

TAXONOMIC OVERVIEW OF THE *HETEROTHECA* *VILLOSA* COMPLEX (ASTERACEAE: ASTEREA)

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ABSTRACT

Heterotheca villosa (as treated by Semple 1996, 2006) is a complex species with nine varieties, most of which are sympatric in various degrees. *Heterotheca villosa* var. *nana* and *H. villosa* var. *scabra* are essentially allopatric and intergrade little, but each is widely sympatric with *H. villosa* and distinct from it. Recognition at specific rank accurately reflects the status of var. *nana* and var. *scabra*, and they are treated here, respectively, as *Heterotheca horrida* (Rydb.) Harms and *Heterotheca polothrix* Nesom, nom. et stat. nov. *Heterotheca stenophylla* sensu stricto is distinct from *H. stenophylla* var. *angustifolia* (sensu Semple) and sympatric with it, and the latter is appropriately treated as *H. villosa* var. *angustifolia* (Rydb.) Harms. The New Mexico endemic *Heterotheca villosa* var. *sierrablancensis* Semple is raised to specific rank as *Heterotheca sierrablancensis* (Semple) Nesom, comb. et stat. nov. Identifications of vars. *villosa*, *foliosa*, *ballardii*, and *minor* (all sensu Semple) require arbitrary judgments because of their broad sympatry and extensive intergradation. The distinction between var. *pedunculata* and *H. zionensis* is not clear, and both taxa apparently intergrade broadly with more typical *H. villosa*. Variety *depressa* is maintained at specific rank as *H. depressa* (Rydb.) Dorn. Maps show the generalized distributions of the taxa of the *H. villosa* complex sensu Semple, and a nomenclatural summary outlines an alternative taxonomy.

RESUMEN

Heterotheca villosa (as treated by Semple 1996, 2006) es un complejo de especies con ocho variedades, la mayoría de las cuales son simpátricas en varios grados. *Heterotheca villosa* var. *nana* y *H. villosa* var. *scabra* son esencialmente alopátricas y se intergradan poco, pero cada una de ellas es ampliamente simpátrica con *H. villosa* y diferente de ella. El reconocimiento a nivel específico refleja con precisión el estatus de var. *nana* y var. *scabra*, y son tratadas aquí, respectivamente, como *Heterotheca horrida* (Rydb.) Harms y *Heterotheca polothrix* Nesom, nom. et stat. nov. *Heterotheca stenophylla* sensu stricto es diferente de *H. stenophylla* var. *angustifolia* (sensu Semple) y simpátrica con ella, y esta última es tratada apropiadamente como *H. villosa* var. *angustifolia* (Rydb.) Harms. La endémica de Nuevo México *Heterotheca villosa* var. *sierrablancensis* Semple se eleva al rango específico como *Heterotheca sierrablancensis* (Semple) Nesom, comb. et stat. nov. Las identificaciones de las vars. *villosa*, *foliosa*, *ballardii*, y *minor* (todas sensu Semple) requieren juicios arbitrarios debido a su amplia simpatria e intergradación extensa. La diferenciación entre var. *pedunculata* y *H. zionensis* no es clara, y ambos taxa aparentemente se intergradan con la más típica *H. villosa*. La variedad *depressa* se mantiene en el rango específico como *H. depressa* (Rydb.) Dorn. En los mapas se muestran las distribuciones generales de los taxa del complejo *H. villosa* sensu Semple, y un resumen nomenclatural delinea una taxonomía alternativa.

Intermediates between taxa of *Heterotheca* are often encountered and unequivocal identifications are correspondingly difficult. Phenotypic plasticity, small

degrees of differentiation, and hybridization apparently underlie the taxonomic difficulties. Tetraploids are common and gene exchange among them apparently occurs frequently. A monograph of *Heterotheca* sect. *Phyllothea* (Semple 1996) provides a detailed view of the taxonomic structure of this group and addresses difficulties in identification.

Heterotheca villosa, as treated by Semple (1996, 2006), is a widespread and complex species with nine varietal taxa, most of which are geographically overlapping or almost completely superimposed. Typical *H. villosa* (var. *villosa*) occupies essentially the northern half of the species range, but it is broadly sympatric with var. *minor*, var. *foliosa*, var. *ballardii*, and var. *nana*. In part of Nebraska and South Dakota, five varieties (sensu Semple) of *H. villosa* occur sympatrically; four varieties occur sympatrically in Saskatchewan; three occur sympatrically in much of Wyoming, Colorado, and Utah. Two are relatively narrow endemics (within a single state); all the others occur in at least four states. All taxa were mapped in detail by Semple (1996, Figs. 39 and 40); generalized outline maps shown here (Figs. 1, 2, 3) are derived in most part from Semple's dot maps.

Regarding the *Heterotheca villosa* complex, Semple (1996, p. 114) noted that it might be "logical to merge all ... varieties together with no infraspecific taxa being recognized ... This would result in the loss from the formal nomenclature of a great deal of information on variation and distribution in what is admittedly a difficult species complex." His approach (as noted by Nesom 1997) has been to recognize sympatric conspecific varieties, using formal varietal names to identify what many (or most) systematists might regard as geographical trends or populational variants. "A variety is characterized by all members of a population exhibiting a particular morphology distinct from other individuals in the species. The distribution of these populations is sympatric with populations whose members are not within the same variety, and also many populations of morphological intermediates exist [citing various references]. ... Van Steenis described varietal level variation as being continuous with other varieties, although the continuum would have pronounced modes" (Semple 1974, p. 8-9). Similarly, and with regard to *Heterotheca villosa*, "the races fit well with the concept of variety in that each occurs in pure form in some populations, and the overall ranges are sympatric to a considerable degree with at least one other variety" (Semple 1996, p. 108).

Semple has used a similar taxonomic approach for *Heterotheca sessiliflora* (Nutt.) Shinnery sensu lato, a primarily Californian complex, and formal changes in taxonomic rank were proposed by Nesom (1997) to clarify its systematics. The taxonomic situation with *H. villosa* (Pursh) Shinnery is considered here. Harms (1968, 1970) also has addressed aspects of the taxonomy of the *H. villosa* complex.

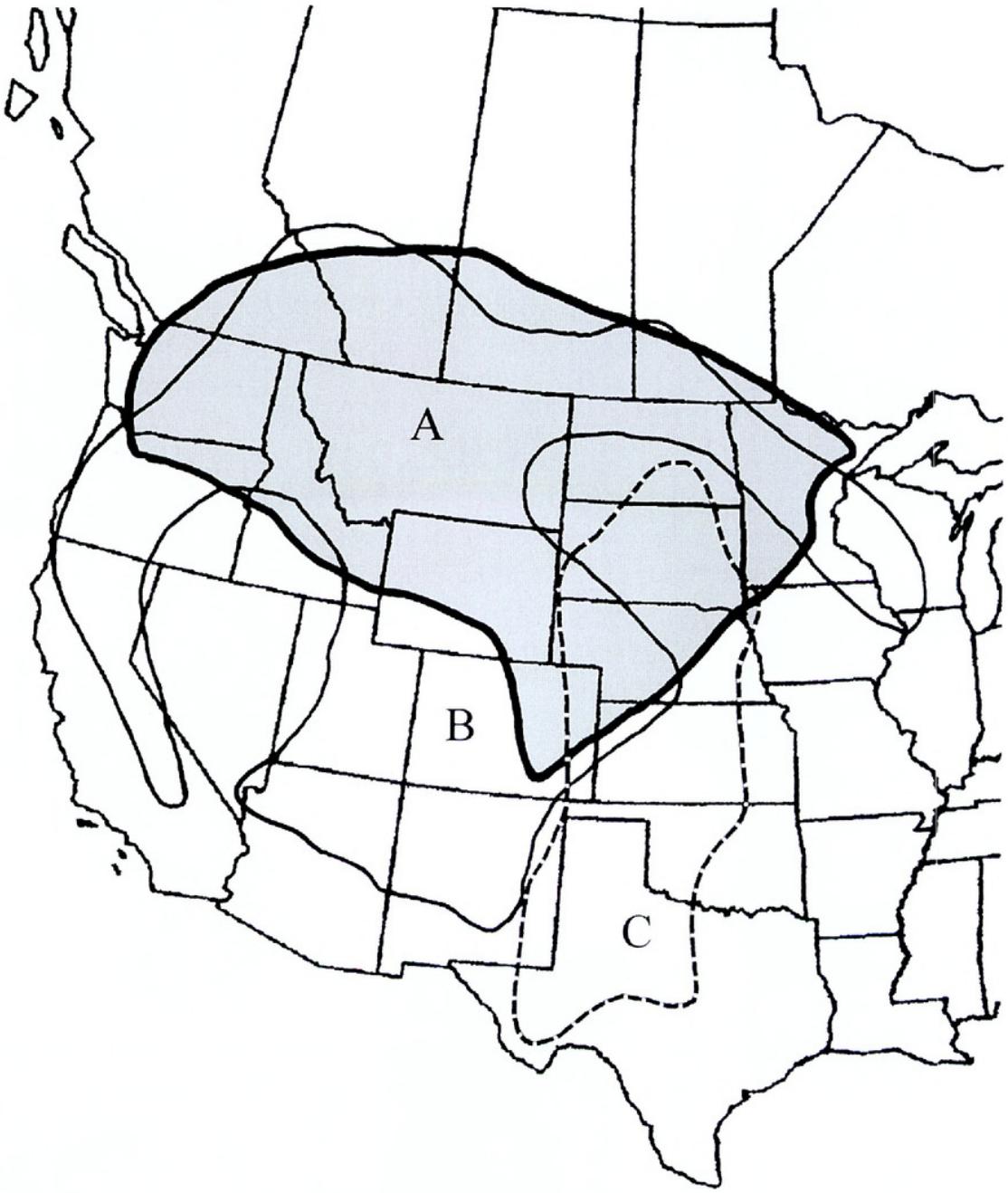


FIG. 1. Generalized distribution of *Heterotheca villosa* (A) var. *villosa* and (B) var. *minor*, both sensu Semple, and (C) *H. villosa* var. *angustifolia*. Illustrated is the broad sympatry of var. *villosa* and var. *minor* and the partial sympatry/allopatry of var. *angustifolia*. The range of *H. villosa*, mapped here as var. *minor*, includes southern Nevada (Clark Co., Excelsior Canyon, 7 Sep 1941, *Clokey* 8759-M0). The range of var. *angustifolia* includes northwestern Iowa (Lyon Co., prairie, among Sioux Quartzite exposures, nw corner of county, 25 Aug 1924, *Shimek* s.n.-M0).

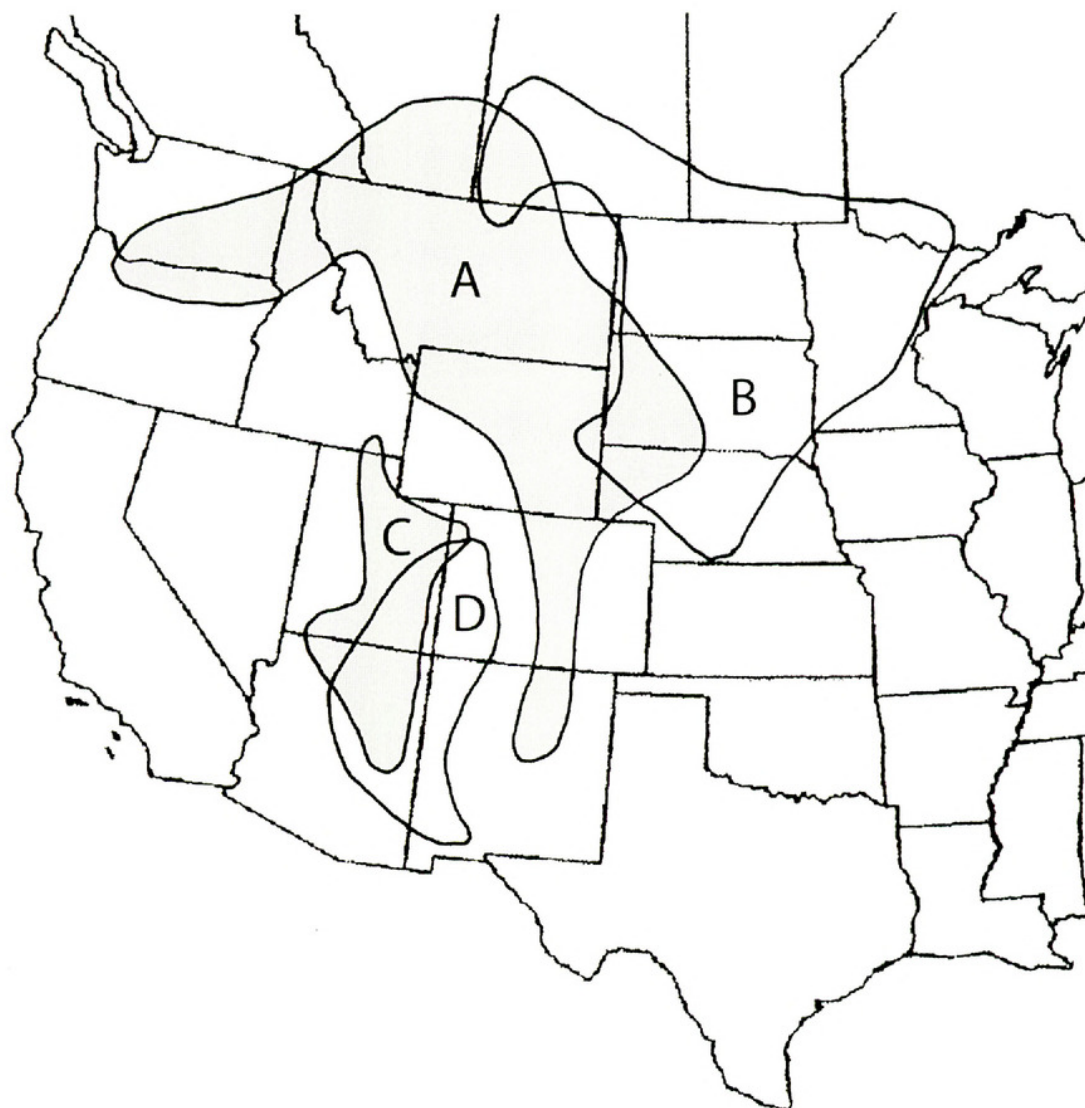


FIG. 2. Generalized distribution of *Heterotheca villosa* (A) var. *foliosa*, (B) var. *ballardii*, (C) *H. zionensis*, and (D) var. *pedunculata*, all sensu Semple. Compare with Fig. 1 to see broad sympatry of var. *foliosa* and var. *ballardii* with var. *villosa* and var. *minor*.

Status of *Heterotheca villosa* var. *pedunculata*

Heterotheca villosa var. *pedunculata* occurs in complete sympatry with *H. villosa* var. *minor* in the Four Corners region, as indicated by Semple (1996) (var. *pedunculata* with upper cauline leaves densely to extremely densely strigose, thus pale green to white, eglandular to very sparsely glandular; $2n = 18, 36$; var. *minor* with upper cauline leaves sparsely to moderately densely strigose, sparsely to densely glandular; $2n = 18, 36$). Variety *minor* "is the most variable [infraspecific taxon] in the species and includes some local distinctive morphotypes that grade into other forms. Plants intermediate between this and all other varieties occur in areas where the ranges are sympatric, and they make infraspecific taxonomy of the species difficult" (Semple 2006). In a study of



FIG. 3. Generalized distribution of (A) *Heterotheca polothrix*, (B) *H. horrida*, (C) *H. stenophylla*, (D) *H. depressa*, and (E) *H. sierrablancensis*. Illustrated are the distributions of taxa recognized here at specific rank.

Four Corners *Heterotheca*, I have been able to make only arbitrary morphological distinctions between var. *pedunculata* and var. *minor*.

Variety *pedunculata* is very similar to *Heterotheca zionensis* Semple and partly sympatric with it. Plants of *H. zionensis* are said to be identified by stems and leaves appearing silvery to whitish from densely strigose vestiture and peduncles and phyllaries usually densely glandular but otherwise glabrate. Such plants are distinguished by Semple from more densely pubescent individuals of *H. villosa* var. *minor* or from plants identified as var. *pedunculata* (with gray to silvery leaves) by glandular peduncles and phyllaries, even though plants of var. *minor* may have glandular phyllaries and populations of *H. zionensis* may

include individuals with eglandular peduncles and phyllaries—"non-glandular forms of *H. zionensis* occur in north-central Utah; glandular and non-glandular forms occur in the Utah-Arizona border region" (Semple 1987, p. 385). The geographic range of *H. zionensis* overlays the range of the western portion of var. *minor* as well as of var. *pedunculata*, and distinctions among these are unclear. It does seem clear that silvery-leaved plants are concentrated in the southwest part of the range of *H. villosa*, but if the silvery-leaved plants are representative of a geographic trend in vestiture, widely intergrading with more typical plants, then it is likely that the names *H. zionensis* and *H. villosa* var. *pedunculata* represent plants shaped by the same trend and the same underlying genetics.

Status of *Heterotheca villosa* var. *nana* and var. *scabra*

Heterotheca villosa var. *nana* (diploid) is almost completely overlaid in its geographic range by var. *foliosa* (diploid and tetraploid but tetraploid in its area of overlap with var. *nana*, many chromosome counts, fide Semple 1996) and by var. *minor* (diploid and tetraploid, many counts, fide Semple 1996). Variety *nana* varies considerably and probably hybridizes with *H. villosa* and *H. fulcrata* (Greene) Shinnars (Semple 2006), but even so, var. *nana* is morphologically consistent and recognizable throughout its range and has previously been treated at specific rank by various botanists as *H. horrida* (Rydb.) Harms (e.g., Harms 1968, 1970; Great Plains Flora Association 1986; Dorn 1988).

Heterotheca villosa var. *scabra* is the westernmost taxon treated by Semple within *H. villosa*, except for the south-reaching extension of the species in California (var. *minor* fide Semple). Semple (1992) noted that var. *scabra* is closely related to the Californian endemic *H. shevockii* (Semple) Semple (originally described as *H. villosa* var. *shevockii*). It seems equally plausible that var. *nana* is closely related to var. *scabra*. All three taxa tend to have spreading leaves and strongly developed glandularity.

The geographic ranges of var. *nana* and var. *scabra* are slightly overlapping along the Utah/Colorado and northern Arizona/New Mexico borders (Fig. 3). Semple (2006) observed that "In the Four Corners area, var. *nana* grades into var. *scabra*, and collections often are difficult to place into one of the two taxa"—but I find the distinction clearer and intermediates not numerous, especially in view of the broad range and relative morphological constancy of var. *scabra*. Plants of var. *scabra* and "aff. var. *scabra*" cited by Semple at a southeastern extension of its range in trans-Pecos Texas are tentatively identified here as forms of *H. viscida* (A. Gray) Harms. New Mexico collections of var. *scabra* well east of the range illustrated in Fig. 3 (San Miguel Co., Rio Arriba Co.; cited but not mapped by Semple 1992) are better identified as var. *nana*. I have not seen records of var. *scabra* from Idaho or Colorado (as indicated on Fig. 3), but it is a distinctive entity and Dr. Semple's citations document its presence there.

Variety *nana* and var. *scabra* are distinguished by Semple by various differences (mostly foliar), and my study corroborates and emphasizes their distinction, as in the following couplet.

1. Cauline leaves usually not contorted upon drying, upper mostly lanceolate to triangular-lanceolate, acute at apex; leaf surfaces moderately to densely glandular, the glands little obscured by the sparsely strigose (nonglandular) vestiture, nonglandular hairs often restricted to midvein area (middle 1/3) of adaxial surfaces or sometimes nearly absent on both surfaces, especially on more distal leaves; phyllaries glabrous to very sparsely strigose, glandular; $2n = 18, 36$ (many counts, fide Semple 1996) _____ ***Heterotheca villosa* var. *scabra***
1. Cauline leaves often contorted (margins undulate) upon drying, upper mostly oblong or oblong-lanceolate, acute to obtuse at apex; leaf surfaces moderately to densely glandular, the glands conspicuous through the sparsely hispid to hispidulous (nonglandular) vestiture; phyllaries sparsely to moderately densely strigose, glandular; $2n = 18$ (many counts; $2n = 27$, one count, fide Semple 1996) _____ ***Heterotheca villosa* var. *nana***

Including some features more difficult to precisely contrast, plants of var. *scabra* (in contrast to var. *nana*) have stems and leaves with much reduced non-glandular vestiture but with denser and more conspicuous glandularity, leaves differently shaped, smaller, and more widely spaced, heads relatively fewer, and phyllaries glabrous (lacking non-glandular hairs) but glandular. The two taxa are different in geography.

In their area of sympatry, var. *scabra* is distinguished from a regional, more typical form of *Heterotheca villosa* (var. *minor* fide Semple) by the following contrasts.

1. Upper cauline leaves lanceolate to triangular-lanceolate, acute at apex; leaf surfaces moderately to densely glandular, the glands little obscured by the sparsely strigose (nonglandular) vestiture, nonglandular hairs often restricted to midvein area (middle 1/3) of adaxial surfaces or sometimes nearly absent on both surfaces; phyllaries glabrous to very sparsely strigose _____ ***Heterotheca villosa* var. *scabra***
1. Upper cauline leaves linear to oblanceolate, oblong-lanceolate, or narrowly obovate, acute to obtuse at apex; leaf surfaces eglandular or sparsely to densely glandular, moderately to densely strigose evenly over both surfaces; phyllaries sparsely strigose _____ ***Heterotheca villosa* var. *minor***

In view of their morphological integrity and apparent reproductive isolation from elements of more nearly typical *Heterotheca villosa*, both *H. villosa* var. *nana* and *H. villosa* var. *scabra* are treated here at specific rank.

Heterotheca polothrix Nesom, nom. et stat. nov. *Chrysopsis villosa* var. *scabra* Eastwood, Proc. Calif. Acad. Sci. 2.6:294. 1896. *Heterotheca villosa* var. *scabra* (Eastwood) Semple, Phytologia 73:453. 1992. TYPE: U.S.A. UTAH. San Juan Co.: Willow Creek, 14 Jul 1895, A. Eastwood 38 (HOLOTYPE: CAS, digital image!). Non *Heterotheca scabra* DC. 1836. The species is named for a resemblance of the medial strip of adaxial leaf vestiture to the mane of a pony (Greek, *polos*, pony, and *thrix*, hair). Blake's varietal epithet ("cinerascens," at varietal rank, as below) is poorly descriptive of the taxon (as also noted by Semple 1987).

Chrysopsis viscida A. Gray subsp. *cinerascens* Blake, Proc. Biol. Soc. Washington 35:173. 1922.
Heterotheca horrida subsp. *cinerascens* (Blake) Semple, Brittonia 39:381. 1987. TYPE: U.S.A.
 UTAH. [Beaver Co.: fide Welsh 1982]: Beaver Creek, among rocks in the oak region, 2 Sep 1901, I.
 Tidestrom 2873 (HOLOTYPE: US, internet image!).

Heterotheca horrida (Rydb.) Harms, Wrightia 4:17. 1968. *Chrysopsis horrida* Rydb.,
 Bull. Torrey Bot. Club 31:648. 1905. TYPE: U.S.A. COLORADO. [Weld Co.]: New Windsor, 8 Aug
 1900, G.E. Osterhout 2326 (HOLOTYPE: NY internet image!; ISOTYPES: RM, WIS).

Chrysopsis canescens var. *nana* A. Gray, Mem. Amer. Acad. Sci. 4[Pl. Fendl.]:78. 1849. *Heterotheca*
villosa var. *nana* (A. Gray) Semple, Novon 4:54. 1994. TYPE: U.S.A. NEW MEXICO. [Mora Co.?]:
 elevated rocky region 2 mi E of the Mora River, Aug 1847, A. Fendler 391c (HOLOTYPE: GH).

Status of *Heterotheca villosa* var. *sierrablancensis*

Heterotheca villosa var. *sierrablancensis* was described by Semple (1996) from the White Mountains and Sacramento Mountains of Lincoln and Otero cos., New Mexico. It is similar to *H. horrida* in its conspicuously glandular vestiture and congested and consistently corymbiform capitulescence but distinct in its leaves more densely strigose, the upper cauline ascending, larger, and differently shaped (lanceolate or oblong-lanceolate to ovate), ray corollas longer, and habitats at higher elevation. It occurs at the southeastern corner of the range of *H. horrida* (*H. villosa* var. *nana*) and Semple indicated (1996, Fig. 3) that the two taxa are most closely related to each other. Both are primarily diploids. The extended population system of var. *sierrablancensis* is morphologically variable but it lies inside the geographic range of *H. horrida* and apparently is isolated from it as well as the regional expression of *H. villosa*, both of which occur at lower elevations. Recognition at specific rank is appropriate for this taxon, especially in view of the parallel rank of *H. horrida*.

Heterotheca sierrablancensis (Semple) Nesom, comb. & stat. nov. *Heterotheca villosa*
 var. *sierrablancensis* Semple, Univ. Waterloo Biol. Ser. 37:146. 1996. TYPE: U.S.A. NEW MEXICO.
 Lincoln Co.: Sierra Blanca, NM 532 8.5 km W of NM 48, rocky outcrop and face of roadcut at
 switchback directly below scenic overlook, 2 Oct 1995, J.C. Semple and Semple 10513-A (HO-
 LOTYPE: WAT; ISOTYPES: MOI, NMC, RM).

Status of *Heterotheca villosa* var. *depressa*.

Semple treated this narrowly endemic taxon at varietal rank because it hybridizes with var. *minor*. Both taxa are tetraploid in their area of sympatry. As noted by Semple (2006), "Var. *depressa* grows in geyser basins in Yellowstone National Park and is locally common in rocky soils in Teton National Park; it is very rare farther south in Wyoming. It is distinguished by its small stature, small heads, and linear-oblong leaves with many hairs and usually some glands. It is similar to some forms of var. *minor*, which occur throughout the range of var. *depressa* and with which it hybridizes. ... Typical var. *depressa* occupies the vicinity of hot springs and geyser basins and nearby river flood banks, while var. *minor* occupies other drier or non-geyserite nearby habitats." Markow (2001,

2004) found that the occurrence of *H. depressa* is strongly correlated with that of another narrow endemic, *Stephanomeria fluminea* Gottlieb.

The geographic range of *Heterotheca villosa* var. *depressa* is relatively discrete, like that of *H. sierrablancensis*, and is essentially imbedded within the much larger distribution of *H. villosa* sensu lato. Although var. *minor* (sensu Semple) hybridizes with var. *depressa*, the latter appears to have its unique ecological niche, maintains its morphological identity, and is justifiably treated at specific rank.

Heterotheca depressa (Rydb.) Dorn, Vasc. Pl. Wyoming (ed. 1) 295. 1988. *Chrysopsis depressa* Rydb., Mem. New York Bot. Gard. 1:381. 1900. *Heterotheca villosa* var. *depressa* (Rydb.) Semple, Novon 4:53. 1994. TYPE: U.S.A. WYOMING. Teton Co.: Yellowstone National Park, Lower Geyser Basin, 7000 ft, 4 Aug 1897, P.A. Rydberg and E.A. Bessey 5067 (HOLOTYPE: NY internet image!; ISOTYPES: CAN, NY, US internet image!).

Status of *Heterotheca stenophylla* var. *angustifolia*.

Semple (1996, 2006) has treated *Heterotheca stenophylla* (A. Gray) Shinnery as comprising two varieties, var. *stenophylla* and var. *angustifolia* (Rydb.) Semple, “based on field studies and the results of multivariate analyses ... The type of var. *angustifolia* is morphologically closer to many individuals of [*H. stenophylla*] var. *stenophylla* than it is to either *H. canescens* or typical *H. villosa*. ... At the very least, the type of var. *angustifolia* belongs in *H. stenophylla*, regardless of where the more *canescens*-like and the more *villosa*-like plants are placed” (Semple 1996, p. 94).

Previous botanists have treated var. *angustifolia* within *Heterotheca villosa* (e.g., Harms 1968, 1970; Great Plains Flora Association 1986). Harms observed (1968, p. 16–17) that “over most its range, including Texas, *Heterotheca stenophylla* appears to represent a quite distinct diploid ($n = 9$) species, but some tetraploid ($n = 18$) populations are known from a narrow band along the eastern edge of the species’ overall distribution reaching from south-central Kansas to the Wichita Mountains of south-central Oklahoma (to ?Archer Co., Texas) which hybridize and intergrade somewhat with [tetraploid] *H. villosa*. As a result, the tetraploid *H. stenophylla* populations as a whole are usually distinguishable from the diploid populations by the presence of such introgressed characters from *H. villosa* as more pubescent involucre, stems, or leaves, but it seems impossible to assign individual plants to a particular ploidy level on this basis. Thus it appears impractical to attempt to taxonomically distinguish the tetraploid from the diploid *H. stenophylla* populations despite the presence of an obvious reproductive barrier based upon different ploidy levels. Neither does it seem logical to taxonomically merge *H. stenophylla* with *H. villosa* [var. *angustifolia*] merely because certain tetraploid populations of the former hybridize more or less extensively with the latter, when most of the *H. stenophylla* taxon is diploid and clearly distinct morphologically and biologically.”

Heterotheca stenophylla (sensu stricto) is broadly sympatric with var. *angustifolia* and I (with Harms) also find that the two are distinct in the field and herbarium. Triploid putative hybrids have been reported (Semple 1996, 2006). In contrast, var. *angustifolia* intergrades with broader-leaved forms of *H. villosa*, especially in Nebraska and the Dakotas, and is reasonably treated within *H. villosa*. "Inclusion of var. *angustifolia* ... only slightly increases the morphological complexity of *H. villosa*, as defined by Semple, and [it] occupies a part of the overall geographic range where its sympatry with conspecific varieties is relatively less" (Nesom 1997, p. 11).

Harms (1970, p. 1567) noted that "most of the Texas material [of *Heterotheca villosa*] belongs to var. *foliosa* (characterized by dense canescent appressed pubescence of involucres and herbage, and larger heads) or to var. *angustifolia* (characterized by narrower leaves, coarser and sparser herbage pubescence and smaller heads); these varieties intergrade on a broad scale, and much Texas material appears to be more or less intermediate between them." Still, a trend within *H. villosa* toward narrow leaves is pronounced in Texas, Oklahoma, and Kansas, and identification of these plants as var. *angustifolia* is justifiable.

1. Stems eglandular; leaves oblong-ob lanceolate to elliptic-ob lanceolate, 3–6 mm wide, eglandular or sessile-glandular on abaxial surface, moderately to densely strigose, hairs usually without inflated basal cells; phyllaries eglandular or inconspicuously and minutely glandular; chromosome counts of $2n = 36$ (fide Semple 1996)

Heterotheca villosa* var. *angustifolia

1. Stems sessile-glandular; leaves linear to narrowly ob lanceolate, 2–3(–4.5) mm wide, sessile-glandular, sparsely hispid-strigose, hairs with conspicuously inflated and viscid basal cells; phyllaries glandular to eglandular, sparsely strigose or essentially without nonglandular hairs; many chromosome counts of $2n = 18$, few of $2n = 36$ (fide Semple 1996)

Heterotheca stenophylla

Consistent distinction between *Heterotheca villosa* var. *angustifolia* and *H. canescens* (DC.) Shinnery is sometimes more difficult than between var. *angustifolia* and *H. stenophylla*. *Heterotheca canescens* is mostly diploid, but some tetraploids have been reported, and as noted by Semple (1996, p. 97), "tetraploids [of *H. canescens* and *H. villosa* var. *angustifolia*] apparently hybridize forming local swarms of parent-like and hybrid individuals." And "in Texas, it sometimes is difficult to clearly distinguish herbarium specimens of [*H. canescens*] from certain canescent, strigose-sericeous, smaller-headed, more narrow-leaved forms of *H. villosa* (Harms 1970, p. 1568).

***Heterotheca villosa* (Pursh) Shinnery var. *angustifolia* (Rydb.) Harms, Wrightia 4:16. 1968. *Chrysopsis angustifolia* Rydb., Bull. Torrey Bot. Club 37:128. 1910. *Chrysopsis villosa* var. *angustifolia* (Rydb.) Cronq., Bull. Torrey Bot. Club 74:150. 1947. *Heterotheca stenophylla* var. *angustifolia* (Rydb.) Semple, Novon 4:53. 1994. TYPE: (Semple 1990): U.S.A. NEBRASKA. Hooker Co.: Middle Loup River, near Mullen, on sandhills, 14 Sep 1893, P.A. Rydberg 1766 (LECTOTYPE: NY internet image!; ISOLECTOTYPES: GH, NY, US).**

Heterotheca stenophylla (A. Gray) Shinnery, 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: U.S.A. TEXAS. [Llano Co.]: Llano, from strong ligneous roots in crevices of smooth granite rocks, Nov 1847, F.J. Lindheimer 631 (HOLOTYPE: GH; ISOTYPES: CAN, DS, GH, K, MO!, ND-G, NY[4 sheets, internet image!], US).

Taxonomic summary of the *Heterotheca villosa* complex

Four taxa treated by Semple as varieties within *Heterotheca villosa* are recognized here at specific rank: *H. horrida*, *H. polothrix*, *H. sierrablancensis*, and *H. depressa*. Intergradation and sympatry among var. *villosa*, var. *foliosa*, var. *ballardii*, and var. *minor* make it impractical and biologically unrealistic to recognize them as more than a single entity. The identity of var. *pedunculata* vs. *H. zionensis* and vs. other densely hairy plants in the region of var. *minor* is not clear. Variety *angustifolia* appears to be justifiably recognized within *H. villosa* (vs. within *H. stenophylla*).

Distinct morphogeographic entities are recognized here with formal names. Relatively stable morphology and sympatry with close relatives indicate that such taxa are reproductively isolated, and they are treated at specific rank. In addition to typical *Heterotheca villosa*, var. *pedunculata* (sensu lato) and var. *angustifolia* appear to be geographically distinct but each intergrades with more typical plants where ranges meet—these latter two are tentatively regarded here at varietal rank. It might be useful to recognize widespread morphological “nodes” within var. *villosa* sensu lato at the rank of forma or with an informal name; the contrasting taxonomic approach (formal recognition of sympatric conspecific varieties) requires a majority of typological and arbitrary judgments.

Local and regional floristic studies may encounter and identify stable sympatric races that call for a more complex nomenclature than proposed here. But because of the geographic mix of hybrids and ploidy levels, biological and morphological patterns in the *Heterotheca villosa* complex may remain more complex than can be adequately circumscribed by traditional nomenclature.

1. *Heterotheca villosa* (Pursh) Shinnery [1951]

Amellus villosus Pursh [1814, NEOTYPE: Missouri River, almost certainly North Dakota]

1a. *Heterotheca villosa* var. *villosa*

Including 1aa, 1ab, and 1ac. The sympatry and intergradation of var. *villosa* sensu Semple with var. *foliosa*, var. *ballardii*, and var. *minor* suggest that these taxa are arbitrarily identified.

[1aa]. *Heterotheca villosa* var. *foliosa* (Nutt.) Harms [1968]

Chrysopsis foliosa Nutt. [1841, TYPE: SW WYOMING]

Chrysopsis villosa var. *foliosa* (Nutt.) Cronq. [1947]

Chrysopsis imbricata A. Nels. [1904, TYPE: COLORADO. El Paso/Teller Co.]

Chrysopsis foliosa var. *imbricata* (A. Nels.) A. Nels. [1909]

If *Chrysopsis foliosa* var. *imbricata* is treated as synonymous with *Heterotheca villosa* var. *foliosa* (as done by Semple 1996, 2006), the earliest name at varietal rank is “var. *imbricata*.” In this context, *H. villosa* var. *foliosa* is an invalid name.

[lab]. *Heterotheca villosa* var. *ballardii* (Rydb.) Semple [1994]

Chrysopsis ballardii Rydb. [1931, TYPE: MINNESOTA. Carver Co.]

“This 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” (Semple 1994, p. 53). “Forms of var. *ballardii* are sufficiently similar to forms of var. *foliosa* that the two taxa might be treated as convarietal races under the name var. *foliosa*” (Semple 1996, p. 114). The geographic range of var. *ballardii* lies within that of var. *villosa* sensu Semple.

[lac]. *Heterotheca villosa* var. *minor* (Hook.) Semple [1994]

Chrysopsis villosa var. *minor* Hook. [1847, TYPE: WYOMING. Sweetwater Co.]

Diplopappus hispidus Hook. [1834, TYPE: SASKATCHEWAN. Carlton House]

Chrysopsis villosa var. *hispida* (Hook.) A. Gray [1884]

Heterotheca villosa var. *hispida* (Hook.) Harms [1974]

Canadian botanists have commonly recognized two varieties of *H. villosa*, var. *villosa* (leaves and involucre with appressed, nonglandular vestiture) and var. *hispida* (leaves and involucre with spreading hairs intermixed with glands), but none has indicated that the taxa are geographically or ecologically distinct or that intergradation and typological identifications are not prevalent in this region.

1b. *Heterotheca villosa* var. *pedunculata* (Greene) Harms ex Semple [1987]

Chrysopsis pedunculata Greene [1900, TYPE: COLORADO. Archeluta Co.]

?*Heterotheca zionensis* Semple [1987, TYPE: UTAH. Washington Co.]

Representing the densely strigose, silvery-sericeous expression of the *H. villosa* complex; common in Utah, northern Arizona, and the Four Corners region. As noted above, I have not been able to distinguish *H. zionensis* from var. *pedunculata*, based on criteria established by Semple.

1c. *Heterotheca villosa* var. *angustifolia* (Rydb.) Harms [1968]

Chrysopsis angustifolia Rydb. [1910, TYPE: NEBRASKA. Hooker Co.]

Chrysopsis villosa var. *angustifolia* (Rydb.) Cronq. [1947]

Heterotheca stenophylla var. *angustifolia* (Rydb.) Semple [1994]

Allopatric and distinct from other expressions of *H. villosa*, at least in Texas, Oklahoma, and most of Kansas, intergrading in Nebraska, South Dakota, and North Dakota.

2. *Heterotheca horrida* (Rydb.) Harms [1968]

Chrysopsis horrida Rydb. [1904, TYPE: COLORADO. Weld Co.]

Heterotheca villosa var. *nana* (A. Gray) Semple [1994]

Chrysopsis canescens var. *nana* A. Gray [1849, TYPE: NEW MEXICO. ?Mora Co.]

3. *Heterotheca sierrablancensis* (Semple) Nesom [2006]

Heterotheca villosa var. *sierrablancensis* Semple [1996, TYPE: NEW MEXICO. Lincoln Co.]

4. *Heterotheca polothrix* Nesom [2006]

Chrysopsis villosa var. *scabra* Eastwood [1896, TYPE: UTAH. San Juan Co.]

Heterotheca villosa var. *scabra* (Eastwood) Semple [1992]

5. *Heterotheca depressa* (Rydb.) Dorn [1988]

Chrysopsis depressa Rydb. [1900, TYPE: WYOMING. Teton Co.]

Heterotheca villosa var. *depressa* (Rydb.) Semple [1994]

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All pertinent specimens at BRIT/SMU, MO, and TEX/LL were studied, and a loan from SJNM was helpful in providing a base of study for plants of the Four Corners region. In all, more than 1350 specimens of the *Heterotheca villosa* complex were examined. Additionally, I have examined all collections of all taxa of *Heterotheca* at these herbaria. Staff at CAS provided an image of the holotype of *Chrysopsis viscida* subsp. *cinerascens* and made observations of details of its vestiture. Robert George lent his digital proficiency toward production of the maps. Constructive review comments of Vernon Harms and an anonymous reviewer are greatly appreciated.

Postscript.—Dr. John Semple has read some or all of the manuscript, and in any case, he is intensely opposed to the approach and its conclusions. But it has not seemed necessary to re-assemble and re-cite the massive number of specimens (10,300) Dr. Semple had on hand for his monographic study of sect. *Phyllothea*. He has noted that his treatment is based on multivariate analyses (yet unpublished), and no statistics are found here (nor do I believe that taxonomic conclusions based on such an approach must necessarily be correct). I do not have the long and focused field experience he has had with this group. Still, because of our strong and basic differences in taxonomic philosophy (regarding concepts of species and varieties) and apparently because of differences in the way in which we perceive and interpret patterns of variation, it obviously is possible to differ in taxonomic conclusions regarding the same group of plants. We agree on the delimitation of some of the taxa but not others. For those we agree should be formally recognized, we disagree at what rank some should be treated. If this taxonomic overview is seen as no more than a “superficial opinion-piece,” at least I have tried to provide a clear rationale for the basis of my opinions and why they differ from those of Dr. Semple. The alternative taxonomy proposed here allows me to identify plants of the *Heterotheca villosa* complex in a consistent and biologically meaningful way, from my point of view. Others also have a choice.

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