collected by Fults and by Lassetter neither leaves, stems, nor phyllaries are glandular. Collections from quartzite habitats in Minnehaha Co., South Dakota (e.g., Fig. 65; adjacent to Lyon Co., Iowa), are similar but have longer hairs on stems and leaves and more the aspect of *H. angustifolia*.

Iowa collections (*H. angustifolia*) examined. Lyon Co.: Gitchie Manitou State Park, clumps in the rocks, 14 Sep 1934, *Fults 2940* (WTU); Gitchie Manitou State Park, dry prairie overlying Sioux quartzite, 13 Jul 1940, *Gleason 9374* (SMU); Gitchie Manitou State Park, quartzite outcrop and open area, dry, thin soil, 20 Sep 1969, *Lassetter 1548* (BRY, Fig. 62) and *Lassetter 1560* (BRY, Fig. 63); granite [probably quartzite], no other locality data, 4 Aug 1896, *Shimek s.n.* (MO, Fig. 64); NW corner of county, Sioux quartzite exposures, 25 Aug 1924, *Shimek s.n.* (MO); Gitchie Manitou State Park, prairie bits among Sioux Quartzite exposures, 27 Aug 1932, *Shimek s.n.* (UC).

Figure 66. *Heterotheca scabrifolia*, Ellsworth Co., Kansas. A diploid chromosome count has been made from Ellsworth County. Photo from Kansas Wildflowers and Grasses (www.kswildflower.org/).

Figure 67. *Heterotheca scabrifolia*, Glass Mts., Major Co., Oklahoma. A diploid chromosome count has been made from Major County. Photo by Pieter Pelser, 26 September 2008, used by permission. See Nickrent, D.L., M. Costea, J.F. Barcelona, P.B. Pelser, and K. Nixon. 2006 onwards. PhytoImages. <http://www.phytoimages.siu.edu>.


Figure 68. *Heterotheca scabrifolia*, Texas Co., Oklahoma. *Semple & Shea 2217* (NY). Voucher for a diploid chromosome count. Typical morphology of relatively small, closely clustered heads, short-ciliate leaves and bracts, glandular phyllaries.


Figure 69. *Heterotheca scabrifolia*, Dewey Co., Oklahoma. *Harms 1700* (KANU). Typical morphology. A diploid chromosome count has been made from Dewey County.


Figure 70. *Heterotheca scabrifolia*, Woods Co., Oklahoma. *Harms 1691* (KANU), diploid. The type of *H. scabrifolia* is from Woods County.


Figure 71. *Heterotheca scabrifolia*, Woods Co., Oklahoma. *Harms 1992-B* (KANU), tetraploid. Noted by the collector to be from an intergrading population with *Heterotheca angustifolia*. Diploid and tetraploid chromosome counts have been made from Woods County


Figure 72. *Heterotheca scabrifolia*, Barber Co., Kansas. *McGregor 15105* (KANU), tetraploid.


Figure 73. *Heterotheca scabrifolia*, Taylor Co., Texas, slightly north of the range of *H. stenophylla*. *Johnston 6515* (LL). Small heads in clusters but long-ciliate vestiture more like typical *H. stenophylla*.


Figure 74. *Heterotheca scabrifolia*, Eastland Co., Texas, slightly north of the range of *H. stenophylla*. *Warnock 46387* (TEX). Small heads in clusters (blue arrows) but long-ciliate vestiture more like typical *H. stenophylla*.


Figure 75. *Heterotheca angustifolia*, Lyon Co., Iowa. *Lassetter 1548* (BRY).


Figure 76. *Heterotheca angustifolia*, Lyon Co., Iowa. *Lassetter 1560* (BRY). See comments in text.


Figure 77. *Heterotheca angustifolia*, Lyon Co., Iowa. *Shimek s.n.* in 1896 (MO).


Figure 78. *Heterotheca angustifolia*, Minnehaha Co., South Dakota. *Stephens 31899* (KANU).

**17. HETEROTHECA WISCONSINENSIS** (Shinners) Shinners, Field & Lab. 19: 71. 1951. *Chrysopsis wisconsinensis* Shinners, Wrightia 1: 218. 1948. **TYPE**: **Wisconsin**. Adams Co.: 15 mi N of Wisconsin Dells on County Trunk D, sandstone bluff, 7 Jul 1947, *H.C. Greene s.n.* (holotype: SMU image!; isotypes: GH, ILL image!, MIL, WIS image!).

**Stems** stiffly hirsute with spreading to spreading-ascending or slightly deflexed hairs in 2 stories, glandular. **Leaves** oblanceolate to oblong-oblanceolate, (1.6–)20–40 mm, relatively even-sized along the stems or slightly reduced distally, not clasping, conspicuously sessile-glandular, coarsely hirsute, margins long-ciliate. **Heads** essentially solitary (loosely arranged on sparsely leafy peduncles mostly 5–8 cm long), usually with 1 or 2 narrow capitular bracts. **Involucres** 8–10 mm wide; phyllaries villous-strigose to villous-hirsute, glandular. **Ray flowers** 14–30. **Chromosome number** 2*n*=18 (Adams Co., 23 Aug 1987, *Semple 8845*, MO).

*Heterotheca wisconsinensis* is an unambiguously distinctive species known only from three contiguous Wisconsin counties (Adams, Marquette, and Waushara), which include most of the Wisconsin "Central Sand Plains" (Wisconsin DNR 2014). Other endemics and disjuncts occur in the area. Many collections of *H. wisconsinensis* have been made (see WIS database, where most are currently identified [following Semple 1996] as *H. villosa* var. *minor*). In the protologue of *Chrysopsis wisconsinensis*, Shinners noted that it is "a dwarf spring-flowering [June to early July] plant [and] locally very common and even weedy." More recent collections show that it continues flowering into October but, even so, flowering during spring months is unusual in *Heterotheca*.

*Heterotheca wisconsinensis* occurs outside of the eastern edge of the range of *H. ballardii*, which is similar in its hirsute stems, oblong-oblanceolate leaves, and heads on relatively long peduncles and subtended by capitular bracts. *Heterotheca wisconsinensis* differs in its more densely hirsute vestiture (often especially noticeable on leaves, bracts, and phyllaries), relatively dense glandularity, much smaller heads, and phyllaries with broad, hyaline margins. Consistent distinctions in vestiture, capitulescence, head size, phyllary morphology, phenology, and disjunct distribution on a specialized habitat provide rationale for the recognition of *H. wisconsinensis* as distinct. *Heterotheca wisconsinensis* is diploid while *H. ballardii* is tetraploid, arguing against a hypothesis that *H. wisconsinensis* originated as a peripheral isolate of *H. ballardii* or of any of the other tetraploid Great Plains populations.


Figure 79. *Heterotheca wisconsinensis*, Adams Co., Wisconsin. *Fassett 16938* (WIS).


Figure 80. *Heterotheca wisconsinensis*, Marquette Co., Wisconsin. *Vazquez G. 5034* (WIS).

**18. HETEROTHECA CAMPORUM** (Greene) Shinners, Field & Lab. 19: 71. 1951. *Chrysopsis camporum* Greene, Pittonia 3: 88. 1896. *Chrysopsis villosa* var. *camporum* (Greene) Cronq., Bull. Torrey Bot. Club 74: 150. 1947. *Heterotheca villosa* var. *camporum* (Greene) Wunderlin, Ann. Missouri Bot. Gard. 59: 471. 1973. **TYPE**: **Illinois**. Prairies of Illinois, 1842, *C.W. Short s.n.* (holotype: NDG image!; isotypes: GH image!, NY, US).

Plants taprooted when young, becoming short-rhizomatous (or with short offsets) and fibrous-rooted and losing the taproot, sometimes retaining a woody caudex. **Stems** erect to ascending-erect, 40–70(–150 in var. *glandulissima*) cm; cauline vestiture with strigose understory of loosely appressed hairs, sometimes with sparsely to moderately coarsely hirsute overstory of spreading hairs, eglandular or sparsely glandular. **Leaves**: surfaces moderately hispid to hispid-hirsute or strigose-hirsute to strigose with loosely appressed hairs, eglandular or very sparsely glandular to densely stipitate-glandular. **Heads** without capitular bracts. **Involucres** 7–10 mm high, glandular-viscid, usually without other vestiture, rarely sparsely strigose. **Ray flowers** 16–32(–38); ligules 10–18(–22) mm long, 1–2.2(–2.6) mm wide. **Chromosome number**, 2*n*=36.

Semple (1996) separated *Heterotheca camporum* from other goldenasters on the basis of its "stem leaves with several serrate teeth along the margins" ("no other species has well developed serrations along the margins of its upper stem leaves"), relatively tall stature, lack of capitular bracts, and its distribution in the eastern USA.

Harms (1963, p. 52) noted that *Heterotheca camporum* is the "coarsest, tallest, and weediest member of the *H. villosa* complex east of the Rocky Mountains" and characterized the species by "(1) its large size [height], generally exceeding 7 dm, and abundant coarse branching, (2) the distinctly toothed larger leaves, (3) the dense, soft-textured, green foliage, (4) fine, non-pustulate, hirsute primary and secondary stem and leaf pubescence, (5) primary stem hairs displaying a definite, but not pronounced, counterclockwise spiral twisting, (6) very small, distinctly stipitate resin glands, at least on phyllaries and stems, (7) phyllary series rather loose, with at least the inner series recurved at anthesis, (8) large, attenuate rather than petiolate leaves, and (9) large, pedunculate heads in open dichasic cymes, the peduncular leaves reduced, distant, linear, the upper ones grading into phyllaries."

Semple noted (essentially following Harms) that a clinal trend is present in *Heterotheca camporum*, the plants in northern to central Illinois tending to have narrower and more entire leaves, increased glandularity, and longer and more divergent phyllary vestiture. Collections from Carroll, Henry, and Joe Daviess counties identified and mapped by Semple (1993) as forms of *H. villosa* ("aff. var. *minor*" and "aff. var. *villosa*") are the narrow-leaved *H. camporum* (e.g., Jo Daviess Co.: Sand prairie, 18 Aug 1898, *Pepoon s.n.*, PH).

Semple (1983) recognized plants with prominent glandularity as *Heterotheca camporum* var. *glandulissima*, distinguished by "stems that are stipitate-glandular above and that are generally 75 cm tall or more, ... densely stipitate-glandular phyllaries and peduncles that are usually sparsely hispid pubescent, ... moderately to densely glandular and hispid pubescent leaves, and often by having fruits with golden to red-brown translucent ridges." Both varieties are consistently tetraploid (2*n*=36), fide counts by Semple.

Among plants grown from seeds by Harms from a St. Louis, Missouri, population (var. *camporum*), "broad- and narrow-leaved forms appeared, as well as forms with resinous and non-resinous leaves and glabrate and persistently pubescent phyllaries." Five plants of var. *glandulissima* transplanted by the author from Wilson Co., Tennessee (*Nesom het2015-13*), to Fort Worth, Texas, and grown for 3 years did not produce glands on the leaf surfaces.


Figure 81. *Heterotheca camporum*, typical form, Greene Co., Missouri. *Yatskievych 91-280* (MO).


Figure 82. *Heterotheca camporum*, narrow-leaved form, Carroll Co., Illinois. *Thieret 60969* (KNK).

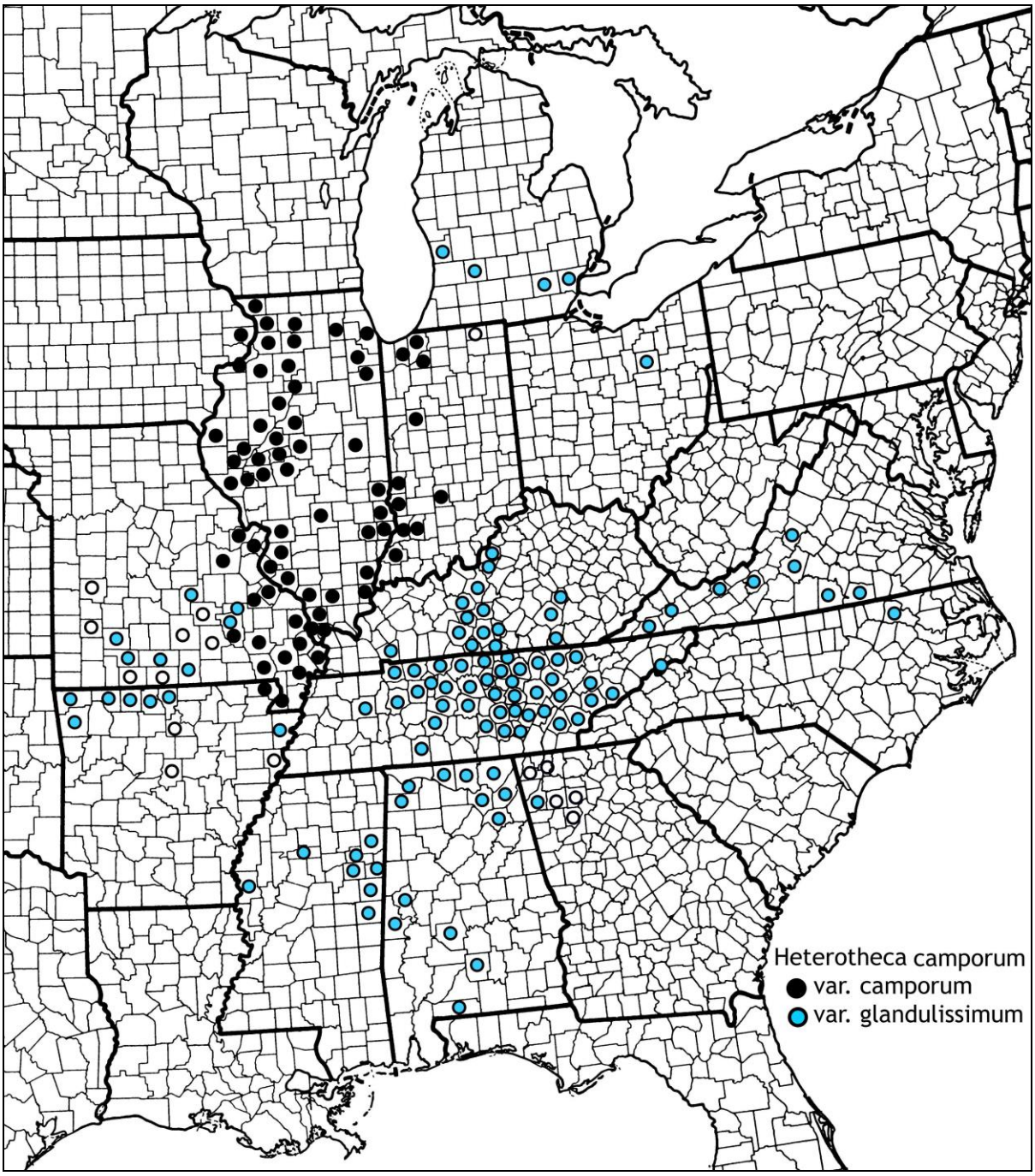


Figure 83. Distribution of *Heterotheca camporum*. Unfilled symbols are records with vouchers not seen by the author.

1. Stems mostly 40–70 cm tall; upper stems and peduncles eglandular to moderately glandular, leaves eglandular ..... 18a. **Heterotheca camporum var. camporum**
1. Stems 65–150 cm tall; stems, peduncles, and leaves prominently stipitate-glandular ..... 18b. **Heterotheca camporum** var. **glandulissima**

**18a. Heterotheca camporum** var. **camporum**

**18b. Heterotheca camporum** var. **glandulissima** Semple, Brittonia 35: 146. 1983. *Chrysopsis camporum* var. *glandulissima* (Semple) Cronq., Man. Vasc. Pl. N.E. U.S. (ed. 2), 863. 1991. **TYPE**: **Tennessee**. Cumberland Co.: Protologue and label: Just S of county line along small river, very large population in disturbed sandy soil, 1 Oct 1977, *J.C. Semple et al. 3010* (holotype: WAT; isotypes: MO!, NY image!). Locality from pers. observ., Nesom 2015: 1 mi S of the center of Clarkrange on US Hwy 127, S side of Clear Creek along the Fentress/Cumberland Co. line, large and dense population on steep, clay-loam road bank immediately between the hwy and maintenance road down to the creek, scattered plants on natural limestone ledges and outcrops on adjacent steep slopes with oak-pine woods.

Flowering Jul–Sep(–Oct). Native range as interpreted here (Alabama, Arkansas, Georgia, Kentucky, Mississippi, Missouri, Tennessee): Limestone, shale, and chalk outcrops and bluffs, rocky limestone slopes, rocky roadcuts, cedar glades and barrens, gravelly roadsides and disturbed sites. Outside of the native range (Michigan, North Carolina, Ohio, Virginia, perhaps eastern Tennessee and southeastern Kentucky): roadsides and disturbed sites.

The observations here show essentially the same historical and present distribution of var. *camporum* as mapped by Semple (1983, his Figs. 2-4). The range of var. *glandulissima*, however, is broader than shown by Semple, perhaps reflecting a greater availability of collections.

Semple (1983, 1996) noted that var. *glandulissima* probably was originally adapted to glades and ecologically similar disturbed areas mostly in central Tennessee and adjacent Alabama. Relatively early collections indicate that the original range probably also included limestone/chalk areas in adjacent east-central Mississippi (e.g., Lowndes Co., Columbus, dry ground, 20 Sep 1931, *Sargent s.n.*, LL). Similar sites in south-central Kentucky may also have been part of the original range. Collections from northwestern Georgia are at the southeastern extremity of the native range: e.g., Floyd Co.: Horseleg Mtn, Marshall Forest, rocks, low ridge woods, 800 ft, 17 Oct 1964, *Demaree 51731* (SMU). I see no clear evidence to support Semple's statement (2006, p. 256) that "The variety appears to have evolved within historic times in Tennessee, or only recently to have evolved the traits necessary to make it a successful roadside weed," but it does seem that the species is expanding in geographic range.

Semple (1996) reckoned that the interstate highway system is the primary corridor for migration of var. *glandulissima*. Collectors Sharp and Iwatsuki (*21624*, LL) noted in 1956 that the taxon was a "recent adventive, rapidly spreading" along roadside banks in Putnam Co., Tennessee. Var. *glandulissima* perhaps has recently colonized northwestern Arkansas and south-central Missouri via the road system, but evidence for such a recent range expansion does not seem unambiguous. Railroad rights-of-way may also have facilitated dispersal, e.g., Mississippi Co.: Along RR in Mississippi valley, Frenchman Bayou, 2 Oct 1949, *Demaree 28579* (SMU). Plants identified as var. *glandulissima* have spread northward into Ohio and Michigan and adventive populations are known from North Carolina and Virginia.

The native range of var. *glandulissima* in Tennessee may have been wider than currently supposed (documentation perhaps existed prior to the 1934 fire that destroyed the TENN collection). The species obviously has increased in abundance in Tennessee through creation of roadway-associated habitats, but it also occurs outside of the main "glades" area in what appear to be natural habitats — limestone bluffs, ledges, outcrops, and rocky slopes (pers. observ.). Such is the case at the type locality in Cumberland County, where a large and conspicuous population is established on a clearly man-made habitat, but other plants are scattered on rocky microsites in undisturbed woods on steep slopes of the surrounding area. It also may be true of Putnam County (see comment above

regarding its recent spread there), where plants can be found in undisturbed microsites (pers. observ. 2015).

Notable variants occur on chalk outcrop areas in Sumter Co., west-central Alabama, and in nearly adjacent Oktibbeha Co., Mississippi. In Sumter Co., most collections document glandular plants (e.g., *Thomas 113860*-BRIT, *Kral 48762*-VDB, *Kral 49779*-VDB), but *Kral 29864* (SMU, VDB) has eglandular stems, leaves, and phyllaries. In Oktibbeha County, *Leidolf 1596* (BRIT, VDB) is glandular while *Bryson 8318* (VDB) and *McDaniel 22925* (BRIT, VDB) are eglandular. All of these collections are identified here as var. *glandulissima*, based on their geography.

**19. HETEROTHECA BRANDEGEEI** (B.L. Rob. & Greenm.) Semple, Syst. Bot. 13: 557. 1988. *Chrysopsis brandegeei* B.L. Rob. & Greenm., Proc. Amer. Acad. Arts 32: 43. 1897 [published 1896]. **TYPE**: **MEXICO**. **Baja California**. San Pedro Mártir, May 1893, *T.S. Brandegee s.n.* (holotype: GH image!; isotypes: OSC image!, RM-fragment!).

*Heterotheca martirensis* R. Moran, Trans. San Diego Soc. Nat. Hist. 15: 289. 1969. **TYPE**: **MEXICO**. **Baja California**. Sierra San Pedro Mártir, common on N slope of "Cerro 2828," 2800 m, 14 Sep 1968, *R. Moran 15612* (holotype: SD; isotypes: CAS!, GH, K, MICH, NY, RSA!, US). Images! of all types.

*Heterotheca brandegeei* is endemic to the Sierra San Pedro de Mártir in Baja California (map in Fig. 1). It is characterized by its tendency to produce slender, scale-leaved rhizomes (or rhizome-like caudex branches), leaves mostly crowded toward the branch tips, solitary, rayless heads on long (2–5 cm), bracteate peduncles without capitular bracts, glabrous phyllaries, and hispid-pilose to hirsute-pilose vestiture of stems and leaves. As observed by Semple (1996), this species, apparently allopatric with all others, exhibits a wide range of density of glandular and non-glandular hairs. It offers an unambiguous view of such variability within a single goldenaster species, presumably without genetic influence (at least contemporary influence) from any other.

Semple (1996) noted that the long peduncles and purple-tinged phyllaries of *Heterotheca brandegeei* suggest a relationship with the "Mucronata group" of continental Mexico, while Moran (1969) emphasized its similarities to *H. jonesii* of southern Utah.

**20. HETEROTHECA JONESII** (Blake) Welsh & Atwood, Great Basin Naturalist 35: 336. 1975 [1976]. *Chrysopsis jonesii* Blake, nom. nov., Contr. U.S. Natl. Herb. 25: 537. 1925; replacing *Chrysopsis caespitosa* M.E. Jones, Proc. Calif. Acad. Sci., ser. 2, 5: 694. 1895 [not *Chrysopsis caespitosa* Nutt. 1834]. **TYPE**: **Utah**. Washington Co.: Springdale, in red sand, 4000 ft, 16 May 1894, *M.E. Jones 5249u* (holotype: RSA!; isotype: US image!). The RSA branch perhaps was originally part of the much larger plant on the US sheet.

*Heterotheca jonesii* is restricted to Garfield, Kane, and Washington counties of southwestern Utah (Map 11, Fig. 106), where it occurs in sandy habitats, often in sandstone crevices. The plants are low (2–6 cm high) and commonly form small cushions, with lateral shoots arising from bracteate (scale-leaved), rhizome-like caudex branches. **Stems** and peduncles loosely strigose-villous, understory eglandular, overstory hispid-hirsute. **Leaves** eglandular, loosely strigose-villous with long-ciliate proximal margins. **Heads** solitary on densely leafy stems, capitular bracts little reduced if any from the leaves. **Involucres** relatively small (5–7 mm long), phyllaries often with purplish margins. **Ray flowers** 7–11, ligules drying purplish. **Chromosome number**, 2*n*=18.