

John C. Semple

Number Thirty-seven

A Revision of
Heterotheca sect. *Phyllotheca* (Nutt.) Harms
(Compositae: Astereae):
The Prairie and Montane Goldenasters
of North America



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The Prairie and Montane Goldenasters
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by

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Abstract

The goldenasters are members of a related group of North and South American genera: *Bradburia*, *Chrysopsis*, *Heterotheca*, *Noticastrum*, *Osbertia*, *Pityopsis* and *Tomentaurum*. *Heterotheca* is the largest of these and includes 28 species in three sections distributed from southern México to southwestern Canada and nearly all of the United States except Alaska. All members of the genus *Heterotheca* have uniseriate osteoform hairs with pustulate surfaces. The largest and most widely distributed section is monographed in this revision. *Heterotheca* sect. *Phyllothea* includes 20 species and 24 varieties of prairie and montane goldenasters. In the type species of the section *H. sessiliflora*, the varieties are grouped into four subspecies. There is a recurring pattern to morphological variation within most species based on variation in leaf indument. At one extreme are species and varieties with many to very many hairs and few or no glands; e.g. *H. canescens*, *H. fulcrata* var. *amplifolia*, *H. gypsophila*, *H. sessiliflora* var. *fastigiata*, and forms of *H. villosa* var. *pedunculata*. At the other extreme are the races with relatively few hairs and comparatively many glands; e.g., *H. fulcrata* var. *arizonica*, *H. mucronata* var. *harmsiana*, *H. sessiliflora* var. *camphorata*, and *H. villosa* var. *nana*. Taxa can also be separated on the basis of differences in leaf shape, stem height, capitulescence form, or the presence or absence of one or more large leaf-like bracts subtending the heads. Generally, combinations of traits define taxa rather than single distinctive features. There are habitat preference differences that also help define taxa, but the ranges of many varieties and species overlap considerably. Nearly all taxa have ranges that differ from those of related taxa. The genus has a chromosomal base number of $x = 9$. Many species include both diploids and tetraploids, while some are known only at the diploid or only at the tetraploid level.

A table summarizing the traits of all genera that have been included in the goldenaster group is presented along with range maps of each genus in North or South America.

A key to all taxa in the genus *Heterotheca* is included.

All taxa in sect. *Phyllothea* are illustrated in detail, and dot distribution maps based on all collections seen are included for each taxon in the section.

The following new names and combinations are proposed: *Bradburia pilosa* (p.7) *Heterotheca fulcrata* var. *amplifolia* (p.74), *H. marginata* (p.83), *H. monarchensis* (p.52), *H. mucronata* var. *harmsiana* (p.60), *H. shevockii* (p.148), and *H. villosa* var. *sierrablancensis* (p.147).

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Introduction

Goldenasters (and camphor weeds) in the usual sense are common wildflowers and weeds of the summer and fall floras of most of the mid and subtropical latitudes of North America. Based on cladistic/phylogenetic analyses of chloroplast DNA data (Suh and Simpson 1990; Morgan and Simpson 1992; Lane et al. 1996) and morphological and anatomical data (Nesom 1991d; pers. obs. and unpublished scanning electron micrographs), there are seven genera (or possible genera) in the “goldenaster group”: *Bradburia* Torr. & Gray, *Croptilon* Raf., *Chrysopsis* (Nutt.) Ell. nom. cons., *Heterotheca* Cass., *Noticastrum* DC., *Pityopsis* Nutt. and *Tomentaurum* Nesom. These mostly herbaceous perennials are aster-like members of the Fam. Compositae: Tribe Astereae that have yellow rays (or sometimes purplish in *Noticastrum*), yellow disc florets and fruits usually with a double pappus consisting of a short outer whorl of generally linear scales a millimeter or less in length and an inner whorl of long barbellate bristles about the length of the corolla tube. Nesom (1994a) proposed treating these genera as the subtribe Chrysopsidineae Nesom. *Osbertia* E.L. Greene was included in the subtribe by Nesom, although it has a single pappus whorl. Using chloroplast DNA data, Lane et al. (1996) did not find that it grouped with the other genera of the Chrysopsidineae included in their study. Thus, there is supporting evidence for the “goldenaster group” being treated as a subtribe with some questions about its membership.

Semple (1977) and Semple et al. (1980) provided the framework on which rests recognition of the three genera historically thought of as the goldenasters: *Chrysopsis*, *Heterotheca*, and *Pityopsis*. Contrasting revisions of the camphor weeds (*H.* sect. *Heterotheca*) were published by Wagenknecht (1960) and Nesom (1990). Semple (1981) revised the eastern goldenasters (*Chrysopsis* sensu Semple 1977). The grass-leaved goldenasters *Pityopsis* were revised by Semple and Bowers (1985). The monospecific *H.* sect. *Ammodia* (Nutt.) was revised by Semple et al. (1988). The at-the-time monotypic *Bradburia* was studied by Semple and Chinnappa (1984). Zardini (1985) monographed *Noticastrum* in South America. *Osbertia* was reviewed by Turner and Sundberg (1986) supplemented with studies by Nesom (1991c) and Garcia-Arévalo (1991). The monotypic *Tomentaurum* was described by Nesom (1991b, 1991e). The objective of this publication is to provide the first comprehensive monograph of the prairie and montane goldenasters, *H.* sect. *Phyllothea* (Nutt.) Harms.

Members of the genus *Heterotheca* have been the subjects of, or included in, ecological, physiological and phytochemical studies (sect. *Heterotheca* - Keever 1955; Burk 1961, 1966; Pinder 1975; Venable 1979, 1985; Venable and Levin 1985a, 1985b; Wollenweber et al. 1985; Mihaliak et al. 1989; Collins and Wein 1990; sect. *Phyllothea* - Wollenweber et al. 1989; Andersen 1993).

MATERIALS AND METHODS

This study was based on more than 10,300 herbarium specimens (6,844 separate collection numbers) borrowed from or examined at 48 herbaria (see Acknowledgments, p. 158). Field observations and nearly 500 collections of *Heterotheca* by JCS were made over the course of more than 25 years throughout the ranges of most taxa in Canada and the United States. No field work was conducted in México.

An attempt was made to examine all possible type specimens and to typify every name adopted or listed in synonymy. Many type specimens were found among general holdings with no indication that they were type material. Explanations for choice of lectotypes and neotypes have been published separately (Semple 1987, 1990, 1993). A complete synonymy including data on typification is given for every taxon.

Notes on the maps

Distribution maps were prepared using location data on all collections examined and field observations. The decision was made to have the maps serve as reasonable indicators of the distribution of each taxon acknowledging that examination of specimens at additional herbaria would have provided more locations.

Location data obtained from herbarium specimen labels were kept in an *askSam* file (*askSam*TM for Windows, vers. 2.0 - Access Stored Knowledge via Symbolic Access Method; Seaside Software Inc., Perry, FL 32347). In frequently collected areas, a single symbol represents more than one collection. Final identifications were made on each specimen independent of duplicates; this approach served as a “test” of previous identifications. In the vast majority of cases, all duplicates were from the same taxon. In the case of specimens of *H. villosa*, duplicates from certain areas, such as southeastern Wyoming where the ranges of four varieties are sympatric, were not assigned to the same variety, or were only tentatively assigned to the same variety. Final maps were prepared with the aid of *Street Atlas USA* vers. 2.0 for WindowsTM and *Map'n'Go*TM (Delorme Mapping, Freeport, ME) and *CorelDRAW*TM vers. 6.0 (Corel Corp., Ottawa, ON).

Notes on the Descriptions and Illustrations

The descriptive terminology used in this treatment is based mainly on Radford et al. (1974) with modifications by Payne (1978), Hardin and Phillips (1985) and Stearn (1995). Indument terminology is discussed in more detail in the section on anatomy in the next chapter (p.19).

The descriptions are based on mature, undamaged specimens supplemented by notes on aberrant specimens showing the consequences of environmental stress or damage. Multivariate morphometric analyses were undertaken on more than 600 specimens including 76 type specimens. The details of these studies will be published separately in order to document conclusions presented in this treatment. Lower stem leaf characteristics are based on a subset of specimens retaining such leaves at the time of collection; lower leaves are often absent.

The range of variation in quantitative characters is expressed in terms of mean (in bold face), normal range and sometimes the extremes of variation. For example, upper leaf length of *H. sessiliflora* is given as (6.5)-8.5-**16.6**-24.7-(39.6) mm where **16.6** is the mean, 8.5-24.7 is the statistically normal range of variation (i.e., minus to plus one standard deviation; $\alpha = 0.05$; in this case $N = 99$) and (6.5)-(39.6) is the extreme range between minimum and maximum measured values. Statistics and numerical analyses were calculated using subroutines in SYSTATTM for Windows (Wilkinson et al. 1992) and *Excel*TM Vers. 5 (Microsoft Corp., Redmond, WA).

Phenological data were recorded for all specimens. The presence of capitulum buds, flowering capitula, and fruiting capitula were determined.

Illustrations were prepared for this treatment from herbarium specimens determined to be suitable representatives for the taxon. Photographs of habits, leaves and heads of most taxa were taken in the field during the course of this study, and these were consulted during the preparation of individual figures. It should be kept in mind that no single set of illustrations can represent all variants of a taxon, and those included should be viewed as guides rather than as absolutes. Figure legends indicate when ranges in character states occur but have not been illustrated.

Scanning electron micrographs were taken using an Hitachi s-570 scanning electron microscope. Micrographs were digitized with a hand scanner (Logitech ScanMan Model 256) at 400 dpi and the *.bmp or *.pcx files were edited to enhance contrast using *Corel PHOTOPAINT*TM Ver. 6 (Corel Corp., Ottawa, ON). Line drawings were digitized using a flatbed scanner (HP-LaserJet 3C) and edited as above. Final illustrations were prepared using *CorelDRAW!*TM Ver. 6 (Corel Corp., Ottawa, ON).

HISTORY OF THE NAME *HETEROTHECA* AND GENERIC DIFFERENCES AMONG THE GOLDENASTER GENERA

The generic name *Heterotheca* was first proposed by Cassini (1817). The name referred to the heteromorphic nature of the ray and disc floret fruits [Greek: $\alpha\lambda\lambda\alpha$ different, $\sigma\tau\alpha\sigma$ case (Gray 1884); see Fig. 2]; the ray fruits lack the double pappus typical of, but not diagnostic for, the goldenasters. The complex history of the nomenclatural relationships of the genera and sections of the goldenaster group are summarized

in Fig. 1. Numerous species were described or transferred into the genus *sensu stricto*; Wagenknecht (1960) described the last species added to what is treated here as *Heterotheca sect. Heterotheca*. Until 1951, the concept of the genus remained unchanged, although the number of species recognized has varied. DeCandolle (1836) described two sections in *Heterotheca sensu stricto*, *H. sect. Chaetactis* DC. and *H. sect. Gymnactis* DC., that differed in achene characters; no one adopted the use of these sections subsequently. Since 1951, there has been considerable debate over what belongs in the genus *Heterotheca*.

Shinners (1951) proposed the merger of the larger genus *Chrysopsis* (Nutt.) Ell. (1824) *sensu* Gray (1884) into *Heterotheca* because he determined that the diagnostic differences in ray fruit traits (Fig. 2E-F) between the genera broke down in some individuals of *Heterotheca chrysopsidis* DC. In such individuals, the ray fruit produced a pappus like that of the disc fruits. Shinners transferred most of the species of *Chrysopsis sensu* Gray to *Heterotheca*; other transfers were made subsequently by various authors as the need arose, often in the preparation of regional floras (e.g., Ahles 1964; Shinners 1969; Long 1970). Thus, all species of the *villosa* complex *sensu lato* (i.e., all of *Chrysopsis sect. Phyllotheca* Nutt.), the two species of *Chrysopsis sect. Ammodia* (Nutt.) Gray and all the grass-leaved goldenasters treated in many floras as members of *Chrysopsis sect. Pityopsis* Nutt. were assigned to a greatly enlarged genus *Heterotheca sensu* Shinners.

Biosystematic studies done by Vernon Harms (1963, 1965a) provided support for the inclusion of at least the *villosa* complex s.l. in *Heterotheca*. Experimental hybrids between *H. latifolia* Buckl. and *H. canescens* (DC.) Shinners (treated by Harms at the time as *C. berlandieri* Greene) were shown to be viable and had a high level of normal pairing of nine bivalents in meiosis. Harms (1968, 1969, 1974a, 1974b) subsequently published floristic treatments that followed Shinners in lumping into *Heterotheca* all species included in *Chrysopsis*.

Floristicians for much of the last 75 years have followed either the Gray scheme (a small *Heterotheca* and a large *Chrysopsis* including *Pityopsis*) or the Shinners scheme (a single genus *Heterotheca* including *Chrysopsis* and *Pityopsis*; Fig. 1). Small (1903, 1933) recognized *Chrysopsis*, *Heterotheca*, and *Pityopsis* as separate genera during a period when splitting was a common practice. Fernald (1950), Munz (1959) Steyermark (1963), Harrington (1964), Cronquist (1968, 1980, 1991, 1994), Scoggan (1979), Martin and Hutchins (1980), the Great Plains Flora Association (1986), and Gandhi and Thomas (1989) accepted Gray's classification of the goldenasters. Radford et al. (1968) and Correll and Johnston (1970) adopted Shinners's single large genus *Heterotheca*. Other floras including members of *sect. Phyllotheca* adopted their placement in *Heterotheca*; e.g., Dorn (1977, 1988), Moss revised by Packer (1983), Welsh et al. (1987), Morton and Venn (1990), and Weber (1990).

An alternative scheme was proposed by Semple (1977) and subsequently modified in Semple et al. (1980). In 1977, two genera were recognized: the genus *Heterotheca* (including sections *Ammodia*, *Heterotheca*, *Phyllotheca* and *Pityopsis*) had a chromosomal base number of $x = 9$, and the genus *Chrysopsis* included those species with either $x = 4$ or 5 and a single allopolyploid species with $x_2 = 9$. With one exception, *C. pilosa* Nutt., all species of *Chrysopsis sensu* Semple (1977, 1981) are native, partly or wholly, to Florida. Anatomical and morphological data were presented by Semple et al. (1980) supporting treatment of *Pityopsis* as a separate genus along the lines followed by Small (1903, 1933). A revision and a cytogeographic study following this concept were published by Semple and Bowers (1985, 1987). Some floristic treatments have adopted the Semple scheme in some form (e.g., Wunderlin 1982, Nesom 1991d) and this scheme will be followed in *Flora North America*.

With the exclusion of the two small genera *Chrysopsis*, the Florida goldenasters, and *Pityopsis*, the grass-leaved goldenasters, the genus *Heterotheca sensu* Semple et al. (1980) retained the majority of the goldenaster species in three sections. Wagenknecht (1960) published a taxonomic treatment of *sect. Heterotheca* and seven species were recognized (see Key I p.25); Nesom (1990) lumped four of these together as *H. subaxillaris* s.l. Semple (1988) transferred one species (*H. breweri* (A. Gray) Shinners) from *H. sect. Ammodia* to *Aster sect. Eucephalus*, where it clearly belonged, based on macro- and micromorphological traits and some cytological traits. Nesom (1994b) treated this species as *Eucephalus*

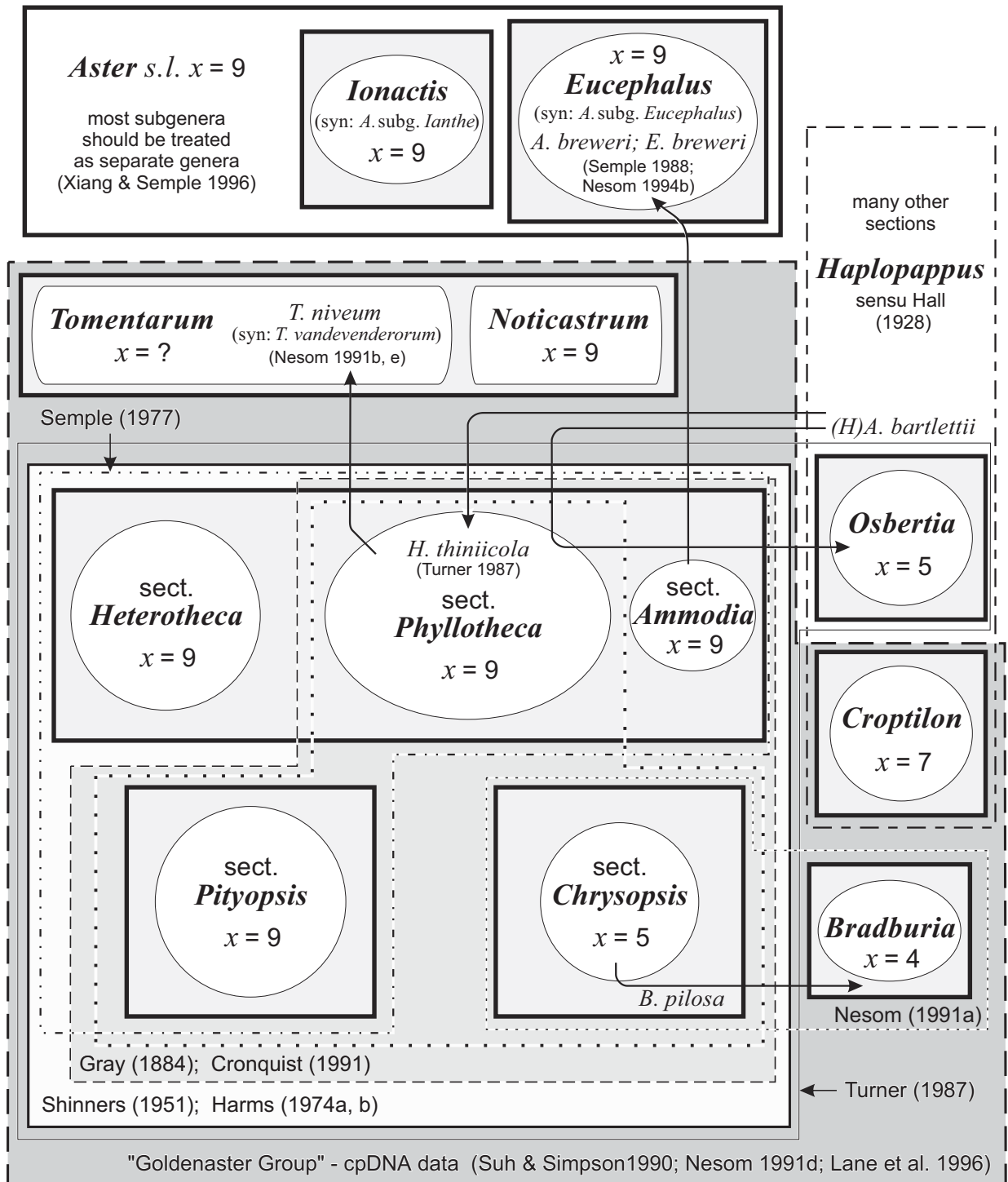


Figure 1. Diagram of the historical nomenclatural relationships among the genera and sections of the goldenaster group. Generic limits followed in this treatment are indicated by heavy dark lines. Alternative generic limits are shown by other kinds of lines with the author(s) who proposed those limits indicated in the figure and discussed in text. *Aster* is a large genus including many subgenera and sections not indicated in the figure. The presumed ancestral chromosomal base number is indicated for each genus; secondarily derived base numbers are not indicated for *Aster*, *Bradburia*, and *Chrysopsis*.

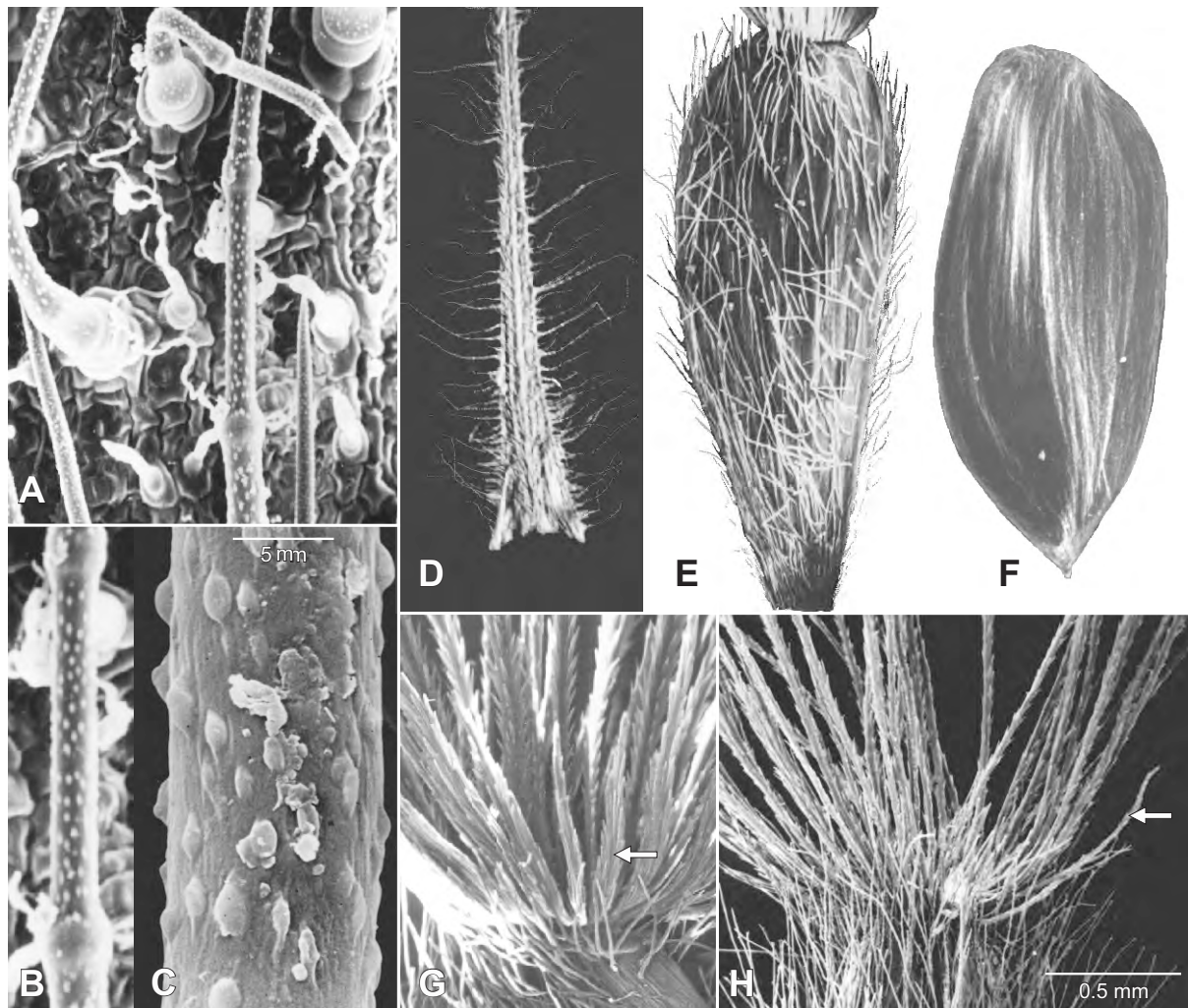


Figure 2. Diagnostic traits of *Heterotheca*. A. Osteoform and other hairs (*H. stenophylla* var. *stenophylla*). B. Single cell of osteoform hair in A. C. Pusticulate surface of hair (*H. thiniicola*). D. Lower leaf petiole with large, hispid, marginal hairs (*H. villosa*). E. Disc floret achene (pappus not shown; *H. psammophila*). F. Ray floret achene (*H. sect. Heterotheca*; *H. psammophila*). G-H. Outer pappus whorl, disc floret. F. Broad scale (arrow; *H. villosa*). G. Short

breweri (A. Gray) Nesom, following his decision to break up *Aster* s.l. into a number of smaller genera. Chloroplast DNA studies by Xiang and Semple (1996) support the recognition of *Eucephalus* and clearly show that the genus is not closely related to *Aster* or *Heterotheca*. Semple et al. (1988) presented a revision of *H. sect. Ammodia* consisting of a single species *H. oregona* (Nutt.) Shinners. That left only the difficult *villosa* complex sensu lato, *H. sect. Phyllotheca* to be revised. Contributions toward this end have been made during the past decade by Turner (1984) and Semple (1987, 1990, 1993).

A proposal to expand the limits of *Heterotheca* and significantly alter which taxa might be included needs comment. Turner (1987) described one new species and transferred two others to *Heterotheca*; only one of these, *H. thiniicola* (Rzedowski & Ezcurra) B.L. Turner, is a member of *H. sect. Phyllotheca*. A second taxon *Heterotheca chihuahuana* (Turner & Sundberg) B.L. Turner belongs in small Mexican genus *Osbertia*, which

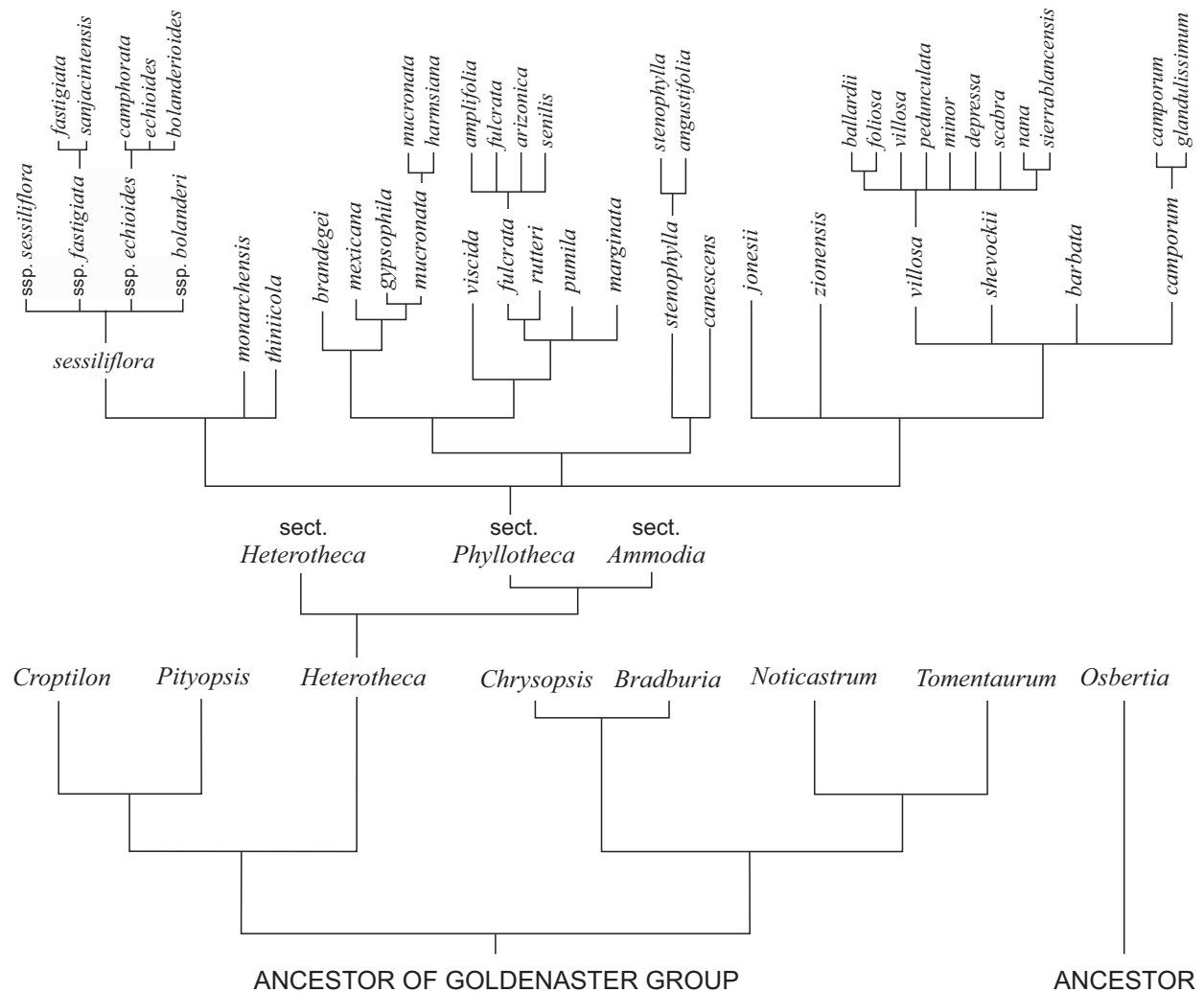


Figure 3. A phylogeny of the goldenasters and the genus *Heterotheca*. The arrangement is intuitive and incorporates published cpDNA and morphological observations summarized in Table 1 and conclusions about relationships among species of section *Phyllothecha* presented in discussions of the taxa in the monograph. The unresolved nodes indicate the lack of sufficient data to speculate on the details of branching at those respective points.

should be recognized separately, along with *O. stolonifera* (DC.) E.L. Greene. These two species lack the double pappus and hair traits typical of all members of *Heterotheca* sensu Semple (Nesom 1991d; Fig. 2 and Table). *Heterotheca vandevenderorum* B.L. Turner also lacks these diagnostic traits and belongs in another genus, possibly the new monotypic genus *Tomentaurum* Nesom (1991b) or *Noticastrum* DC., a genus of South American yellow and purple rayed goldenasters. Regardless of placement, the name *Heterotheca vandevenderorum* must go into synonymy under *Haplopappus nivea* S. Watson, an identical plant (Nesom 1991e). If *H. vandevenderorum* or the species of *Osbertia* are retained in *Heterotheca*, then an entirely new way to delimit the genus must be found because neither the Semple nor Shinnors concepts encompass the traits of these species. It appears that *Heterotheca* was being used as a repository for taxa that did not fit well into other possible 'homes' for distinctive species from central México; previously *Haplopappus* s.l. and later to a much lesser extent *Machaeranthera* s.l. have served as repositories for yellow, white or purple rayed

Astereae that were difficult to assign (Hall 1928 and Hartman 1990, respectively).

Circumscription of all the generic limits of the goldenasters remains in turmoil. For example, Nesom (1991a) transferred the single species of *Bradburia*, *B. hirtella* Torr. & Gray, into *Chrysopsis* sect. *Bradburia* (Torr. & Gray) Nesom under the new name *C. texana* Nesom on the basis of a cladistic analysis. *Chrysopsis pilosa* Nutt. was also included in the new section. However, using the same cladistic analysis, an alternative solution to the generic limits problem surrounding the goldenasters is to transfer *C. pilosa* to the genus *Bradburia* as ***Bradburia pilosa*** (Nutt.) Semple (**comb. nov.** based on *Chrysopsis pilosa* Nutt., J. Acad Sci Phila. 7: 66-67. 1834. non (Walt.) Britt. 1894.). This would place the two annual species¹ with less to non-flagelliform hairs and disc corolla throat cells with small or no crystals in a separate genus, native to eastern Texas and adjacent states. *Chrysopsis*, then, is reserved for the perennials with distinctly flagelliform hairs and disc corolla throat cells with large elongate crystals; all species occur totally or in part in Florida.

Most recently, Nesom (1993) discussed the possible nomenclatural priority of *Diplopappus* Cass. over *Chrysopsis* (Nutt.) Ell. The problem lies with the identity of unseen, and possibly no longer extant, types for three species of *Diplopappus*. Nesom noted that discovery of the types might result in the need to either conserve *Chrysopsis* over *Diplopappus* or the treatment of *Diplopappus* as a synonym under *Heterotheca*. Neither alternative will change the nomenclature of taxa in *Heterotheca* sect. *Phyllotheca*, unless one or more of the three species of *Diplopappus* turn out to be based on epithets having priority over *H. villosa* or *H. camporum*, the only two species of the section that could possibly have been collected in eastern North America.

Diagnostic features of *Heterotheca* are illustrated in Fig. 2. Differences among the genera and some sections of the goldenaster group summarized in Table 1. An intuitive phylogeny of the goldenasters based on data in Nesom (1991d), Lane et al. (1996) and my conclusions on relationships within *Heterotheca* sect. *Phyllotheca* is presented in Fig. 3.

EXCLUDED TAXA

The following taxa are excluded for various reasons from the genus *Heterotheca* as it is delimited here:

Goldenaster taxa excluded from *Heterotheca*

Heterotheca sect. *Chrysopsis* (Nutt.) Harms
 = *Chrysopsis* (Nutt.) Ell. nom cons. [see Semple, Rhodora 83: 323-384. 1981.]
Heterotheca sect. *Pityopsis* (Nutt.) Harms
 = *Pityopsis* Nutt. [see Semple & Bowers, U. Waterloo Biol. Ser. 29: 1-34. 1985.]
Heterotheca adenolepis (Fern.) Ahles
 = *Pityopsis aspera* (Shuttlew. ex Small) Small var. *adenolepis* (Fern.) Semple & Bowers
Heterotheca aspera (Shuttlew. ex Small) Shinn.
 = *Pityopsis aspera* (Shuttlew. ex Small) Small
Heterotheca correllii (Fern.) Ahles
 = *Pityopsis graminifolia* (Michx.) Nutt. var. *tenuifolia* (Torr.) Semple & Bowers
Heterotheca falcata (Pursh) Harms
 = *Pityopsis falcata* (Pursh) Nutt.
Heterotheca flexuosa (Nash) Harms
 = *Pityopsis flexuosa* (Nash) Small

Heterotheca floridana (Small) Long
 = *Chrysopsis floridana* Small
Heterotheca graminifolia (Michx.) Shinners
 = *Pityopsis graminifolia* (Michx.) Nutt.
Heterotheca graminifolia (Michx.) Shinners var. *graminifolia* sensu auth.
 = *Pityopsis graminifolia* (Michx.) Nutt. var. *latifolia* (Fern.) Semple & Bowers
Heterotheca graminifolia (Michx.) Shinners var. *tracyi* (Small) Long
 = *Pityopsis graminifolia* (Michx.) Nutt. var. *tracyi* (Small) Semple
Heterotheca gossypina (Michx.) Shinners
 = *Chrysopsis gossypina* (Michx.) Ell.
Heterotheca hyssopifolia (Nutt.) Harms
 = *Chrysopsis gossypina* (Michx.) Ell. ssp. *hyssopifolia* (Nutt.) Semple

¹ Semple and Chinnappa (1994) reported the existence of an $n = 4$ perennial form in *B. hirtella*, which was otherwise found to be $n = 3$ and annual.

Heterotheca hyssopifolia (Nutt.) Long
 = *Chrysopsis gossypina* (Michx.) Ell. ssp.
hyssopifolia (Nutt.) Semple
Heterotheca hyssopifolia (Nutt.) Long var. *subulata*
 (Small) Long
 = *Chrysopsis subulata* Nutt.
Heterotheca latisquamea (Pollard) Harms
 = *Chrysopsis latisquamea* Pollard
Heterotheca mariana (L.) Shinnery
 = *Chrysopsis mariana* (L.) Ell.
Heterotheca mariana (L.) Shinnery ssp. *floridana*
 (Small) Harms
 = *Chrysopsis floridana* Small
Heterotheca microcephala (Small) Shinnery
 = *Pityopsis graminifolia* (Michx.) Nutt. var.
tenuifolia (Torr.) Semple & Bowers
Heterotheca nervosa (Willd.) Shinnery
 = *Pityopsis graminifolia* (Michx.) Nutt. var.
tenuifolia (Torr.) Semple & Bowers
Heterotheca pilosa (Nutt.) Shinnery
Chrysopsis pilosa Nutt. non (Walt.) Britton
 = *Bradburia pilosa* (Nutt.) Semple
Heterotheca pinifolia (Ell.) Ahles
 = *Pityopsis pinifolia* (Ell.) Nutt.
Heterotheca ruthii (Small) Harms
 = *Pityopsis ruthii* (Small) Small
Heterotheca scabrella (T & G.) Harms
 = *Chrysopsis scabrella* T. & G.
Heterotheca trichophylla (Nutt.) Shinnery
 = *Chrysopsis gossypina* (Michx.) Ell. ssp. *gossypina*
 f. *trichophylla* (Nutt.) Semple

**Taxa that do not belong in *Heterotheca*, *Chrysopsis*
 or *Pityopsis* sensu Semple et al., Can. J. Bot. 58: 147-
 163. 1980.**

Chrysopsis acaulis Nutt., J. Acad. Sci. Phila. 7: 33.
 1834.
 = *Stenotus acaulis* (Nutt.) Nutt.
Chrysopsis alpina Nutt., Journ. Acad. Phila. 7: 34,
 pl.III f.2. 1834.
 = *Ionactis alpina* (Nutt.) Greene, Pittonia 3: 245.
 1897.
Chrysopsis amygdalina (Lam.) DC., Prod. 5: 272.

1836.
 = *Doellingeria umbellata* (Mill.) Nees
Chrysopsis caespitosa Nutt., J. Acad. Sci. Phila. 7: 33.
 1834.
 = *Stenotus acaulis* (Nutt.) Nutt.
Chrysopsis gracilis Eastwood, Bot. Gaz. 41: 291. 1906.
 = *Eucephalus brickellioides* (Greene) Nesom
Chrysopsis breweri A. Gray var. *multibracteata*
 Jepson, Man. Fl. Pl. Calif. 1037. 1925.
 = *Eucephalus brickellioides* (Greene) Nesom
Chrysopsis obovata (Nutt.) Nutt. ex Ell., Sketch. 2:
 368. 1824. *Doellingeria obovata* (Nutt.) Nees,
 Gen. et Sp. Aster. 182. 1832.
 = *Doellingeria reticulata* (Pursh) Greene
Chrysopsis divaricata (Nutt.) Elliot, Bot. Sketch 2: 338.
 1824. *Inula divaricata* Nutt. Gen. 2: 152. 1818.
 = *Croptilon divaricata* (Nutt.) Raf.
Heterotheca bartlettii (S.F. Blake) M.C. Johnston,
 Southwest. Nat. 2: 172. 1958. Based on:
Haplopappus bartlettii S.F. Blake, Journ. Wash.
 Acad. Sci. 22: 328. 1932.
 = *Osbertia bartlettii* (S.F. Blake) Nesom
Heterotheca breweri (A. Gray) Shinnery, Field & Lab.
 29:71. 1951. Based on *Chrysopsis breweri* A. Gray,
 Proc. Amer. Acad. 6: 542. 1866. *Aster breweri* (A.
 Gray) Semple, Syst. Bot. 13: 545. 1988.
 = *Eucephalus breweri* (A. Gray) Nesom, Phytologia
 77: 254. 1994.
Heterotheca chihuahuana (Turner & Sundberg)
 B.L. Turner, Phytologia 63:128. 1987.
 = *Osbertia chihuahuana* Turner & Sundberg, Pl. Syst.
 Evol. 151:233. 1986.
Heterotheca deltoidea Klatt., Ann. K. K. Natur. Hoff. 9:
 258. 1894. Excluded by Wagenknecht (1960)
 = ??
Heterotheca grievii Benson, Bot. Gaz. 74: 121. 1922.
 Excluded by Wagenknecht (1960)
 = Lower Carboniferous organ genus, seedfern stem.
Heterotheca vandevederorum B.L. Turner, Phytologia
 63: 127. 1987.
 = *Tomentaurum nivea* (S. Watson) Nesom

Table 1. Summary of the characteristics of the goldenaster genera.

TRAIT	<i>Heterotheca</i> Cass. (1817) sect. <i>Heterotheca</i>	<i>Heterotheca</i> sects. <i>Phyllotheca</i> & <i>Ammodia</i>	<i>Pityopsis</i> Nutt (1841)	<i>Croptilon</i> Raf. (1836)	<i>Brauburia</i> T. & G. (1841) [including <i>C. pilosa</i>]	<i>Chrysopsis</i> (Nutt.) Ell. (1824) nom. cons.	<i>Noticastrum</i> DC. (1836)	<i>Tomentaurum</i> Nesom (1991b)	<i>Osbertia</i> Greene (1895)
Spp.; taxa	7; 10	21; 54	7; 14	3; 5	2; 2	9; 19	19; 19	1; 1	3; 3
Range	coastal plain Long Is, NY to México; S & C prairies of US.; California to Texas to S México	SW Canada (B.C. to Ont.) to C México; midwestern US and piedmont of SE U.S. west of Appalachians	New Jersey to S Florida and E Texas in US; SE México, Guatemala, NW Honduras	Coastal plain SE Virginia to Texas and inland Arkansas, Oklahoma and Kansas	E Texas; W Ozarks to S Texas	most spp. in Florida; Atlantic Coastal Plain to E Texas inland to Ohio	E Andes and Austro-brasilëña South America	rare Chihuahua, México	scattered locations in México
Habit	herbaceous perennial; annuals	herbaceous perennials	short-lived herbaceous perennials	short-lived perennials; annual	annuals, very rarely perennial	biennials or short-lived perennials	herbaceous perennials, small shrubs	herbaceous perennials	herbaceous perennials
Root system	tap root	tap root	fibrous root system	short tap root	short tap root	short tap root, 1 with fibrous root system; 1 with adventitious roots	short tap root	tap root	short tap root
Stems	decumbent to erect; from woody caudex in perennials	decumbent to erect from branching woody caudex in perennials; infrequently rhizomatous	erect; infrequently to commonly rhizomatous	erect	erect	mostly erect, decumbent	erect, decumbent, stoloniferous	erect, decumbent, stoloniferous	erect, decumbent, stoloniferous

Table 1. Summary of the characteristics of the goldenaster genera. (Cont.)

TRAIT	<i>Heterotheca</i> Cass. (1817) sect.	<i>Heterotheca</i> sects. <i>Phyllothea</i> & <i>Anmodia</i>	<i>Pityopsis</i> Nutt. (1841)	<i>Croptilon</i> Raf. (1836)	<i>Bradburia</i> T. & G. (1841) [including <i>C. pilosa</i>]	<i>Chryopsis</i> (Nutt.) Eill. (1824) nom. cons.	<i>Noticastrum</i> DC. (1836)	<i>Tomentaurum</i> Nesom (1991b)	<i>Osbertia</i> Greene (1895)
Capitules- cence	paniculiform or corymbiform, upper portion of stem, extend- ing downward with age, compact to lax	paniculiform or corymbiform, upper portion of stem, lax to compact	paniculiform or corymbiform upper portion of stem, compact	paniculiform or corymbiform upper portion of stem	paniculiform, branches long, upper portion of stem, lax	paniculiform or corymbiform, upper portion of stem, compact, extending downward with age in 1 sp.	usually scapose solitary heads	usually scapose solitary heads	usually scapose solitary heads
Basal leaves	auriculate, petiolate; hispid-strigose	petiolate hispid-strigose, rarely woolly	mostly grass- like; sessile; silky	petiolate	petiolate; sparsely hispid or pilose	sessile, cuneate or subclasping; densely wooly	subpetiolate to sessile cuneate; sparsely pilose to densely wooly	subpetiolate to sessile cuneate; densely woolly	subpetiolate to sessile cuneate; sparsely pilose to densely wooly
Venation	reticulate; veins raised below	reticulate; veins raised below	pseudo-parallel, veins sunken	reticulate; veins raised below	reticulate; veins raised below	reticulate; veins raised below	reticulate; veins raised below	reticulate; veins raised below	reticulate; veins raised below
Upper stem leaves	sessile, clasping; indument similar to basal	sessile, indument similar to basal, rarely sub- clasping	similar to basal, often much smaller	greatly reduced upward; indument similar to basal or more glandular, less hispid	sessile, much reduced upward; indument similar to basal	sessile, subclasping cuneate; indument often very different from basal leaves	sessile, cuneate	sessile, cuneate	sessile, cuneate; sparsely woolly or pilose

Table 1. Summary of the characteristics of the goldenaster genera. (Cont.)

TRAIT	<i>Heterotheca</i> Cass. (1817) sect.	<i>Heterotheca</i> <i>Phyllotheca</i> & <i>Ammodia</i>	<i>Pityopsis</i> Nutt (1841)	<i>Croptilon</i> Raf. (1836)	<i>Bradburia</i> T. & G. (1841) [including <i>C. pilosa</i>]	<i>Chrysopsis</i> (Nutt.) Ell. (1824) nom. cons.	<i>Noticastrum</i> DC. (1836)	<i>Tomentaureum</i> Nesom (1991b)	<i>Osbertia</i> Greene (1895)
Mesophyll features	adaxial palisade; no enlarged storage cells	adaxial palisade; no enlarged storage cells	isolateral palisade; enlarged central storage cells	no enlarged storage cells	adaxial palisade; no enlarged storage cells	adaxial palisade; no enlarged storage cells	not determined	not determined	not determined
Petiole margin hairs	very large hairs	very large hairs	normal hairs	normal hairs	normal hairs	normal hairs	normal hairs	normal hairs	normal hairs
Primary Indument Hairs (PIH)	stiff, uniseriate; cells terete osteoform - TYPE A	stiff, uniseriate; cells terete osteoform; often two categories - TYPE A	flattened, anastomosing, often like cobwebs; uniseriate; cells flattened - TYPE B	osteoform, stiff, uniseriate - TYPE A	very weakly flagelliform, or osteoform, stiff, uniseriate - TYPE A	flagelliform, uniseriate, woolly below to various above; cells terete to flattened, twisted - TYPE A	flagelliform, uniseriate; woolly, cells flattened, twisted - TYPE A	flagelliform, uniseriate; woolly, cells flattened, twisted - TYPE B	more or less flagelliform, uniseriate; woolly, cells flattened, twisted - TYPE A
PIH cell surface	densely tuberculate	densely tuberculate	smooth-striate	sparsely tuberculate	sparsely tuberculate to smooth	smooth	smooth to weakly striate	smooth to striate	smooth to densely tuberculate
Secondary Indument Hairs (SIH)	minute or absent - TYPE B	minute or absent - TYPE B	minute or absent - TYPE B	minute or absent - TYPE B	minute or absent - TYPE B	minute or absent - TYPE B	minute or absent - TYPE B	absent or like PIH	minute or absent - TYPE B

Table 1. Summary of the characteristics of the goldenaster genera. (Cont.)

TRAIT	<i>Heterotheca</i> Cass. (1817) sect.	<i>Heterotheca</i> sects. <i>Phyllotheca</i> & <i>Ammodia</i>	<i>Pityopsis</i> Nutt (1841)	<i>Croptilon</i> Raf. (1836)	<i>Bradburia</i> T. & G. (1841) [including <i>C. pilosa</i>]	<i>Chrysopsis</i> (Nutt.) Ell. (1824) nom. cons.	<i>Nothocastrum</i> DC. (1836)	<i>Tomentaurum</i> Nesom (1991b)	<i>Osbertia</i> Greene (1895)
	Involucre	campanulate	campanulate	narrowly campanulate	narrowly campanulate	campanulate	campanulate	hemispheric to campanulate	hemispheric
Phyllaries	keeled; glandular, strigose- hispid	keeled; variously glandular, strigose-hispid	variously glandular and pilose	densely glandular, sparsely hispid	sparsely glandular and pilose	variously glandular, pilose to glabrous	herbaceous; variously glandular, pilose	herbaceous to slightly keeled; densely glandular, glabrate	sparsely glandular, sparsely pilose
Ray strap	yellow; dries curled	yellow; dries curled; absent	yellow; dries curled	yellow; dries curled	yellow; dries curled	yellow; dries curled	yellow tinged with reddish purple, 1 sp yellow; dries straight	yellow ; dries curled	yellow tinged with reddish purple; dries straight
Disc floret indument	short hairs on lobes and tube; small glands	short/ long hairs on lobes and tube; small glands	short hairs on lobes and tube	small to large glands on lobes	a few glands on lobes and tube	small glands on lobes and tube	glabrous or band of hairs on mid tube (Zadini 1985)	a few long hairs and small glands on lobes and tube	a few minute hairs and glands on lobes and tube
Disc corolla throat cells	radial walls straight	radial walls straight	radial walls straight	radial walls straight	radial walls straight	radial walls straight	radial walls straight	radial walls sinuate	radial walls straight

Table 1. Summary of the characteristics of the goldenaster genera. (Cont.)

TRAIT	<i>Heterotheca</i> Cass. (1817) sect.	<i>Heterotheca</i> sects. <i>Phyllotheca</i> & <i>Ammodia</i>	<i>Pityopsis</i> Nutt (1841)	<i>Croptilon</i> Raf. (1836)	<i>Bradburia</i> T. & G. (1841) [including <i>C. pilosa</i>]	<i>Chrysopsis</i> (Nutt.) Ell. (1824) nom. cons.	<i>Nothocastrum</i> DC. (1836)	<i>Tomentaureum</i> Nesom (1991b)	<i>Osbertia</i> Greene (1895)
Hetero- carpy	ray and disc achenes distinct	monocarpic	monocarpic	monocarpic	monocarpic or only ray fruit develop	monocarpic	monocarpic	monocarpic	
Achene shape	compressed obconic	compressed obconic	terete fusiform	terete obconic	rhombic, broadly obconic or compressed, obconic	compressed, mostly broadly obconic	compressed narrowly obconic	terete obconic	
Achene ribs - number	4-10	4-10	9-15	6-10	3-6	4-6 (-10 in 1 species)	7-9	4-10 (-16)	
Achene ribs - swollen and resinous	thin, shallow, sometimes resinous	thin shallow, sometimes resinous	thin, shallow, sometime resinous	thin, shallow, not resinous	both thin and thick, shallow, not resinous	thin to swollen, sometimes resinous	thin, shallow, not resinous	thin, shallow, not resinous	
Ray achene pappus	absent; rarely like disc pappus	like disc pappus	like disc pappus	like disc pappus	flat lanceolate scales of vary- ing length or like disc pappus	like disc pappus	like disc pappus	like disc pappus	

Table 1. Summary of the characteristics of the goldenaster genera. (Cont.)

TRAIT	<i>Heterotheca</i> Cass. (1817) sect.	<i>Heterotheca</i> sects. <i>Phyllotheca</i> & <i>Ammodia</i>	<i>Pityopsis</i> Nutt. (1841)	<i>Croptilon</i> Raf. (1836)	<i>Bradburia</i> T. & G. (1841) [including <i>C. pilosa</i>]	<i>Chrysopsis</i> (Nutt.) Ell. (1824) nom. cons.	<i>Noticastrum</i> DC. (1836)	<i>Tomentaurum</i> Nesom (1991b)	<i>Osbertia</i> Greene (1895)
Disc achene pappus bristles - cross section	outer whorl of short lanceolate to linear scales; inner whorl of long barbellate bristles	outer whorl of short lanceolate to linear scales; inner whorl of long barbellate bristles	outer whorl of short linear scales; inner whorl of long barbellate bristles	single whorl of long barbellate bristles	aborted or outer whorl of short broad lanceolate scales; inner whorl of long barbellate bristles	outer whorl of short lanceolate to linear scales; inner whorl of long barbellate bristles	outer whorl of short linear scales; inner whorl of long barbellate bristles	outer whorl of a few short linear scales; inner whorl of long barbellate bristles	single whorl of long barbellate bristles
Long pappus bristles - cross section	flattened	flattened	terete	terete	flattened	terete to flattened	terete	terete	terete
Chromo- some base number	$x = 9$	$x = 9$	$x = 9$	$x = 7$ (or 5?) $n = 7, 6, 5,$ $4, 3$	$x = 4$ $n = 4, n = 3$	$x = 5, 4; x_2 = 9$ $n = 5,$ $4(8, 12, 16), 9$	$x = 9$	$x = \text{unknown}$	$x = 5$ $n = 5, 4$
Polyploidy	unknown	common; diploids and tetraploids in many species	common; diploids and tetraploids in some species; hexaploids in 1 species	unknown	unknown	1 autopoly- ploid series; 1 allopolyploid	unknown (limited data)	no data	unknown (limited data)

Natural History

DISTRIBUTION PATTERNS AND RARE SPECIES

Goldenasters occur throughout much of temperate and subtropical North America. The general distributions of the three sections of *Heterotheca* are shown in Fig. 4. *Heterotheca* is by and large a western North American genus with only a few taxa occurring east of the Great Plains. Section *Ammodia* is restricted to the Coastal and Cascade Mts. of the Pacific states. Section *Heterotheca* is centered in central México with annual species occurring across the central and southern United States; *H. subaxillaris* and *H. grandiflora* are weedy introductions in a few other parts of the world. Section *Phyllothea* occupies nearly the entire range of the genus from western Canada to central México and from California to the Appalachian Mts. With the exception of the polytypic *H. villosa*, each species occupies a much smaller range within a sub-area of southwestern North America. The distributions of individual taxa are summarized in Table 2 and illustrated

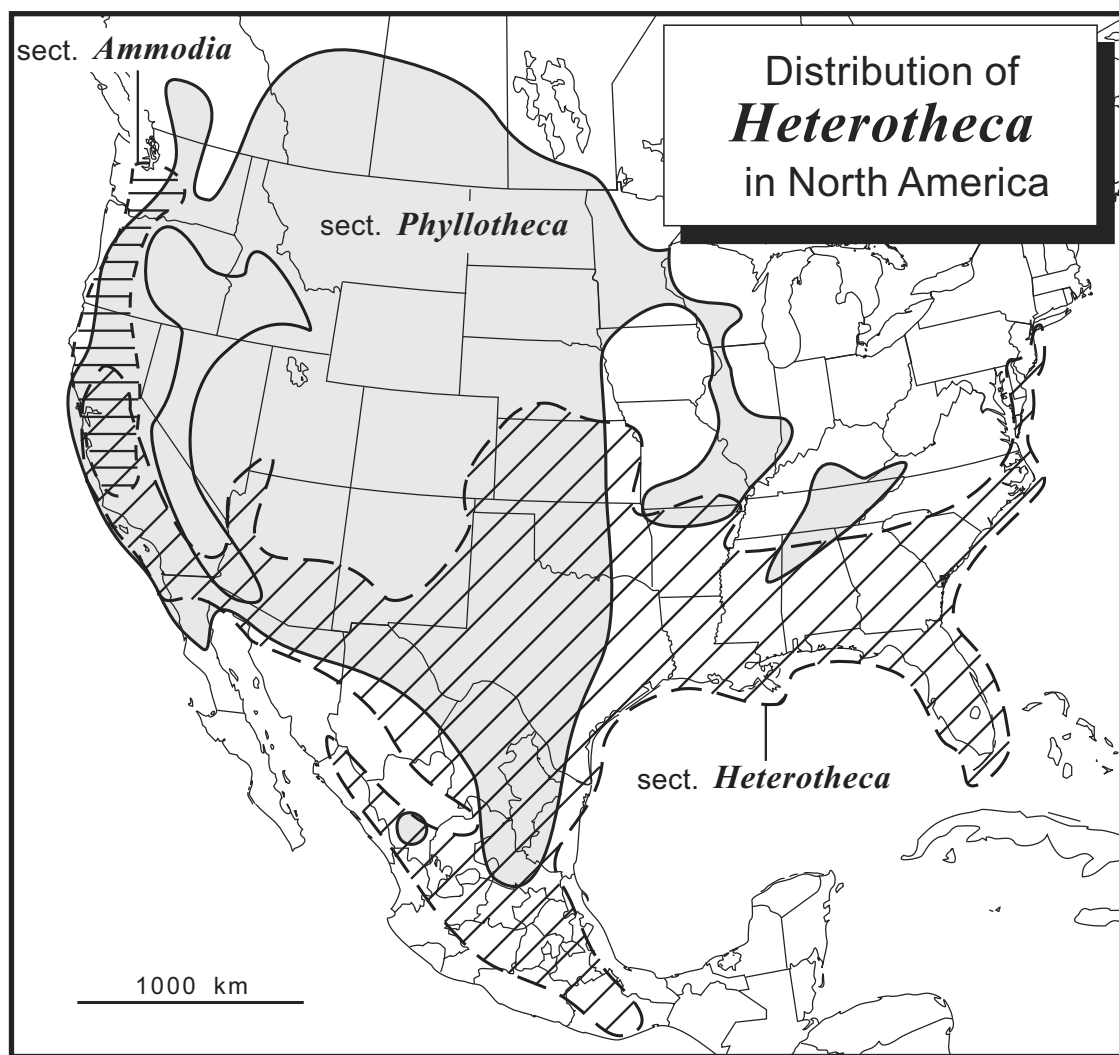


Figure 1. Distribution of the three sections of the genus *Heterotheca* in North America.

separately in the section on species descriptions. *Heterotheca jonesii* is one of the rarer species of the section and is confined to a restricted habitat type within a restricted range. Nonetheless, it has unknowingly been seen by a very large number of people¹ who were enjoying the view of Checkerboard Mesa in Zion National Park, Utah (Fig. 38). The least accessible species are *H. brandegei* in northern Baja, México (Fig. 26), and *H. monarchensis* (the rarest species²) in the Monarch Wilderness in the Sierra Nevada of California (Fig. 20).

For comparison, the ranges of distribution of the other genera of the "Goldenaster Group" are presented below; *Croptilon* and *Pityopsis* are shown in Fig. 5, *Bradburia* and *Chrysopsis* are shown in Fig. 6, *Noticastrum* in Fig. 7, and *Osbertia* and *Tomentaurum* are shown in Fig. 8. The first five genera occur in the southeastern United States and the Atlantic Coastal Plain. *Bradburia hirtella* is now restricted to a small area in eastern Texas, and *B. pilosa* ranges from eastern Texas and Louisiana to Missouri and eastern Kansas (Semple and Chinnappa 1984). *Chrysopsis* is centered in Florida with two polyploid species occupying the remainder of the range in the eastern United States (Semple 1981). *Croptilon* and *Pityopsis* have similar

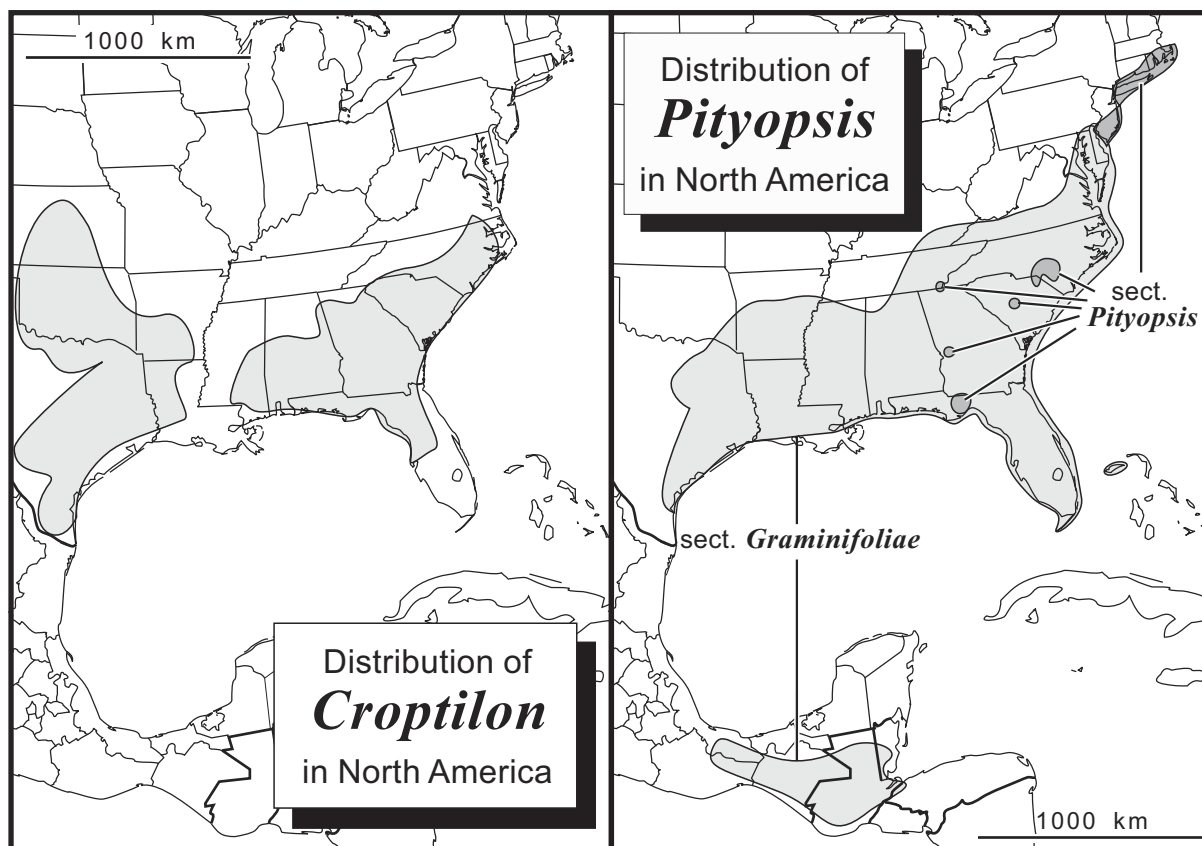


Figure 5. Distribution of *Croptilon* and *Pityopsis* in the southeastern United States and Central America.

¹ I remember seeing the mesa on a visit to the park in 1961, but I have no recollection of the dwarf plants growing in the cracks of the "checkerboard". Having gained an enlightened state, I saw the species on the mesa in 1987 and 1995.

² *Heterotheca barbata* is believed to be extinct; it is only known from the type collection and two "aff." collections.

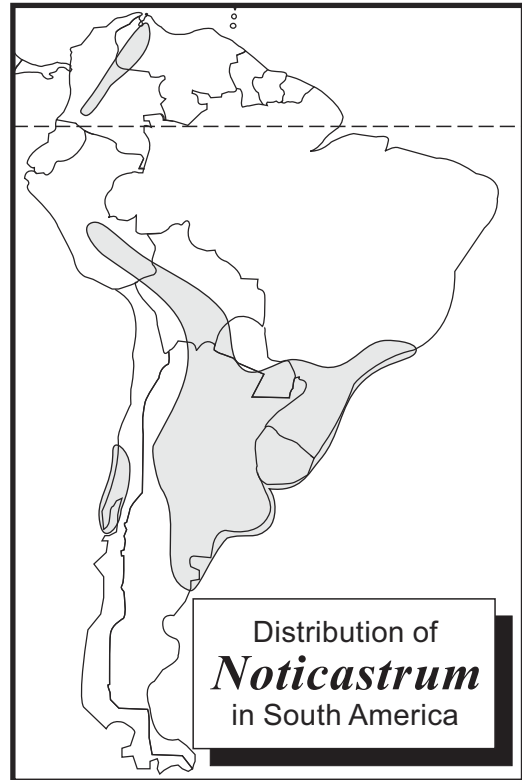
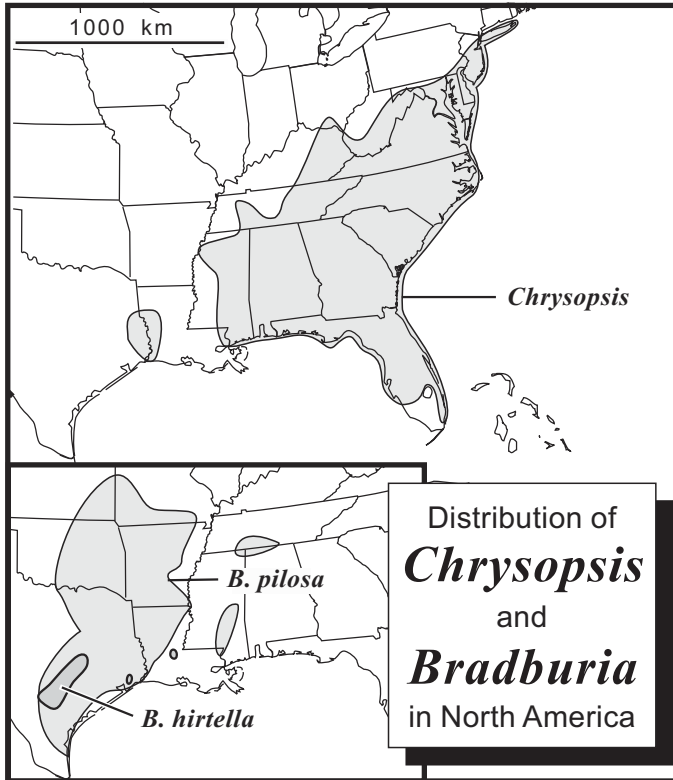


Figure 3. Distribution of *Bradburia* and *Chrysopsis* in the southeastern United States.

Figure 3. Distribution of *Noticastrum* in South America. After Zardini (1985).

ranges with the former centered in Texas and the latter centered in Florida, Georgia and the Carolinas (Smith 1965, 1981; Semple and Bowers 1985). *Osbertia* and *Tomentaurum* are narrowly distributed endemics in México (Turner and Sundberg 1986; García-Arévalo 1991; Nesom 1991b, c), and *Noticastrum* occurs in South America (Zardini 1985).

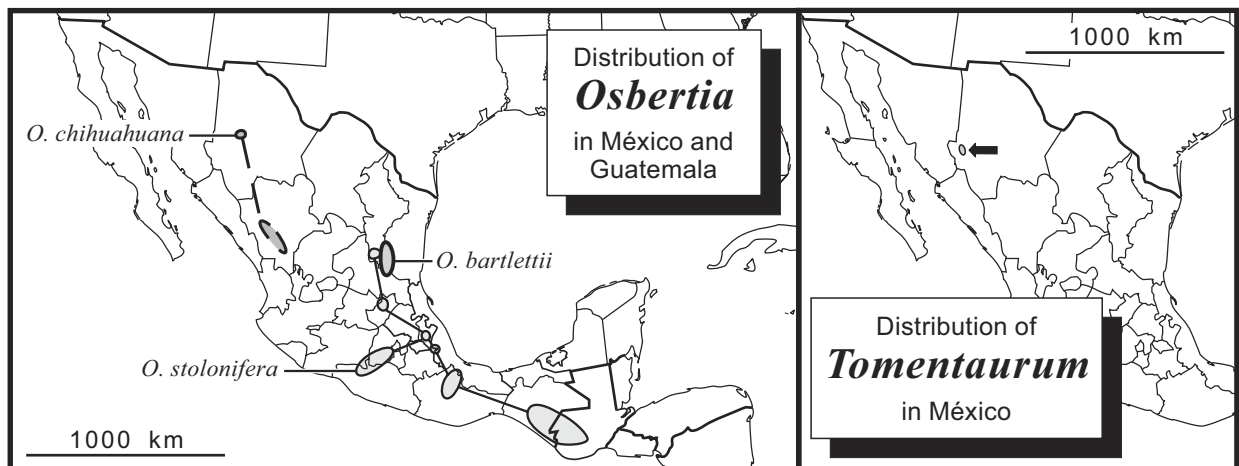


Figure 3. Distribution of *Osbertia* and *Tomentaurum* in the México and Guatemala.

Table 2. Summary of the distributions of the taxa of *Heterotheca* sect. *Phyllothea*.

Taxon	Frequency	Habitat and Distribution
<i>H. barbata</i>	very rare	possibly extinct; Spokane R. Valley, Idaho
<i>H. brandegei</i>	rare	upper elevations of Sierra San Pedro Martir, Baha Norte, México
<i>H. camporum</i>		
var. <i>camporum</i>	uncommon	glades, bluffs along Mississippi R.; Iowa, Illinois and Missouri; sand hill prairies, Illinois and W Indiana
var. <i>glandulissimum</i>	locally common	disturbed areas, streams banks, C and E Tennessee and adjacent states, range expanding into S Missouri, N Arkansas, rare disjuncts elsewhere
<i>H. canescens</i>	common	prairies, rocky soils, S Kansas to S Texas; rare in Chisos Mts., Texas
<i>H. fulcrata</i>		
var. <i>amplifolia</i>	locally common	pine forests, central Rocky Mts.
var. <i>arizonica</i>	rare	rocky areas, Arizona, W New Mexico, E of El Paso, Texas
var. <i>fulcrata</i>	locally common	pine forests and rocky slopes, central Rocky Mts., Wyoming to E Nevada and S to N México
var. <i>senilis</i>	locally common	rocky areas, S Arizona to Trans-Pecos Texas and N Mexico
<i>H. gypsophila</i>	rare	gypsum soils; central Nuevo Leon, México
<i>H. jonesii</i>	very rare	sandy pockets in sandstone cliffs; SW Utah
<i>H. mexicana</i>	locally common	pine forests; W of Durango, México
<i>H. monarchensis</i>	very rare	rock outcrops; Kings R. Canyon, Fresno Co., California
<i>H. marginata</i>	locally common	rock outcrops; Superstition Mts. region, Arizona
<i>H. mucronata</i>		pine forests; S Nuevo Leon and adjacent states, México
var. <i>harmsiana</i>	uncommon	pine forests, cactus hills, S Nuevo Leon and adjacent states, México
var. <i>mucronata</i>	locally common	pine forests, S half of Nuevo Leon and adjacent states, México
<i>H. pumila</i>	uncommon	rocky soils; 9500-11000 ft el., S Wyoming S to E Arizona
<i>H. rutteri</i>	rare	plains, SC Arizona and adjacent México
<i>H. sessiliflora</i>		
ssp. <i>bolanderi</i>	locally common	dunes, headlands Mendocino to Santa Cruz, California
ssp. <i>echioides</i>		
var. <i>bolanderioides</i>	uncommon	mid to upper elevations in hills, San Francisco Bay area, California
var. <i>camphorata</i>	uncommon	Santa Cruz, Santa Clara and N San Benito Co's, California
var. <i>echioides</i>	common	inland hills and valleys; Central Valley, C and S coastal mts., California
ssp. <i>fastigiata</i>		
var. <i>fastigiata</i>	common	mid el., San Gabriel and San Bernardino Mts., California
var. <i>sanjacintensis</i>	uncommon	San Jacinto Mts. and Mt. Palomar, California
ssp. <i>sessiliflora</i>	uncommon	
<i>H. shevockii</i>	rare	Kern R. Canyon, Kern Co., California
<i>H. stenophylla</i>		
var. <i>angustifolia</i>	common	rocky plains; north central Texas to E Colorado and S Dakota
var. <i>stenonophylla</i>	common	rocky plains; central Texas to SE S. Dakota, NW Iowa
<i>H. thiniicola</i>	rare	sand dunes; Desierto de Altar, NW Sonora, México
<i>H. villosa</i>		
var. <i>ballardii</i>	common	NE Great Plains; Saskatchewan to Minnesota and S to Nebraska
var. <i>depressa</i>	rare	hot springs; Yellowstone and Teton N.P. region
var. <i>foliosa</i>	common	hills and valleys of central Rocky Mts, NW Great Plains
var. <i>minor</i>	common	wide spread; Canada to N México
var. <i>nana</i>	common	rocky soils lower foothills, plains; SE Wyoming, SW Nebraska S to Arizona, S New Mexico and W Texas
var. <i>pedunculata</i>		SW Colorado, W New Mexico, S Utah, N & E Arizona
var. <i>scabra</i>	common	rocky soils; Utah, Arizona, Nevada; rare California
var. <i>sierrablancensis</i>	rare	rocky soils, montane pine forests; E New Mexico
var. <i>villosa</i>	common	N Great Plains, Rocky Mts., S Canada to central U.S.
<i>H. viscida</i>	rare	rocky outcrops; SE Arizona to Trans-pecos Texas
<i>H. zionensis</i>	locally common	hot pots, rocky flood plains, Provo-Salt Lake City area; sandy and rocky soils, S Utah, N Arizona; adventive in SW New Mexico and SE Idaho

ANATOMY AND INDUMENT

The leaf anatomy and trichome features of *Chrysopsis*, *Heterotheca* and *Pityopsis* were discussed by Semple et al. (1980). These features in *Bradburia hirtella* were discussed by Semple and Chinnappa (1984). Only *Pityopsis* had distinct leaf anatomy (Fig. 9D-E); both surfaces tended to be furrowed along the veins and the mesophyll had isolateral zones of palisade and a central zone of large parenchyma cells presumed to

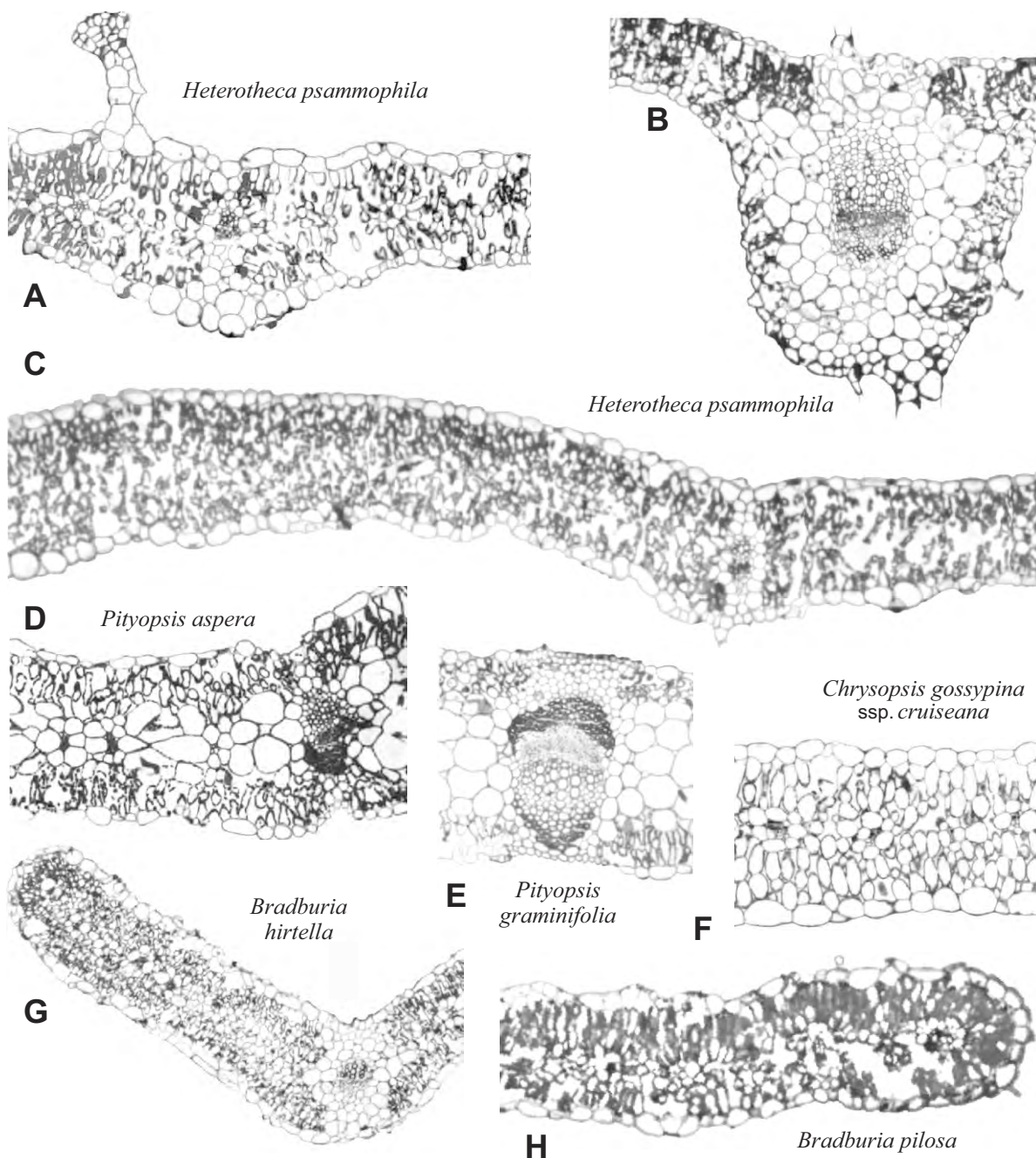


Figure 9. Leaf anatomy in some goldenaster genera. A-C. *Heterotheca*. D-E. *Pityopsis*. F. *Chrysopsis*. G-H. *Bradburia*. Surface hairs have broken off; these are best seen in scanning electron photomicrographs.

to be storage tissue. The main veins in *Pityopsis* are “parallel” and the leaves often are grass-like in general appearance, especially basal rosette leaves. *Heterotheca*, *Bradburia* and *Chrysopsis* are similar in having a well developed mid vein region consisting of a central vascular bundle surrounded by a bundle sheath of large parenchyma cells (Fig. 9B, G). The sheath extends to the upper and lower epidermal layers (Fig. 9A-C, G). The vascular bundles was collateral with an abaxial zone of sclerenchyma. The mesophyll is either bifacial (Fig. 9C), more clearly isolateral (Fig. 9G), or not distinctly zoned (Fig. 9F).

Trichome traits are distinctive in *Heterotheca*, although indument appearance varies greatly within sect. *Phyllothea* (Fig. 10; Semple et al. 1980, figures 2-30). All species of *Heterotheca* have small to large uniseriate hairs with osteoform (bone-shaped) cells covered with small pustulate knobs (Figs. 2A-C, 10B). These hairs were treated as TYPE-A trichomes by Nesom (1991d), along with some other kinds of hairs occurring in other goldenaster genera, e.g., the flagelliform hairs of *Chrysopsis* (Semple et al. 1980, figure 3). The osteoform hairs of *Heterotheca* are stiff-walled and remain terete even in air dried specimens. They are very large and several millimeters long when produced along the lower margins of lower stem leaves. In some species, e.g., *H. fulcrata* and *H. marginata*, such large hairs are produced along most of the leaf margin even on upper stem and branch leaves. In other taxa, few or no large hairs occur along the upper stem and branch leaf margins, e.g., *H. sessiliflora* var. *fastigiata* (Fig. 10E). The density of the osteoform hairs varies between varieties within species and between species. Osteoform hair density was found to be very useful in distinguishing varieties within variable species, e.g., *H. fulcrata*, *H. sessiliflora*, and *H. villosa* and as a diagnostic feature of some species, e.g. *H. canescens*. Osteoform hair density accounts for the differences in leaf color among species. Dark or bright green leaves have few hairs/mm² (Fig. 10A), while species whose leaves are very light green tend to have 30-70 hairs/mm², and silvery to white leaves have 90-250 hairs/mm² (Fig. 10D). Hair density can vary from lower to upper stem and branch leaves, and from one part of a leaf to another in some taxa. For example, in *H. sessiliflora* var. *fastigiata*, upper stem and branch leaves have a very dense indument of 100-250 hairs/mm² (Fig. 10D), except along the margins where hair density can be very low and glandular trichome density moderate to high.

In this treatment, the orientation of the indument of osteoform hairs is described as either hispid or strigose. In the hispid condition, the osteoform hairs tend to stick out from the surface and are labelled “spreading” and may even be slightly reflexed. In the strigose condition, the osteoform hairs are more closely appressed to the stem, leaf or phyllary surface. The size of the hairs varies greatly in each kind of indument and the two conditions are really only ends of a continuum in hair orientation. Nonetheless, in some cases nearly all hairs are appressed and in others many hairs are relatively erect. The difference is obvious when the hairs are long as in the hispid leaves of *H. sessiliflora* var. *echioides* versus short as in the strigose leaves of *H. sessiflora* var. *fastigiata*. In all species, obviously larger spreading hairs occur along the bases of the leaves. These spreading hairs may also occur on the upper margins, or they may be absent from the margins on the uppermost stem branch leaves.

Species of *Heterotheca* produce two other kinds of leaf and stem trichomes: stipitate glands and minute delicate uniseriate soft-walled hairs (Fig. 10B-C, respectively). Nesom (1991d) referred to the biseriate glands as TYPE-C trichomes and the usually small hairs as TYPE-B. In most goldenasters TYPE-A hairs make up the primary indument, often sharing dominance with TYPE-C glandular trichomes, except in the case of glabrous individuals and taxa. The TYPE-B hairs usually go unnoticed in *Heterotheca*, *Bradburia* and *Chrysopsis*. Nesom (1991d) stated that TYPE-B trichomes made up the primary indument of *Pityopsis* (Semple et al. 1980, figures 25-30) and *Tomentaurum* rather than TYPE-A trichomes. Nesom (1991d) also discovered other trichomes features of the goldenaster group. In the case of *Heterotheca* the distinction between TYPE-A and TYPE-B hairs is very clear. In some of the other goldenaster genera, however, the distinction may not be as clear and scanning electron microscopy may be needed to confirm that very large TYPE-B hairs are not just very thin uniseriate TYPE-A hairs. It may ultimately be demonstrated that TYPE-A and TYPE-B hairs are extremes of a single continuous category.

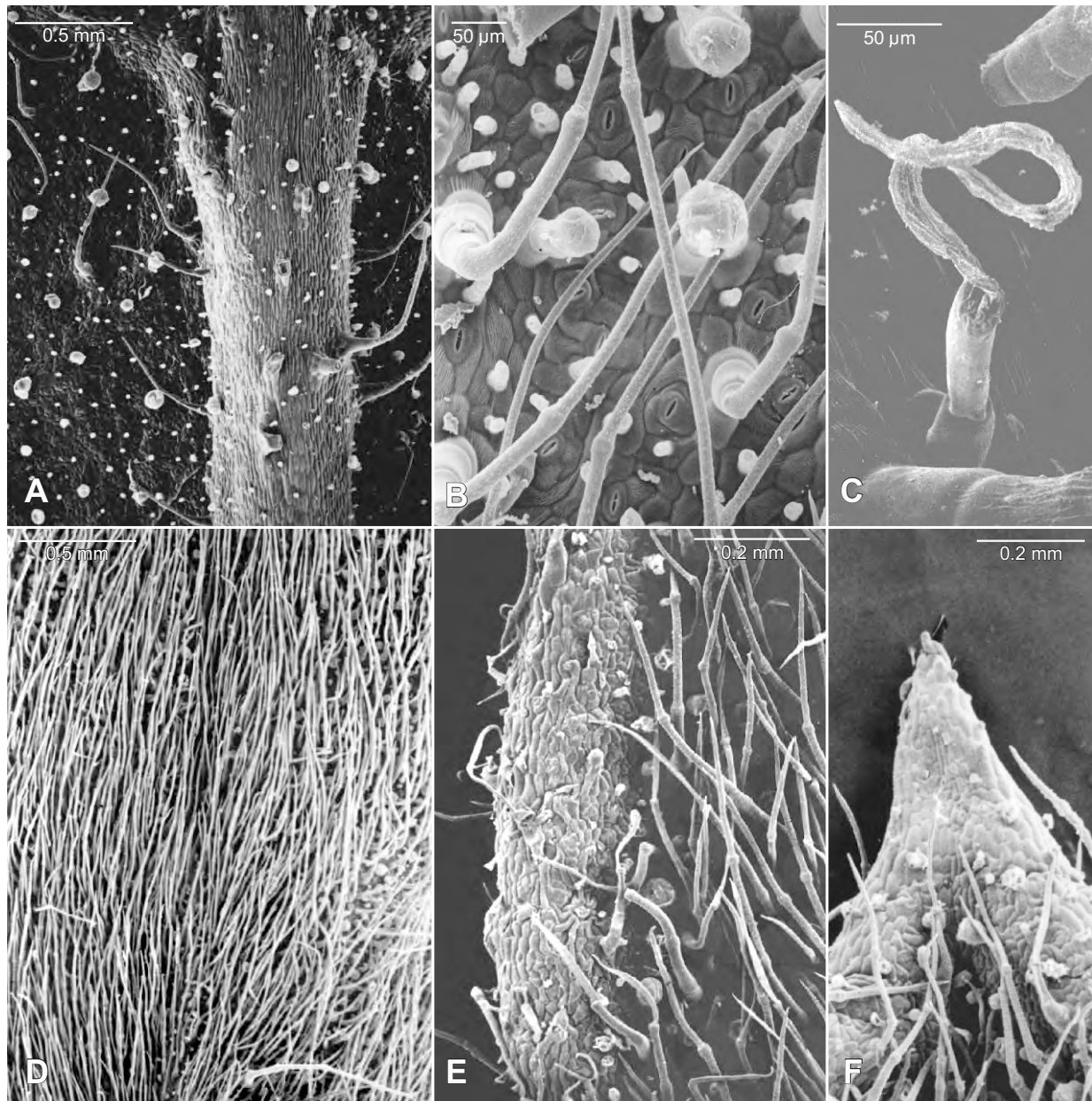


Figure 10. Leaf surfaces and trichomes: *Heterotheca* sect. *Phyllothea*. A. Mid vein region, sparsely pubescent, densely glandular leaf, *H. shevockii*. B. Three kinds of trichomes, *H. sessiliflora* var. *bolanderioides*. C. Small non-osteiform hair, *H. villosa* var. *scabra*. D-F. *H. sessiliflora* var. *fastigiata*. D. Mid vein region, very densely pubescent, moderately glandular leaf. E. Leaf margin, sparsely pubescent and glandular. F. Mucronate tip. (Scanning electron photomicrographs; scale bars indicated).

The presence or absence of long hairs on the corolla lobes was found to be significant in distinguishing species in sect. *Phyllothea* (Semple 1993). These differences are clearly seen in Figs. 11A-D. *Heterotheca sessiliflora* (Figs. 11A-C) and the newly discovered *H. monarchensis* produce relatively long (0.5-2.0 mm) osteiform-pusticulate hairs (TYPE-A) on the corolla lobes, while all other species produce either TYPE-B

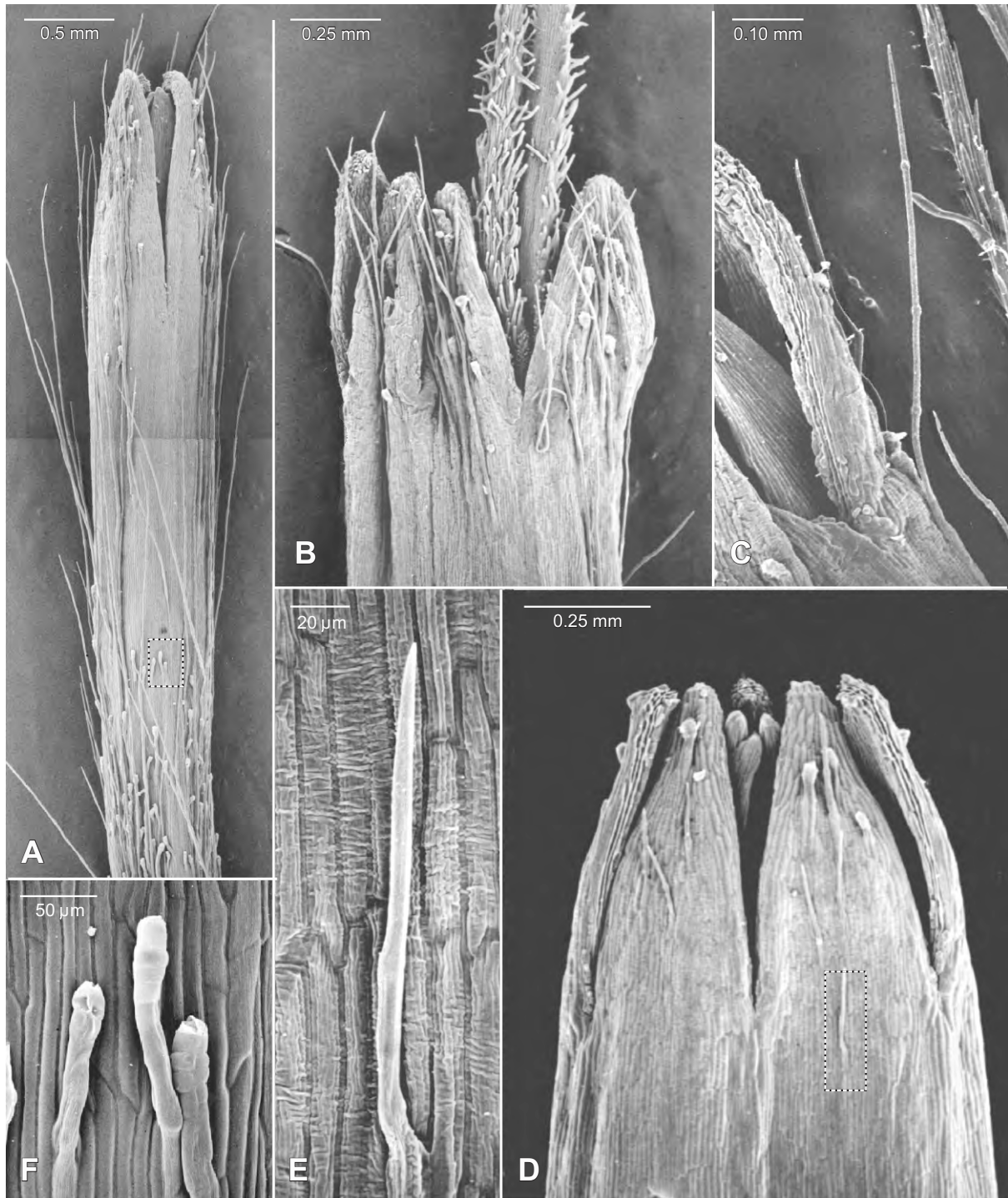


Figure 8. Corolla limb and lobe traits. A. Corolla limb, *H. sessiliflora* var. *bolanderioides*. B-C. Corolla lobes and long lobe hair, respectively, *H. sessiliflora* var. *bolanderioides*. D-E. Corolla lobes and short lobe hair (in box in D), *H. villosa* var. *minor*. F. Small glandular hairs in box in A. (Scanning electron micrographs; scales indicated)

hairs or minute to small (0.1-0.25 mm long) TYPE-A hairs (Figs. 11D-E). TYPE-B glandular trichomes also are produced on corolla lobes and tubes; these vary from very small (Figs. 11F) to modest in size compared to those on leaves and stems, where the glands can be several millimeters in height and are clearly visible to the naked eye as bright yellow resinous structures (Fig. 11A).

Members of sect. *Phyllothea* produce on the achene body the biseriate hair (Zwillingshaare) typical of Astereae. These hairs lack the pusticulate surface knobs of the osteoform hairs and are much smaller than the osteoform hairs of leaf margins. The density of these hairs is high at anthesis but decreases as the fruit body enlarges. At maturity achenes may be sparsely to densely pubescent.

CYTOLOGY

The genus *Heterotheca* has been the subject of a number of cytological studies with early major investigations by Vernon Harms (1963, 1965a, 1974a). Artificial hybrids between *H. canescens* and *H.* (sect. *Heterotheca*) *latifolia* Buckl. var. *macgregoris* Wagenk. demonstrated the genomic similarity of the members of sections *Phyllothea* and *Heterotheca* (Harms 1965a). The chromosomal base number of *Heterotheca* is $x = 9$ with all species being diploid ($2n = 18$) and many including both diploids and tetraploids ($2n = 36$), with the exception of the entirely tetraploid *H. camporum*. Since the first chromosome number report for the genus by Heiser and Whittaker (1948; *H. grandiflora* in sect. *Heterotheca*) more than 650 counts have been determined. More than 250 chromosome number reports have been published under various synonyms for *H.* sect. *Phyllothea* by (Jackson 1959; Raven et al. 1960; Turner et al. 1961; Turner et al. 1962; Turner and Flyr 1966; Harms 1965a, 1974a; Solbrig et al. 1964; Chuksanova et al. 1968 cited in Kovanda 1972; Moran 1969; Solbrig et al. 1969; Powell and Sikes 1970; Kovanda 1972; Watson 1973; Anderson et al. 1974; Hartman 1977; Keil and Stuessy 1977; Taylor and Taylor 1977; Semple 1977, 1983, 1985b, 1987, 1988; Powell and Powell 1978; Gallagher and Parfit 1982; Ward 1984; Semple and Chmielewski 1987; Semple, Chmielewski and Lane 1989; Semple, Chmielewski and Xiang 1992).

A cytogeographic study of the genus with a review of all previously published counts and new reports for several hundred individuals is in preparation. In most cases, diploids and tetraploids occur over much of the range of a taxon. Overall, tetraploids are more common on the prairies than diploids, except in *H. canescens* in which diploids are much more widely distributed than tetraploids. In the mountains, diploids and tetraploids are common, but the frequency of each differs among varieties within individual species and among species. In the case of *H. sessiliflora*, tetraploids are known in only one of the four subspecies and these are confined mostly to ultramaphic soil types in the greater San Francisco Bay area. In *H. villosa*, tetraploids are generally more widely distributed than diploids in each of the varieties with large ranges.

Meiotic and mitotic karyotype illustrations (camera lucida or photomicrographs) have been published by Harms (1965a) and Semple (1977). Mitotic metaphase chromosomes are metacentric or acrocentric. A representative idiogram karyotype of *H. stenophylla* var. *stenophylla* is shown in Fig. 12; nucleolar organizer region and centromere positions vary among the species. Individual chromosomes range from 1-3 μm in length in squash preparations using a 0.01% colchicine or saturated para-dichlorobenzene pretreatment. No detailed study of karyotypes in *Heterotheca* has been published.

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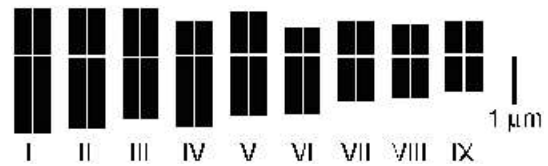


Figure 12. Idiogram karyotype of *H. stenophylla* var. *stenophylla*.

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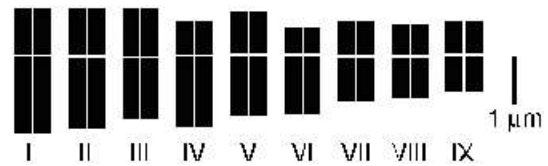


Figure 12. Idiogram karyotype of *H. stenophylla* var. *stenophylla*.

HYBRIDIZATION

The western and montane goldenasters have pollen (Fig. 13) typical of Astereae that are pollinated by bees, wasps, butterflies, and flies mimicking bees. Similarities in appearance among sympatric species undoubtedly facilitates the occasional transfer of pollen from one species to another. Interspecific hybridization between diploids does not appear to be a common phenomenon in *H. sect. Phyllotheca*. Hybridization between tetraploids is a more likely occurrence with a number of collections from the central and southern Great Plains being putative hybrids. There is some documentation of naturally occurring hybridization. Harms (1963, Ph.D.) discussed several possible cases involving *H. stenophylla* var. *stenophylla* and *H. canescens* with each other or *H. villosa*. Possible hybrids between *H. fulcrata* and *H. villosa* have been collected as well. Within species, intervarietal hybrids are common in areas of sympatry. For example, numerous putative inter-varietal hybrids in *H. villosa* have been collected throughout the range of the species.

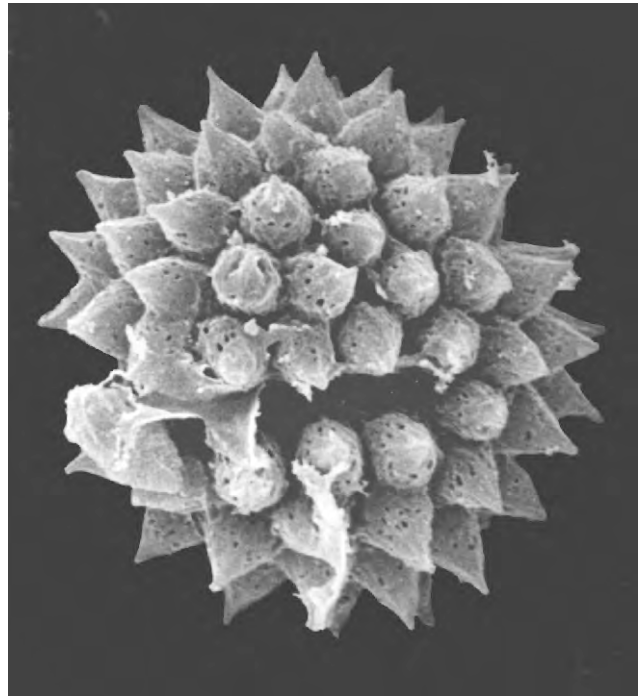


Figure 10. SEM of pollen grain, *H. sessiliflora* var. *fastigiata*.

Taxonomic Treatment

Heterotheca Cass., Bull. Soc. Philom. 137. 1817. Goldenasters, Telegraph Weeds

Herbaceous annuals and herbaceous perennials from woody taproot, sometimes forming ramets at ends of short to long rhizomes; shoots sometimes persisting and becoming shrubby. STEMS ascending-erect, 0.05-2 m, usually 0.3-0.6 m tall, branching above, indument appressed strigose and hispid, longer spreading hairs few to many; hairs with knobs (pusticulate) on cell walls. LEAVES simple, basal and cauline; lower ovate-oblongate, petiolate to sessile, variously hairy but always with some coarse spreading hairs along basal margins of petioles; upper sessile, smaller, variously hairy and stalked-glandular. CAPITULESCENCE cymose-corymbiform, heads solitary to many. Heads radiate or discoid; involucre campanulate-hemispheric upon drying, 3-14 mm; phyllaries in 3-5 overlapping series. RAY FLORETS pistillate, fertile, (4)-30, absent in one species; corolla yellow, glabrate to short pilose and glandular. DISK FLORETS many; corolla 5-lobed, yellow, glabrate to sparsely hairy, sometimes minutely glandular; style branches finely papillate, appendages narrowly triangular, 1-2 times the length of stigmatic lines. RAY FRUIT obconic, often 3-angled; pappus absent or double, outer short (0.2-1 mm) narrow scales (sometimes few, obscure), inner 30-45 long (3-7 mm) barbellate bristles. DISK FRUIT compressed obconic; pappus double, similar to ray fruit, always present. RECEPTACLE alveolate, subulate.

Mostly western North America, 3 sections and 28 species. Most taxa in sect. *Phyllotheca* were previously included in *Chrysopsis villosa* (Pursh) Nutt. at one time or another by various authors.

KEYS TO THE SECTIONS AND SPECIES OF *HETEROTHECA*

- 1 Heterocarpic ray and disc floret achenes; heads radiate; perennials and annuals . **sect. *Heterotheca* I**
- 1' Pappus of ray and disc similar or heads radiate; perennials
 - 2 Heads discoid and a few obscure or no obvious short outer pappus bristles; Pacific coast states
..... **sect. *Ammodia* II**
 - 2' Heads radiate or heads discoid and outer pappus whorl well developed, very thin bristles to narrow scales; throughout much of North America **sect. *Phyllotheca* III**

I. KEY TO *HETEROTHECA* SECT. *HETEROTHECA* (after Wagenknecht, 1960, with modifications)

- 1 Habit strict, to (0.1)1-2.5 m tall; stems 0.9-1.7 cm in diameter; cauline leaves petiolate below, sessile above, coarsely serrate to entire; capitulescence of short, paniculiform axillary branches; peduncles and phyllaries densely glandular; CA, eastern AZ, Baha and Sonora México, introduced in Hawaii
..... ***H. grandiflora* Nutt.**
- 1' Habit erect to procumbent, if strict; capitulescence corymbiform to paniculiform; stems < 0.9 cm diameter, of if larger, with cordate clasping leaves; peduncles and phyllaries sparsely to moderately glandular
 - 2 Habit erect or of several strict stems from a central caudex; lateral branches not well developed; capitulescence corymbiform; leaves lanceolate; peduncles elongate and leafless
 - 3 Annual; heads 0.5-1.2 cm in diameter, narrowly campanulate; Chihuahua and Sinaloa south to state of México
..... ***H. leptoglossa* DC.**
 - 3' Perennial, several strict stems; heads 1.5-3.0 cm diameter, broadly campanulate; central and southern México
..... ***H. inuloides* Cass.**

- 4 Stem and leaves sparsely pilose; phyllaries glandular, sparsely villous; Veracruz, Puebla and Oaxaca, México, 1550-2300 m *H. inuloides* var. *viridis* Nesom
- 4' Stem and leaves moderately to densely pilose or villous
- 5 Stem and leaves densely pilose to villous; phyllaries densely villous, hairs large; S Nuevo Leon W to Durango and S to Puebla, México, 2000-3000 m *H. inuloides* var. *inuloides*
- 5' Stem and leaves pilose; phyllaries with sparse slender hairs; Durango, Zacatecas, Nayarit, Jalisco, Michoacán, and Colima, México, 1200-2400 m *H. inuloides* var. *rosei* Wagenknecht
- 2' Habit erect to decumbent; lateral branches well developed; capitulescence paniculiform to paniculiform-corymbiform; leaves ovate, elliptical to lanceolate; peduncles sparsely to densely foliar (*H. subaxillaris* complex)
- 6 Perennial from well-developed woody caudex; blades of basal and cauline leaves ovate to elliptical, serrate to rarely entire, petiolate, the petioles of lower leaves to 4 cm long; pappus a deep reddish-brown; central and northeastern México *H. chrysoptidis* DC.
- 6' Annual or weakly perennial, caudex not developed; leaves elliptical to lanceolate, serrate to entire, the petioles of basal leaves < 3 cm long; pappus tan to white
- 7 Habit erect to procumbent, to 1 m tall; stem scabrous; lower leaf surfaces scabrous; phyllaries with a well-defined subapical tuft of short thick hairs; outer coastal plain of SE US into northeastern México *H. subaxillaris* (Lam.) Britt. & Rusby
- 7' Habit erect, to 2 m tall; stem and lower leaf surfaces velutinous or pilose, the upper leaf surfaces scabrous to hispid-strigose; phyllaries sericeous and sparsely glandular
- 8 Stem to 12 mm diameter; the lateral branches coarse; leaves cordate-clasping, sparsely pilose above; phyllaries densely glandular hispid-strigose; southern UT, AZ, northern México; western TX, introduced into CA *H. psammophila* Wagenknecht
- 8' Stem 4-9 mm diameter; lateral branches slender, or if coarse then leaves long-pilose; phyllaries sparsely to moderately glandular *H. latifolia* Buckley
- 9 Leaves scabrous above; heads < 0.9 mm wide *H. latifolia* var. *latifolia*
- 9' Leaves densely long hispid-strigose above; heads > 0.9 mm wide
- 10 Lateral branches slender; leaves oblanceolate, the veins not prominently raised; AZ, NM, CO, northern TX, KS, OK and introduced across the SE US *H. latifolia* var. *macgregoris* Wagenknecht
- 10' Lateral branches coarse; leaves elliptical to lanceolate, the veins prominently raised; eastern TX and OK, AR, MO and introduced in the E US (MD) *H. latifolia* var. *arkansana* Wagenknecht

II. KEY TO THE VARIETIES OF *HETEROTHECA* SECT. *AMMODIA* (Nutt.) Harms:

- H. oregona* (Nutt.) Shinnars (after Semple et al. 1988)
- 1 Branch leaves glabrate to sparsely hispid (<5 hairs/mm²), obviously glandular
- 2 Branch leaves usually larger than 13 × 3 mm; outer phyllaries deltoid-lanceolate; Cascades from central WA to coastal ranges of northern and central CA *H. oregona* var. *oregona*
- 2' Branch leaves usually smaller than 13 × 3 mm; outer phyllaries deltoid; inner coastal ranges San Francisco Bay to San Luis Obispo, CA *H. oregona* var. *scaberrima* (A. Gray) Semple
- 1' Branch leaves moderately to densely hispid (>5 hairs/mm²), not obviously glandular
- 3 Stems usually open branching above middle; leaves short-hispid, appearing green; coastal to lower mountains of southern OR and northern CA *H. oregona* var. *rudis* (Greene) Semple
- 3' Stems usually branching near base or below middle; leaves long-villose, appearing gray-green; lower el. In mountains of northern and central CA. *H. oregona* var. *compacta* (Keck) Semple

III. ARTIFICIAL KEY TO TAXA OF *HETEROTHECA* SECT. *PHYLLOTHECA*

- 1 Upper corolla tube and lobes sparsely hairy (sometimes obscurely so), longest hairs generally 0.4-1 mm and very thin; coastal and transverse ranges, central valley and foothills of adjacent mountains in California, coastal NW Baha California Norte, México
 - 2 Upper leaves narrowly oblanceolate, moderately hispid, marginal hairs large, numerous; stems 9-18 cm tall; rare Kings R. canyon, Monarch Wilderness, Fresno Co., California
 - *H. monarchensis* (2, p.52)
 - 2' Upper leaves not as above; leaf margins often wavy; coastal and transverse ranges, central valley, Tehachapi Mts. of California, coastal NW Baha, México *H. sessiliflora* (1, p.34)
 - 3 Upper leaf margins distinctly wavy, hairs ca. 1mm long
 - 4 Heads subtended by large foliar bracts; upper stem leaves green, not stiff; along coast, dunes of south coastal range, < 100 m el.; southern California to NW Baha, México
 - *ssp. sessiliflora* (1.1, p.36)
 - 4' Heads not subtended by large foliar bracts; upper stem leaves whitish, stiff; > 200 m el.; Ventura east to E San Bernadino Mts., Mt. Palomar *ssp. fastigiata* (1.2, p.38)
 - 5 Stems and leaves densely short stigose-canescens (whitish), sparsely glandular to densely so capitulescence; San Gabriel and San Bernardino Mts, rarely along washes below mountains in Imperial Valley *ssp. fastigiata var. fastigiata* (1.2.1, p.40)
 - 5' Stems and leaves sparsely to moderately hispid-strigose, densely glandular (green); San Jacinto Mts. and Mt. Palomar *ssp. fastigiata var. sanjacintensis* (1.2.2, p.41)
 - 3' Upper leaf margins weakly wavy to flat, hairs 1.2-2.5 mm
 - 6 Lower stem sparsely woolly; upper leaves oblanceolate, hairs long woolly-strigose, not much smaller upward; dunes and headlands Mendocino to Santa Cruz, lower el. San Francisco Bay area
 - *ssp. bolanderi* (1.4, p.49)
 - 6' Lower stem hispid; upper leaves elliptic to lanceolate, much smaller upward in tall plants, margins sometimes somewhat wavy, hairs strigose and hispid, not woolly; inland hills and valleys of central and southern California *ssp. echioides* (1.3, p.42)
 - 7 Upper stems and leaves densely glandular and very sparsely hispid; Santa Cruz, Santa Clara and northern San Benito Co's *ssp. echioides var. camphorata* (1.3.2, p.46)
 - 7' Upper stems and leaves moderately to densely hispid-strigose or hispid-villous
 - 8 Stems and leaves densely hispid-villous; 5-40 cm tall; mid to upper elevations of hills around San Francisco Bay *ssp. echioides var. bolanderioides* (1.3.3, p.47)
 - 8' Stems and leaves moderately to densely hispid; 20-110 m tall; lower and mid el. central valley, central and southern coastal ranges, Tehachapi Mts.
 - *ssp. echioides var. echioides* (1.3.1, p.44)
- 1' Upper corolla tube and lobes hairless or very sparsely so, longest hairs > 0.3 mm (rarely longer in *H. rutteri* and *H. mexicana*); leaf margins usually not very wavy; indument various
 - 9 Shrubs to subshrubs; branch leaves suborbicular, sessile, 3-12 mm long, margins undulate; sand dunes of Desierto de Altar, NW Sonora, México *H. thiniicola* (3, p.54)
 - 9' Herbaceous perennials not forming shrubs
 - 10 Heads eradiate, solitary; peduncles often 25-50% of height, moderately to densely glandular; low mat-forming plants; leaves sparsely to densely glandular, sparsely to moderately strigose; phyllary margins or entire distal portion tinted red; 200-2900 m el., Sierra San Pedro Martir, Baha California Norte, México *H. brandegei* (7, p.64)
 - 10' Heads radiate; other locations in México and north to western Canada

- 11 Upper stem leaves narrowly to linearly oblanceolate (rarely broader or oblong), sparsely to moderately strigose and moderately densely glandular **OR** moderately strigose and usually glandless, usually ascending and exceeding heads, large marginal hairs often present along distal portion of blade; lower stems becoming brittle, often dark brown, upper stems sparsely to densely long hispid; fascicles of leaves often present in leaf axis along stem; central and southern Great Plains, central Texas to E Colorado, S South Dakota and extreme NW Iowa *H. stenophylla* (13, p.88)
- 12 Leaves dark to bright green, hairs bases often broad (pustulate), glands many; phyllaries usually sparsely strigose and glandular; Nebraska and NW Iowa, Kansas to central Texas *H. stenophylla* var. *stenophylla* (13.1, p.89)
- 12' Leaves pale green, hairs rarely pustulate, glands absent or very few; phyllaries usually moderately strigose and glandless; central Texas to Colorado, S South Dakota [can hybridize with or be similar to *H. canescens* in S and *H. villosa* vars. in N] *H. stenophylla* var. *angustifolia* (13.1, p.92)
- 11' Leaves not linear oblanceolate, variously oblong, ovate or (ob-)lanceolate; range other than central and southern Great Plains
- 13 Leaves ovate-obovate, somewhat petiolate, sparsely to moderately hispid-strigose and moderately to densely glandular; heads solitary on well-defined peduncles; stems less than 30 cm tall
- 14 Upper leaves broadly oblanceolate to obovate, moderately hispid-strigose (12-33 hairs/mm²); peduncles 1-2 cm long; rocky cactus hills and open pine oak forests; Coahuila, Nuevo Leon, W Tamaulipas NE Zacatecas, México *H. mucronata* var. *harmsiana* (5.2, p.60)
- 14' Upper leaves (ob)ovate, subclasping, sparsely hispid-strigose (1-6 hairs/mm²); rock crevices of mts. of SE Arizona, SW New Mexico and Trans-Pecos, Texas *H. viscida* (8, p.66)
- 13' Not as above
- 15 Some heads subtended by one or more ovate-lanceolate leafy bracts that are distinct from the upper stem leaves and usually exceeding involucre (obscure in narrow-leaved hairier plants)
- 16 Upper leaves densely long-villous-strigose (silvery-white), very sparsely glandular, lanceolate, usually sharply acute; heads large, rays long; stems erect; rare, grassy plains below mts., S Arizona and adjacent México *H. rutteri* (10, p.80)
- 16' Leaves sparsely to densely short hispid-strigose, sparsely to densely glandular, ovate to lanceolate, usually bluntly acute to obtuse; open areas in pine and oak forests, central Rocky Mts in the U.S. and northern México *H. fulcrata* (9, p.68)
- 17 Distal margins of uppermost leaves with numerous long hispid-strigose hairs, leaves moderately hispid, moderately glandular; S Arizona to Trans-Pecos Texas and adjacent areas in México *H. fulcrata* var. *senilis* (9.4, p.79)
- 17' Leaf margins of upper leaves lacking long hairs or only a few basally, leaves variously pubescent and glandular
- 18 Upper stem leaves sparsely hispid-strigose and moderately glandular; heads usually small, rays short; subtending foliar bracts not well differentiated from obovate-lanceolate leaves (12-20 mm long); rare in SE Nevada and adjacent Utah, scattered lower-mid el. of Mogollon Escarpment in Arizona, scattered in SW New Mexico and mts of Trans-Pecos, Texas and adjacent México *H. fulcrata* var. *arizonica* (9.3, p.76)
- 18' Heads larger, rays long; subtending ovate foliar bracts usually large; upper stem leaves ovate, lanceolate or oblong (18-40 mm long); front ranges Wyoming and Colorado, mts of N Utah to SE Arizona, rare in NE Nevada and into NE México
- 19 Leaves and stems sparsely to moderately glandular and hispid-strigose; Front Range in Colorado and SE Wyoming, scattered in mts of Utah, N and E Arizona, S New Mexico and Chihuahua and Coahuila, México *H. fulcrata* var. *fulcrata* (9.1, p.70)
- 19' Leaves and stems moderately to densely short-strigose and glandless or nearly so, small leaves sometimes nearly white; Front Range, Wyoming and Colorado, SW Utah to SW New Mexico *H. fulcrata* var. *amplifolia* (9.2, p.74)

- 15' Heads not subtended by one or more leafy obvate-lanceolate bracts distinct from the upper stem leaves and exceed the involucre in height (sessile heads can be exceeded by upper stem leaves); when present subtending bracts oblanceolate to linear oblanceolate
- 20 Stem leaves with several serrate teeth along the margins; bluffs of Mississippi R. in Iowa and Missouri, N Ozark Mts. and eastward in disjunct locations from Michigan to North Carolina and south excluding the S.E.U.S. coastal plain. *H. camporum* (20, p.152)
- 21 Stems less than 0.7 m tall; upper stems and peduncles eglandular to moderately glandular; prairies, sandy banks, limestone bluffs and ledges along the Mississippi R. in Iowa, Illinois and Missouri to W Indiana *H. camporum* var. *camporum* (20.1, p.153)
- 21' Shoots to 1.4 m tall; upper stems and peduncles and leaves moderately to densely glandular; roadsides and disturbed sandy habitats, streams banks, C and E Tennessee and adjacent states, range expanding into S Missouri, N Arkansas, especially in disturbed areas, disjuncts in Michigan and E North Carolina *H. camporum* var. *glandulissimum* (20.2, p.156)
- 20' Mid and upper stem leaves toothless; lower leaves may have one or two serrate teeth along the apical margins; mountains and prairies from British Columbia to Manitoba and south to México, rare in northwestern Ontario and southern Wisconsin and northern Illinois
- 22 Dwarf cushion plants, 3-6 cm tall, stems usually decumbent, often buried in sand; heads solitary, peduncles < 1 cm long, involucre 3-5 mm high; mid stem leaves 3-6 mm long, oblanceolate; sandy pockets in sandstone cliffs, rare in SW Utah *H. jonesii* (15, p.100)
- 22' Plants usually more than 10 cm tall; habitat not as above
- 23 Stems and leaves densely short-strigose (appearing white); upper leaves sparsely to moderately glandular beneath hairs; peduncles and phyllaries densely glandular and glabrate (sometimes only sparsely glandular and moderately strigose); hot spring margins, rocky river beds, disturbed soils Provo to N and E of Salt Lake City, sandy soils, rock outcrops in S Utah and N Arizona, scattered locations E Arizona and SW New Mexico, hot springs SE Idaho [see also *H. villosa* var. *pedunculata*] *H. zionensis* (16, p.101)
- 23' Leaf and phyllary indument similar or phyllaries less glandular than leaves
- 24 Upper stem leaves linear oblanceolate, densely short-strigose canescent (90-200 hairs/mm²), glandless; involucre much shorter than disc corollas; leaves ascending, congested on stems and branches; heads often subtended by long linear oblanceolate bracts; rocky soils and outcrops, S Kansas to S Texas, disjunct in Chisos Mts. of Trans-Pecos Texas *H. canescens* (14, p.97)
- 24' Not as above
- 25 Outer pappus of a few easily-overlooked bristles of varying lengths; leaves strigose-canescens; peduncles of mature heads 2-5 cm; near Durango, México *H. mexicana* (4, p.56)
- 25' Outer pappus of narrow to broader scale-like easily seen bristles
- 26 Leaf hairs long silky; capitulescence of 1-few heads on peduncles 2-5 cm long; plants of pine forests of NE México
- 27 Phyllaries densely strigose, hairs obscuring glands; leaves white, very densely strigose; rare endemic of gypsum soils in south central Nuevo Leon, México *H. gypsophila* (6, p.62)
- 27' Glands of phyllary tips not obscured by hairs; leaves pale green to silvery-green, not white; stems sometimes sprawling; wide spread on non-gypsum soils in western and southern Nuevo Leon and adjacent states of México *H. mucronata* var. *mucronata* (5.1, p.56)
- 26' Leaf hairs not appearing silky, capitulescence usually branched, heads on short to long peduncles; prairies and mountains of W Canada and the U.S.

- 28** Upper stem leaves linear oblanceolate, often longer than lower leaves and exceeding the short peduncled heads, moderately strigose and sparsely glandular; rays usually showy; heads usually solitary or few; alpine, 9500-12,500 ft. el., Colorado, very rare in Carbon Co., Wyoming and possibly in the LaSalle Mts., SE Utah
..... *H. pumila* (12, p.85)
- 28'** Not as above
- 29** Stems, peduncles, bract and leaf margins with numerous long to very long spreading hairs; upper stem leaves stiff, lanceolate to narrowly elliptic, coarsely hispid-strigose and very sparsely glandular; stems to 80 cm tall, often with long ascending lateral branches; locally common in Superstition Mts. and adjacent areas in S Arizona
..... *H. marginata* (11, p.83)
- 29'** Not as above; plants may have long spreading hairs but not on most parts
- 30** Leaves broadly elliptic-lanceolate, acute, large, sparsely strigose, sparsely glandular; endemic to Spokane R. valley in Idaho and adjacent Washington, very rare, possibly extinct [see also *H. villosa* var. *minor*]
..... *H. barbata* (19, p.150)
- 30'** Leaves not as above, variously (ob-)lanceolate or oblong; much of central and western North America
- 31** Stems to 120 cm tall; upper stem leaves sessile, deltoid-lanceolate, margins usually inrolled, moderately to densely glandular, sparsely to moderately hispid-strigose; rocks along river, disturbed areas, lower Kern R. Canyon, California [short plants similar to *H. villosa* var. *scabra*]
..... *H. shevockii* (18, p.148)
- 31'** Stems usually less than 50 cm tall; upper leaves various but not as above, indument highly variable with many intermediate forms among varieties; widely distributed in western mts and Great Plains
..... *H. villosa* (17, p.105)
- 32** Stems and leaves moderately to densely strigose (25-200 hairs/mm²), very sparsely glandular to eglandular (rarely more glandular)
- 33** Leaves narrowly to broadly oblanceolate; bracts subtending heads small or absent
- 34** Upper stem leaves moderately strigose (25-60 hairs/mm²); stems 10-50 cm tall, with few to many longer spreading hairs and many appressed hairs; peduncles sometimes elongated and with few bracts; northern Great Plains Minnesota to Alberta south to Nebraska, scattered in hills and mts., British Columbia to Colorado
..... *H. villosa* var. *villosa* (17.1, p.108)
- 34'** Upper stem leaves densely to very densely strigose (80-270 hairs/mm²)
- 35** Stems erect, 5-20 cm tall, long spreading hairs few, short appressed hairs many; leaves narrowly oblanceolate, moderately densely strigose (80-150 hairs/mm²), very sparsely to moderately glandular; involucre campanulate, disc florets few (11-24-(31)); hot springs, geyser basins, Yellowstone Nat' Park and gravelly river banks, eastern Teton Natl. Park, rare further south in W Wyoming [plants approaching var. *minor* are common in range] *H. villosa* var. *depressa* (17.4, p.121)
- 35'** Stems erect, (12)-30-50-(75) cm tall, long spreading hairs few, rarely to many; leaves narrowly oblanceolate, densely to extremely densely strigose (60-270 hairs/mm²), glandless to sparsely glandular; involucre cylindrical to narrowly campanulate; grasslands and wooded hillsides and mountains, SW Colorado and SE Utah to SE Arizona, NW and W New Mexico [sparsely glandular forms of *H. zionensis* can be similar but leaves more oblong] .. *H. villosa* var. *pedunculata* (17.5, p.126)
- 33'** Leaves narrowly to broadly oblong; bracts subtending heads often exceeding involucre, stems often with numerous long spreading hairs

- 36 Rays showy, often numerous; involucre broadly campanulate; leaves strigose, hairs not generally obscuring leaf surface; northeastern Great Plains Saskatchewan to Manitoba and Minnesota, rare northwestern Ontario [similar to but more robust than next variety]
 - *H. villosa* var. *ballardii* (17.2, p.113)
- 36' Rays less showy; involucre narrowly campanulate; leaves hispid-strigose, hairs sometimes obscuring leaf surface; foothills New Mexico to Wyoming; infrequent on prairies of western Canada into western mountains Wyoming to British Columbia [frequently hybridizes with var. *minor* and var. *villosa*]
 - *H. villosa* var. *foliosa* (17.3, p.117)
- 32' Upper stem leaves sparsely to moderately densely hispid-strigose (2-100 hairs/mm²) and sparsely to densely glandular (2-60 glands/mm²), oblanceolate, oblong, lanceolate, ovate; heads few to many
- 37 Upper stem leaves narrowly to broadly oblong to narrowly ovate; capitulescence cymose to somewhat umbelliform
- 38 Upper leaves broadly oblong-lanceolate to ovate, moderately to densely strigose (usually 40-68-90 hairs/mm²) and sparsely to densely glandular (usually 4-21-40 glands/mm²); rays showy; scattered and locally abundant, mid elevations of Sierra Blanca, New Mexico and mts. to the south and west
 - *H. villosa* var. *sierrablancensis* (17.9, p.146)
- 38' Upper leaves linear to broadly oblong, often oriented nearly at right angles to stem, sometimes very small (< 1 cm long), moderately hispid-strigose (usually 12-28-44 hairs/mm²) and moderately to densely glandular (usually 9-18-27 glands/mm²) sometimes more than hairs, often; long spreading hairs on stems often numerous, lower elevations in mountains and foothills of Colorado and northern New Mexico, Great Plains of Wyoming to New Mexico to western Nebraska, possibly disjunct in Wisconsin [plants treated by authors as *H. horrida* included here]
 - *H. villosa* var. *nana* (17.8, p.141)
- 37' Upper stem leaves ovate to oblanceolate or lanceolate, apex obtuse to acute, numbers of glands sometimes > the number of hairs/mm²; much of range of the species
- 39 Upper stem leaves narrowly lanceolate to deltoid-lanceolate, apex acute, mid stem leaves ascending not reflexed, margins not inrolled, glands sometimes abundant and more than number of hairs/mm²; branches of capitulescence often very long; phyllaries very sparsely strigose, hairs short, sparsely to moderately glandular; rocky outcrops, margins of arroyos, rocky embankments, Utah, Nevada, Arizona and disjunct in Little San Bernardino Mts., S California [gland density varies depending on growth conditions and time of blooming]
 - *H. villosa* var. *scabra* (17.7, p.136)
- 39' Upper stem leaves narrowly to broadly oblanceolate, sometimes ovate in mts., indument very sparse to moderately dense, highly variable, glands fewer than hairs; capitulescence cymose, branches not usually very long; heads small to large; capitulescence more or less compact, not lax in undamaged plants; phyllaries usually moderately strigose, hairs to 1 mm long, often glandular; common in much of range of the species, except most of Nevada [the most variable taxon in the section, numerous intermediates with other varieties of the species; plants treated by authors as var. *hispidula* included here] *H. villosa* var. *minor* (17.6, p.126)



***Heterotheca* sect. *Phyllotheca* (Nutt.) Harms**, Castanea 39: 158-159. 1974. *Chrysopsis* subg. *Phyllotheca* Nutt., Trans. Amer. Philos. Soc. Ser. 2. 7: 315. 1841. TYPE SPECIES: *Chrysopsis sessiliflora* Nutt. = *Heterotheca sessiliflora* (Nutt.) Shinnery
Sideranthus Nutt. in Fras., Cat. 1813. pro parte; nom. nudum.
Hectorea DC., Prod. 5: 95. 1836.

PERENNIALS from stout woody taproots, sometimes producing short to long rhizomes from which develop additional taprooted ramets. STEMS one to many, decumbent to ascending-erect, 2-154 cm tall, usually 20-40 cm tall, sparsely to densely appressed strigose, hispid hairs few to many, glandless to moderately glandular above. LOWER STEM LEAVES broadly spatulate to narrowly oblanceolate, 8-75 mm long, 1.5-18 mm wide, 2-11.5 times as long as wide, usually petiolate sometimes sessile and broadly to narrowly cuneate, sparsely to very densely strigose on both surfaces, glandless to densely glandular; margins entire or sometimes sparsely serrate apically, sometimes somewhat undulate, a few large longer hispid to hispid-curved hairs along petiole and near base. UPPER STEM LEAVES sessile, (ob)ovate to narrowly (ob)lanceolate or broadly to very narrowly linear elliptic, generally reduced upward, rarely larger than mid to lower stem leaves, rarely much reduced, very sparsely to very densely strigose, rarely more hispid than appressed, glandless to densely stipitate glandular, margins entire except serrate in *H. camporum*, usually flat, rarely weakly to strongly undulate. CAPITULESCENCE cymose-corymbiform, heads solitary to many, sometimes on long bracteate pedunculate branches. Peduncles 0-77 mm long, usually moderately to densely hispid-strigose, sometimes sparsely to densely glandular; bracts few, lower ones like leaves, becoming linear and less pubescent and more glandular near heads, sometimes one to several larger bracts subtending heads, these linear oblanceolate to ovate and subpetiolate. INVOLUCRES cylindrical to turbinate when fresh, cylindrical to campanulate-hemispheric upon drying, 4-15 mm high; phyllaries in 4-5 imbricate series, outer ones 1/5 to 1/3 length of inner, narrowly triangular or lanceolate, mid series very sparsely to densely strigose, especially near the apex, glandless to densely stipitate-glandular, especially near the apex, margins narrowly to broadly hyaline, fimbriate-ciliate apically; inner ones similar, apex and upper margins sometimes purplish-red tinted (anthocyanotic), rarely much of phyllary tinted. RAY FLORETS 4-38, absent in one species; strap yellow, 3.5-21.5 mm long, 0.5-3.0 mm wide, tube and base of strap sometimes sparsely glandular and strigose. DISC FLORETS 9-110, yellow, corolla barely to somewhat ampulate, 3.5-9.5 mm long, glabrous to sparsely strigose and stipitate-glandular, lobes 0.3-1.1 mm long, glabrous to sparsely strigose and glandular, hairs generally about 0.25 mm long, rarely to 1 mm long. ACHENES 1-4.3 mm long, sparsely to moderately strigose, 5-10 ribbed, ribs sometimes resin-filled, orange-brown and translucent; pappus off-white to rust colored, double, outer whorl of linear scales 0.1-1.0 mm long, linear and terete to narrowly lanceolate and flat, inner whorl of 25-45 barbellate bristles, 3.4-10 mm long, 80-140% the length of corolla tube at anthesis. Chromosome numbers: $2n = 18, 36$; more than 400 reports.

Flowering Period: (March)-MAY-OCTOBER-(December)

Distribution and habitat: Prairies, pine forests, chaparral, rarely in Upper Sonoran Zone deserts, (Figs. 4, 14, 20-28, 31-40, 50-52); sea level to 3800 m (0-12,500 ft) elevation

Discussion: *Heterotheca* sect. *Phyllotheca* includes mostly herbaceous perennials that die back to overwinter as hemi-chryptophytes. A few taxa in the subtropical areas become more woody and form 0.5-1 m tall shrubs when climatic conditions do not cause seasonal die back. Stem height varies from a few cm in *H. Jonesii* (Fig. 37A) to nearly 1.5 m in *H. camporum* (Fig. 52C) and *H. shevockii* (Fig. 50A), although most taxa produce shoots which are 30-50 mm long. Stem height is greatly influenced by growing conditions, and individuals may produce dwarf shoots one season and robust ones in another or in the same year. The upper limit of stem height does appear to be under genetic control.

Stem pubescence varies greatly as well. Most taxa produce some shorter, appressed, osteoform hairs (strigose indument) and some longer, large spreading osteoform hairs (hispid indument). The ratio of these two hair types determines whether the stem is described as strigose or hispid-strigose. The trait is variable

and although it has been used in the past as being diagnostic, it is too variable to be diagnostic by itself. In combination with other traits, stem indument can be helpful in separating taxa.

Most species produce similar looking basal stem leaves as seedlings; the leaves have a moderate number of hairs (10-40/mm²) and few or no glands. A few serrations are sometimes present near the apex. As development proceeds new leaves rapidly take on the characteristics typical of the upper portion of shoot of older plants. Upper stem leaves vary greatly in size, shape and indument features. Upper stem and branch leaves can less than 5 mm long, e.g., *H. jonesii* (Fig. 37B) and some forms of *H. villosa* var. *scabra* (Fig. 47F) as much as 140 mm long, e.g., *H. camporum* var. *glandulissimum* (Fig. 52D).

Leaf indument varies greatly in the section between and within taxa. Nonetheless, most taxa have leaf indument traits that are useful in characterizing and often diagnosing the taxon. A repeated pattern within species is distinctive races to have distinctive indument, usually a more densely glandular and less pubescent variety or race and a less glandular and more pubescent race. In some species the range is sufficiently large that extremely densely glandular and extremely densely pubescent varieties can also be recognized. These differences make the visual appear of the leaves range from bright or dark green to grayish-green to even nearly white. Thus, species need to be defined on traits other than leaf indument, although indument might be important in the set of traits defining a particular taxon, e.g., the high leaf hair density in *H. canescens* is critical in separating it from *H. stenophylla* var. *angustifolia*, but not the only features that disquish the two taxa. Hair density ranges from very low to very high. Most taxa produce between 10-50-(70) hairs/mm² of leaf surface. Some taxa have much higher densities of hairs ranging from (60)-80-250 hairs/mm². The difference in appearance of leaves between 60-90 hairs depends as much on the length of the individual hairs as the density. Leaves with 90 short hairs/mm² will look greener than leaves with 50-60 long hairs/mm². This makes it difficult to describe leaf appearance in a few words and care should be taken when considering this feature. Leaves with very high hair densities regardless of hair length are silvery to white, e.g., *H. canescens*, *H. villosa* var. *pedunculata* and *H. zionensis*. The greatest range in leaf indument density and leaf appearance occurs in *H. villosa* var. *minor*, which can have a very sparse indument of hairs and glands, but other forms have a moderately dense indument of both short to long hairs (40-60 hairs/mm²) and glands. Gland density rarely exceeds 20-30 hairs/mm², but gland size variation is great and this can make less glandular individuals with large glands seem more glandular than more densely glandular individuals with smaller glands. Crushing leaves in the field can reveal the presence of glands by the camphor odor that is detected.

Some taxa have large distinct foliar bracts subtending the heads, and others do not but may have normal leaves exceeding the involucre. The foliar bracts of *H. fulcrata* (Figs. 29-30) and *H. rutteri* (Fig. 31) are the extremes and diagnostic for the taxa. When small, such bracts normally have a different shape (usually ovate) than the upper stem leaves rather than just being smaller versions of the leaves. Heads can be subtended by oblanceolate upper stem leaves and similar peduncular bracts such as in *H. pumila* (Fig. 33), *H. stenophylla* (Figs. 34B and 35C), *H. villosa* var. *foliosa* (Fig. 43D) and some individuals of *H. villosa* var. *minor* (Fig. 46G), while other individuals in these taxa can have very small or no subtending bracts or leaves. Immature heads may be surrounded by leaves and bracts but by anthesis the peduncle has elongated and carried the head above and free of the foliage. This is true even in taxa typically considered to have elongated peduncles, e.g., *H. mexicana* (Figs. 22A,D).

Involucres vary in size and indument features within and between taxa. Size is influenced by ploidy level. Tetraploids within a taxon have larger heads than diploids of the same taxon, e.g., *H. villosa* var. *minor* (Figs. 46F-G), but between taxa diploids can have larger heads than tetraploids of other taxa. Phyllary indument may be constant or variable within a taxon. In nearly all taxa phyllary indument is similar to that of upper leaves or less glandular, i.e., taxa with densely stigose-canescens leaves have relatively densely strigose phyllaries (e.g., *H. canescens*, Fig. 30A) and taxa with hispid glandular leaves tend to have relatively more glandular phyllaries (e.g., *H. fulcrata* var. *arizonica*, Fig. 30A). In some taxa phyllary and leaf indument do not correlate in all individuals (e.g., *H. villosa* var. *minor*, Figs. 46H and *H. zionensis*, Fig. 38E-F). This reduced the value of phyllary traits in distinguishing taxa and is representative of many variable features.

Species Descriptions

1. *Heterotheca sessiliflora* (Nutt.) Shinnery, Field & Lab. 29: 71. 1951. *Chrysopsis sessiliflora* Nutt., Trans. Amer. Philos. Soc. Ser. 2. 7: 215. 1841. *Chrysopsis villosa* (Pursh) Nutt. var. *sessiliflora* (Nutt.) A. Gray, Synopt. Fl. N. Amer. 1, 2: 123. 1884. TYPE: U.S.A. CALIFORNIA. [Santa Barbara Co.:] Santa Barbara, [April 1836] *Nuttall s.n.* (Holotype: BM!; isotypes: GH!, K!)

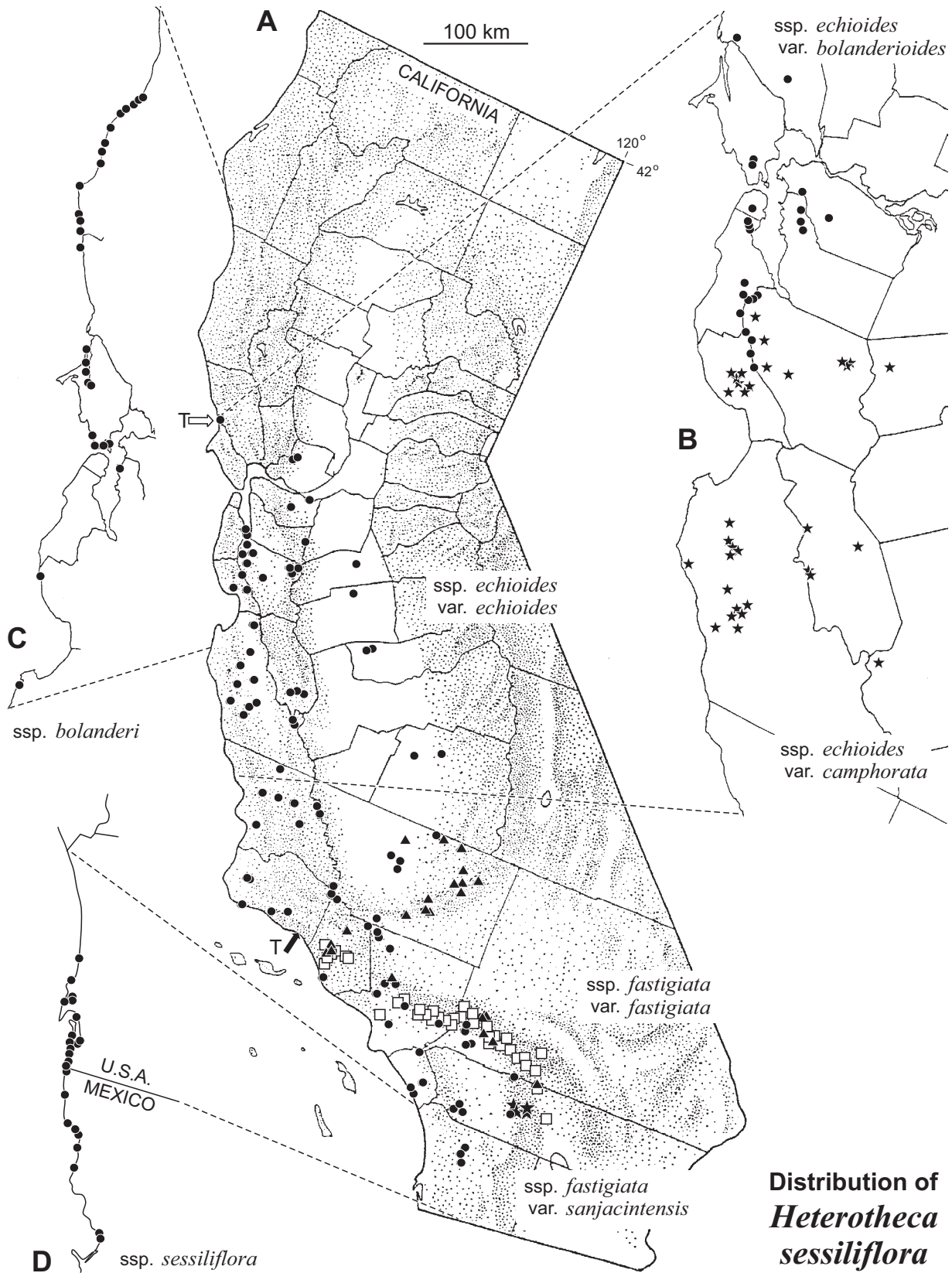
Perennial from stout woody taproots, STEMS several to many, ascending-erect, (10)-21-44-67-(106) cm tall, moderately to densely hispid/strigose (long spreading hairs often broken off), sometimes becoming densely glandular and moderately pubescent above; (9)-22-43-63-(90) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (8)-15-26-36-(57) mm long, (2.4)-4.3-6.2-8.1-(11) mm wide, subsessile, cuneate, acute, moderately to densely hispid-strigose on both surfaces; margins entire, strigose, longer spreading hairs near base, flat to undulate. UPPER STEM LEAVES narrowly to broadly lanceolate, sessile, usually reduced upward, (6.5)-8.5-16.6-24.7-(39.6) mm long, mm (1.5)-3.3-4.8-6.4-(7.7) wide, bases rounded, sparsely to densely glandular (0)-7-17-28-(50) glands/mm², sparsely to densely hispid-strigose or short-strigose (5)-19-80-140-(245) hairs/mm², margins flat to strongly undulate. CAPITULESCENCE corymbiform or paniculiform, branches ascending, heads 1-17-36-(126); peduncles densely hispid, strigose or glandular, bracts few, lower ones lanceolate, leaf-like or reduced upward and phyllary-like (1.9)-2.7-5.6-8.4-(13) mm long, (0.3)-0.5-1.2-1.8-(4) mm wide, sometimes with a few large foliaceous bracts just below head. INVOLUCRES cylindrical, turbinate or campanulate when fresh, campanulate upon drying, (6.3)-7.6-9.2-10.7-(15) mm high; phyllaries in 4-6 imbricate series, outer 1/5-1/4 length of inner, mid series narrowly triangular, very sparsely to moderately glandular, very sparsely to moderately strigose, margins hyaline, fimbriate-ciliate apically. RAY FLORETS (4)-7-11-15-(24), strap yellow, (3.5)-4.6-7.5-10.4-(18.5) mm long, (0.7)-1-1.4-1.7-(2.4) mm wide. DISC FLORETS (9)-20-35-50-(81), yellow, corolla somewhat ampliate, (4)-5.7-6.4-7.2-(9.5) mm long, lobes (0.4)-0.5-0.6-0.75-(1.0) mm long, very sparsely to sparsely pilose, hairs on lobes (0.1)-0.25-0.4-0.6-(1.0) mm long. ACHENES (12.3)-1.9-2.5-3.2-(4.5) mm long, moderately strigose; pappus off-white, double, outer whorl of a few linear scales 0.25-0.5 mm long, inner whorl of 25-45 barbellate bristles (4.9)-5.7-6.7-7.7-(10.2) mm long. Chromosome numbers: $2n = 18, 36$; numerous reports.

Flowering Period: (April)-MAY-NOVEMBER

Distribution and habitat: Much of California west of the Sierra Nevadas and Mohave and Colorado Deserts (Fig. 14); sea level to 2100 m elevation. Details of the distribution and habitats are discussed below under each subspecies and variety.

Discussion: *Heterotheca sessiliflora* is distinguished by the relatively long thin hairs on the corolla lobes and less so by its undulate sessile upper stem leaf margins (Figs. 15-19). It is the only species of the section native to the central and southern coastal ranges and valleys of California. The species is divided into four subspecies and five varieties differentiated on the basis of indument features and degree of waviness of the leaf margins and to a lesser extent stem height and leaf shape. Semple (1992) revised the nomenclature of the species and described two new varieties. A brief treatment of the species was presented by Semple (1993). With the exception of *H. monarchensis*, *H. sessiliflora* is the only species in the section with the long, fragile, osteoform hairs on the corolla lobes.

Figure 14. Distribution of *Heterotheca sessiliflora*; California and adjacent Baja California. **A.** Ssp. *echioides* var. *echioides*, lowland form, ●, (open arrow-type locale), montane form, ▲; ssp. *fastigiata* var. *fastigiata* (□), var. *sanjacintensis* (★). **B.** Ssp. *echioides* var. *camphorata* (★), var. *bolanderioides* (●). **C.** Ssp. *bolanderi*, ●; enlargement of coastline in A. **D.** Ssp. *sessiliflora* (●), enlargement of coastline in A (solid arrow - type locale). ➔



1.1 *Heterotheca sessiliflora* (Nutt.) Shinnars ssp. *sessiliflora*

Herbaceous or subshrubby perennials, STEMS several to many, decumbent to ascending-erect, (17)-23-**31**-38-(100) cm tall, moderately hispid-strigose, usually becoming densely glandular and sparsely to moderately pubescent above; (22)-29-**43**-57-(70) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, 16-**20**-24-(28) mm long, (4.7)-5.7-**7.0**-8.3-(10) mm wide, subsessile, cuneate, acute, moderately to densely hispid-strigose on both surfaces, sparsely to moderately glandular; margins entire, strigose, longer spreading hairs near base, undulate. UPPER STEM LEAVES lanceolate, sessile, reduced upward, (9)-10-**13**-16-(21) mm long, (4)-4.5-**5.5**-6.5-(7) mm wide, bases rounded, indument like lower leaves or becoming densely glandular, (10)-15-**25**-34-(36) glands/mm² and moderately hispid-strigose 7-**17**-27-(50) hairs/mm², margins, strongly undulate. CAPITULESCENCE corymbiform, branches ascending, heads (1)-3-**5**-8-(10); peduncles densely glandular, bracts few, lower ones lanceolate, leaf-like, reduced upward, (6.0)-6.7-**8.3**-9.9-(11) mm long, (1.0)-1.1-**1.5**-1.9-(2.2) mm wide, phyllary-like or foliaceous and subtending head. INVOLUCRES campanulate when fresh, hemispheric upon drying, (7)-8.4-**9.4**-10.4-(11) mm high; phyllaries in 5-6 imbricate series, outer 1/5-1/4 length of inner, mid series narrowly triangular, moderately glandular, very sparsely strigose, margins hyaline, fimbriate-ciliate apically. RAY FLORETS 14-**17**-20-(24), strap yellow, (5)-6-**7.4**-8.9-(11) mm long, 1.0-**1.5**-1.8-(2.3) mm wide. DISC FLORETS (38)-46-**58**-69-(79), yellow, corolla somewhat ampliate, (5.3)-5.6-**6.2**-6.7-(7.2) mm long, lobes (0.4)-0.5-**0.6**-0.75-(1.0) mm long, sparsely pilose, hairs 0.15-**0.3**-0.4 mm long. ACHENES 1.8-**2.2**-2.6-(2.9) mm long, sparsely strigose; pappus off-white to light brown, double, outer whorl of a few linear scales 0.25-0.5 mm long, inner whorl of 30-40 barbellate bristles, (4.9)-5.3-**5.7**-6.1 mm long. Chromosome number: $2n = 18$; one report.

Flowering Period: (March)-JUNE-SEPTEMBER-(October-January); the peak blooming period is mid to late summer, but individuals can produce some heads throughout much of the year.

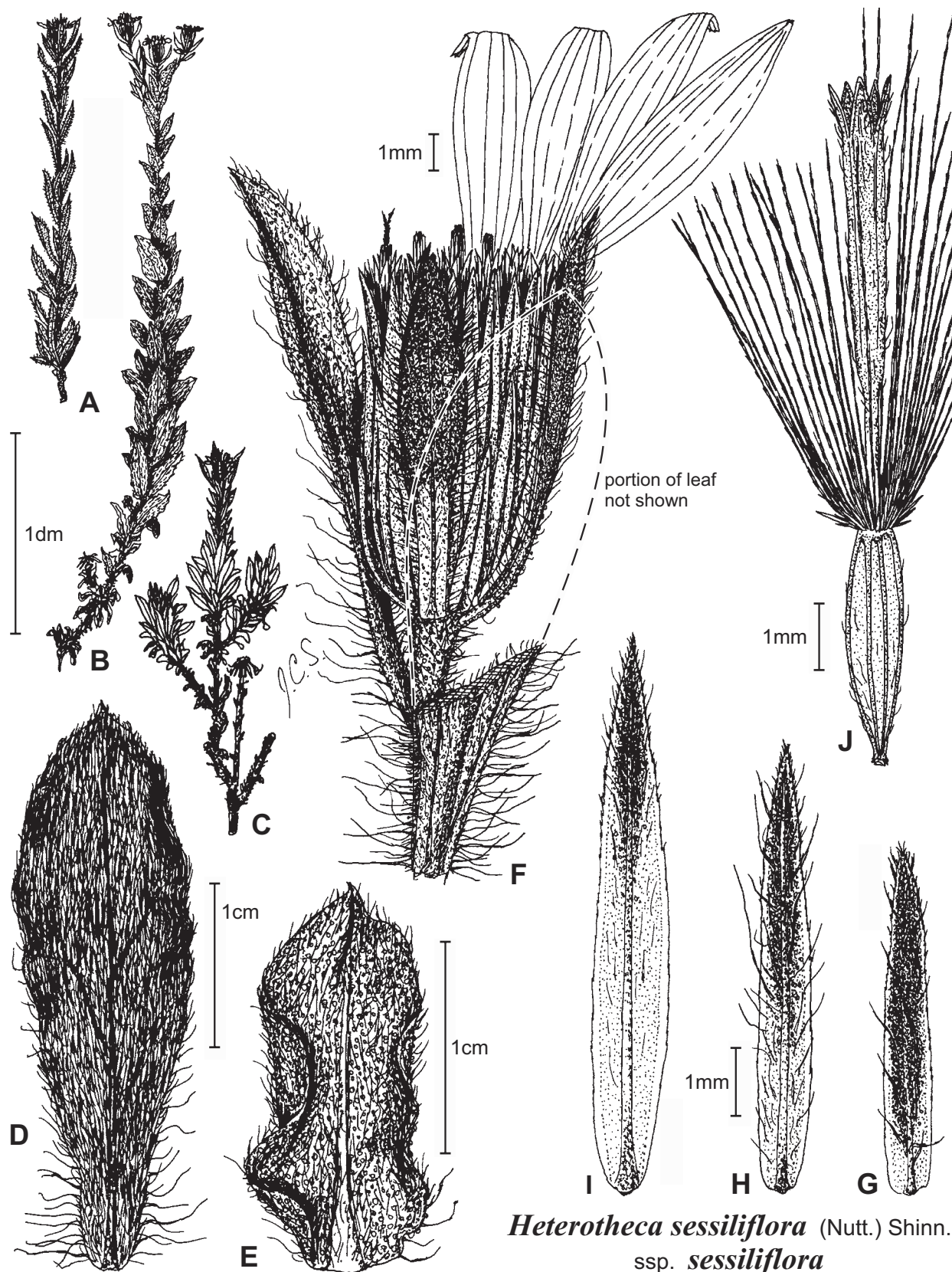
Distribution and habitat: San Diego Co., California to northern Baja Norte California, México; coastal dunes and strand, mud flats; sea level to 60 m elevation. The type comes from Santa Barbara where the subspecies now appears to be extinct (Fig. 14D). The lack of any specimens of the subspecies north of San Diego Co. except for the type specimen might indicate a possible location data error for the Nuttall type. He was in San Diego in early May of 1836 (Graustein 1967).

Discussion: Subspecies *sessiliflora* is distinguished by its usually densely glandular and sparsely to moderately pubescent upper stem and branch leaves which have wavy margins and by the usually relatively large foliaceous bracts subtending the involucre (Fig. 15). The plants vary greatly in habit. Some are short and herbaceous, the shoots dying back at the end of the growth season. Others in the northern Baja coastal dunes are meter high shrubs whose shoots have not been killed back to rootstock level.

The type collection is from an early blooming plant that is unusual because the shoot has elongated in a manner suggesting that it arose from near the base of a plant without much intervening stem. This can be seen in more complete specimens from the San Diego strand. The shift from densely pubescent lower stem leaves to densely glandular upper stem leaves occurs abruptly in some collections and gradually in others. The difference is likely the result of different environmental conditions under which the shoots developed. This can be seen in more complete specimens from the San Diego strand.

Specimens examined: MÉXICO. BAJA CALIFORNIA NORTE. *Cooper 95* (MIN). Descanso, *Higgins & Harbison s.n.* (CAS);

Figure 15. Morphology of *Heterotheca sessiliflora* ssp. *sessiliflora*. A. Spring shoot ; leaves glandular. B. Shoot from 1 m tall plant; leaves mostly densely pubescent. C. Branching shoot from small plant with short internodes, lower leaves pubescent, upper leaves glandular. D. Lower-mid stem leaf. E. Mid-upper stem leaf. F. Peduncle and head (only some florets drawn). G-I. Outer, mid and inner series phyllaries, respectively, with chlorophyllous zone dark. J. Mature achene with disc corolla attached. ➔



Higgins (SD). N of Descanso, *Moran 13255* (SD). Descanso Bay, *Fosberg 55686* (PH). Ensenada, *Brandege s.n.* (UC), *Rose 36758* (CAS). W of La Mision, *Moran 19118* (ASU, CAS). N of Rosarito Beach, *Wiggins & Gillespie 3877* (CAS(2), DS, F, NY). Between mouth of Tia Juana R. and international boundary, *Howe 296* (SD). Playas de Tijuana, *Moran 18547* (RSA, SD, UC). Tijuana, *Smith 5203* (F). *Stokes 13468* (SD). S of the U.S. boundary, near 32°19'N, 117°06'W, *Moran 16708* (SD); S of Tijuana near rd to Ensenada, *Wiggins & Thomas 342* (CAS). **U.S.A. CALIFORNIA.** San Diego Co.: *Palmer 129* (NY(2), PH). Chula Vista, *Cooper s.n.* (MIN). Del Mar, *Brandege s.n.* (UC), *Cooper 182* (CAN). Imperial Beach, *Peirson 3368* (RSA). La Jolla, *Spencer 10161* (NY). National Monument, *Johnson 989* (CAS, RSA). N of monument, *Wolf 10914* (RSA). Ocean Beach, *Brandege s.n.* (RSA, UC). San Diego, *Brandege s.n.* (UC), *Degener s.n.* (NY). *Eastwood 9275* (CAS), *Cleveland 9119* (SD), *Spencer 77* (NY, UC). *Stokes s.n.* (SD); mud flats on bay, *Cohen 455A,B* (RSA), ocean beach, *Brandege s.n.* (RSA, UC, WIS). Mission Bay, *Woodcock s.n.* (LL), *Wordeck 5298* (SD). Mission Valley, *Brandege s.n.* (UC), Pacific Beach, *Ganders 12209* (SD). Rockwell Field, Aristine Station, *Wordeck 5303* (SD). Silver Strand, *Purer 2307* (RSA), *Purer 5565* (DS, GH), *Semple & Chmielewski 8991* (DAO, MT, JCS, RSA, UC, WAT). South San Diego, *Chandler 4117* (CAS). Tijuana River, *Herre s.n.* (DS). Torrey Pines Beach, *Roos & Roos 4938* (CAS, DS, GH, RSA, UC).

1.2 *Heterotheca sessiliflora* (Nutt.) Shinners ssp. *fastigiata* (E.L. Greene) Semple, *Phytologia* 73: 451. 1992. *Chrysopsis fastigiata* E.L. Greene, *Pittonia* 3: 296. 1898. *Chrysopsis villosa* (Pursh) Nutt. var. *fastigiata* (E.L. Greene) H.M. Hall, *Univ. Calif. Publ. Bot.* 3: 43. 1907. *Heterotheca fastigiata* (E.L. Greene) Harms, *Brittonia* 26: 61. 1974. TYPE: U.S.A. California. San Bernardino Mts, 1000-1500' [not 10000-15000 as in protologue], 15 Oct 1895, *Parish 3815* (Holotype: NDG!; isotypes: CAS!, GH!, UC!, US!)

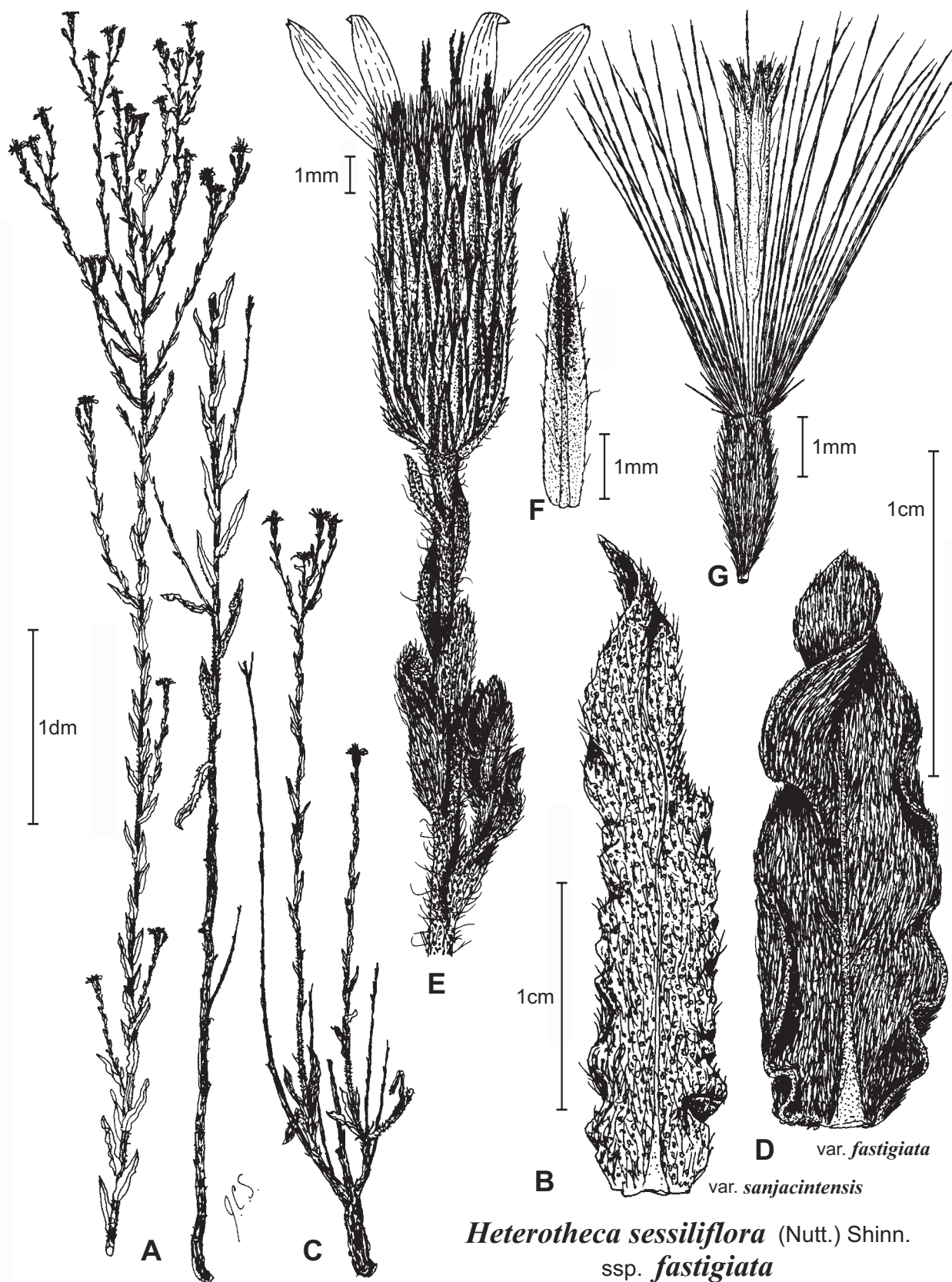
Perennial from stout woody taproots, STEMS several to many, ascending-erect, (24)-37-**60**-84-(106) cm tall, densely strigose, longer spreading hairs few to many, usually becoming densely glandular and moderately pubescent above; (25)-38-**56**-73-(90) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (12)-17-**23**-29-(38) mm long, (3)-4.7-**6**-7.2-(8.5) mm wide, subsessile, cuneate, acute, moderately to densely hispid-strigose on both surfaces, very sparsely to moderately glandular; margins entire, strigose, longer spreading hairs near base, undulate. UPPER STEM LEAVES lanceolate, sessile, reduced upward, (10)-10.6-**13.7**-16..8-(20) mm long, (2)-3.7-**4.5**-5.4-(6) mm wide, bases rounded, sparsely to densely glandular (0)-5-**16**-27-(42) glands/mm², moderately to extremely densely short-strigose (27)-48-**115**-182-(245) hairs/mm², margins usually strongly undulate, often more glandular and less pubescent than leaf surfaces. CAPITULESCENCE corymbiform to paniculiform, branches ascending, heads 5-**27**-50-(102); peduncles moderately glandular, bracts few, reduced upward, (1.9)-2-**2.9**-3.9-(6) mm long, 0.3-**0.6**-0.9-(1.5) mm wide, not foliaceous. INVOLUCRES cylindrical when fresh, cylindrical to campanulate upon drying, (7)-7.8-**9.1**-10-(12) mm high; phyllaries in 5-6 imbricate series, outer 1/5 length of inner, mid series lanceolate, usually sparsely glandular and strigose. RAY FLORETS (4)-5-**8**-12-(14), strap (3.5)-3.6-**4.7**-5.9-(8.8) mm long, (0.7)-0.9-**1.2**-1.5-(1.8) mm wide. DISC FLORETS (20)-26-**33**-40-(47), corolla ampliate, (5)-5.9-**6.4**-6.9-(7.5) mm long, lobes (0.4)-0.45-**0.5**-0.6-(0.6.5) mm long, sparsely pilose, hairs (0.2)-0.25-**0.4**-0.5-(0.6) mm long. ACHENES 1.9-**2.5**-3.1-(4.2) mm long, moderately strigose; inner pappus whorl of 25-40 barbellate bristles, (5.2)-6.2-**6.6**-7-(7.1) mm long. Chromosome number: $2n = 18$; many reports.

Flowering Period: JULY-OCTOBER-(December); very rarely in spring.

Distribution and habitat: San Gabriel, San Bernardino and San Jacinto Mts. and Mt. Palomar of southern California; arroyos and embankments in oak scrub and pine forests, rarely adventive in desert arroyo below mountains; (150)-300-1800-(2200) m ((500)-1000-6000-(7000) ft.) elevation (Fig. 14A).

Discussion: Subspecies *fastigiata* is distinguished by its undulate leaf margins (Fig. 16), heads not subtended by large peduncular bracts and generally low number of ray florets for the species. Two varieties are recognized on the basis of the density of leaf hairs and glands. In var. *fastigiata*, the leaves appear

Figure 16. Morphology of *Heterotheca sessiliflora* ssp. *fastigiata*. A-B. Var. *sanjacintensis*. A. Habit. B. Lower-mid stem leaf. C-G. Var. *fastigiata*. C. Older plant with a large rootstock and short shoots. D. Mid-upper stem leaf. E. Peduncle and head (only some florets drawn). F. Mid series phyllary with chlorophyllous zone dark. G. Mature achene with disc corolla attached. ➔



Heterotheca sessiliflora (Nutt.) Shinn.
ssp. *fastigiata*

silvery-white due to the very dense indument of tightly appressed short hairs obscuring any underlying glands. In var. *sanjacintensis*, the leaves are not nearly as densely pubescent and are more glandular giving them a light green appearance.

1.2.1 *Heterotheca sessiliflora* (Nutt.) Shinnery var. *fastigiata*

Perennial from stout woody taproots, STEMS several to many, ascending-erect, (24)-48-74-(90) cm tall, densely strigose-hispid, longer spreading hairs few, usually becoming densely glandular and moderately pubescent above; (40)-47-61-75-(80) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, 16-21-26-(32) mm long, (4)-4.6-6.1-7.6-(8.5) mm wide, subsessile, cuneate, acute, moderately (rarely densely) hispid-strigose on both surfaces; margins entire, strigose, longer spreading hairs near base, undulate. UPPER STEM LEAVES lanceolate, sessile, reduced upward, (8)-9-12-15-(18) mm long, (2)-3.3-4.5-5.6-(6) mm wide, sparsely to densely glandular (0)-2-14-25-(35) glands/mm², densely to extremely densely short-strigose (75)-110-180-245 hairs/mm², margins usually distinctly undulate, more glandular and less pubescent than leaf surfaces. CAPITULESCENCE corymbiform to paniculiform, branches ascending, heads (1)-5-31-64-(102); peduncles moderately glandular, bracts few, reduced upward, 1.9-2.4-2.8-(3) long, 0.3-0.4-0.5 mm wide. INVOLUCRES (7)-7.6-8.5-9.4-(10) m high; mid series phyllaries sparsely glandular, sparsely strigose. RAY FLORETS (3)-4-6-9-(15), strap 3.5-4.2-4.8-(5.5) mm long, (0.7)-0.9-1.0-1.2-(1.3) mm wide. DISC FLORETS 20-29-37-(47), corolla (5)-5.5-6.3-6.8-(6.9) mm long, lobes (0.45)-0.5-0.55-0.6-(0.7) mm long, sparsely pilose, hairs (0.2)-0.3-0.4-0.5-(0.6) mm long. ACHENES 2-2.4-2.7-(3) mm long, moderately strigose; inner pappus whorl of 25-40 barbellate bristles, (5.2)-6.1-6.4-6.8-(7.1) mm long. Chromosome number: $2n = 18$; many reports.

Distribution and habitat: San Gabriel Mts., San Bernardino Mts., Santa Monica Mts. (Fig. 14A); dry sandy washes in pine forests and transition chaparral, road embankments, rarely adventive in desert washes at lower elevations; sandy, rocky, alluvial or coarse granitic or gravel-adobe soils; (150)-300-1800-(2200) m ((500)-1000-6000-(7000) ft.) elevation.

Discussion: Variety *fastigiata* is distinguished by its relatively small upper stem leaves that are densely strigose and very sparsely if at all hispid on the upper and lower surfaces and that are moderately to very wavy along the margins (Fig. 16D). The rays are short for the species and few in number.

Representative Specimens: U.S.A. CALIFORNIA. *Lee 164* (UC). Los Angeles Co.: *Blake 1473* (LL), *Chamberlain s.n.* (NY), *Davidson s.n.* (NDG). Azusa, *Abrams 2653* (DS, GH(2), NY(2), RSA). Big Tujunga Cyn E Lucas Creek, *Ross 5803* (TEX). Burbank, San Fernando Valley, *Hutchinson s.n.* (RM). Cajon Cyn, *Thorne et al. 42437* (RSA). Camp Lupine near Prairie Fork, *Thorne & Olmstead 35382* (RSA). Clam Shell Cyn above Monrovia, *Ewan 3472* (DS, RSA). E of Claremont, *Munz 12171* (RSA, WTU); near Claremont, *Baker 3669* (CAN, CAS, DS, GH, LL, NY, RM, RSA, UBC, UC, UT, WTU), *Crawford s.n.* (UC), *Peirson 5274* (RSA), *Finch 211* (UBC), *Grinnell 5* (DS). N of Claremont, *Semple & Heard 8629* (JCS, MT, NY, OBI, RSA, UC, WAT). Dalton Cyn Wash near C.C.C. Camp, *Horton 237* (UC). Delta Cyn., Tujunga Trib., *Peirson 4735* (DS). Echo Park, *Brauton 706* (DS). El Monte, *Fosberg S3101* (NY). mouth of Evey Canyon, *Fosberg S1638* (PH). Glendora, *Glowenke 4315* (PH). NE of Glendora, *Horton H-237* (RM). Hollywood, Mulholland Dr., *Rose 46239* (CAS, GH, NY). NE of La Verne, *Wheeler 1372* (DS, ND). Los Angeles, *Blake 386* (GH), *Blake 1313* (LL), *Blake 1338* (LL), *Lynn s.n.* (GH); Elysian Park, *Abrams 4175* (DS, GH, NY, RSA). Monrovia, *Abrams 851* (DS). N of La Canada, *Semple et al. 5592* (JCS, MO, NY, WAT), *Semple et al. 5598* (JCS, UC, WAT). Pasadena, *Grant s.n.* (CAS, DS, IN, RSA, UC, WIS); Arroyo Seco, *Peirson s.n.* (UC), *Peirson 5263* (RSA). Pomona, *Johnson s.n.* (RSA). Near San Fernando, Pacoima Wash, *Grinnell s.n.* (DS, RSA), *Peirson 285* (JEPS, RSA). San Gabriel Mts., Switzer Camp, *Grinnell s.n.* (DS), mouth of Burro Canyon, *Ross & Fritsch 3616* (TEX), Prairie Fork Ranger Station, *Ewan 8452* (UC). San Gabriel Wash, *Ramsey & Ramsey 1912* (herb??). W Fork of San Gabriel R., *Peirson 1226* (RSA). Santa Monica Mts, *Raven 14732* (CAS, GH, JEPS, RSA). E of Van Nuys, Tujunga Wash, *Keck 1951* (DS, DS ex Carneg. Wash.), *Ewan 11048* (CAS, GH), *Peirson 5273* (RSA). Upper San Antonio Cyn, *Johnston 1701* (DS, RSA, UC(2)). Venedo Canyon, *Ross & Mistretta 3306* (NY). Near Verdugo, *Blake 1617* (LL). Riverside Co.: Banning Cyn., *Wilder 1114* (UC). N of Whitewater, *Ferris 12601* (DS), Whitewater Wash, *Roos & Roos 4657* (RSA), *Thorne, Wright & Benjamin 55400* (RSA, UC); Whitewater Cyn, *Prigge 3819* (RSA). Near Thousand Palms, *Clary 715* (CAN). San Bernardino Co.: Cajon Junction, *Semple & Chmielewski 8973* (WAT). Cajon Pass, *Grant & Grant 9013* (RSA), *Rose 36756* (WIS, WTU), Camp Cajon, *Fosberg 7068* (ND), *Raven 16692* (CAS, RSA), *Fosberg 7068* (LL). Near Forest Home, *Rusby s.n.* (NY). Hesperia, Lady Bug Cyn, *Ramsey & Ramsey 163* (RSA). Lone Pine Valley, *Thorne & Dourley 37324* (RSA). Mill Creek, *Raven &*

Snow 11070 (GH, CAN), *Munz 7582* (GH, NY, RSA, UC), *Roos s.n.* (CAS). Mt. Baldy, *Semple & Heard 8632* (JCS, RM, RSA, SD, WAT). Mohave Desert, *Spencer 626* (RSA). Patton, *Perkins s.n.* (CAS). S of Running Springs, *Semple & Chmielewski 8978* (CAS, GA, RSA, WAT, WIS). San Antonio Cyn, *Aven s.n.* (CAN), *Peirson 5274* (RSA), *Shields s.n.* (UT). San Bernardino Mts, CA-38, *Tilforth & Dourley 1052* (RSA, TEX). San Bernardino Valley, *Parish s.n.* (NDG), *Parish & Parish 570* (DS, UC), *Parish 5327* (RM), *Parish 6483* (RM, UC), *Parish 11624* (RSA, UC, WTU), *Parish & Parish s.n.* (UC). San Gabriel Mts, *Wolf 2503* (CAS, DS, RSA, UC), *Pierson 4734* (DS, RM, RSA). Santa Ana River, *Parish 6483* (TEX). White Mts., *Parish 746* (GH). NE Wrightwood, *Thorne & Tilforth 52322* (RSA). SW of Wrightwood, *Hensel 287* (ASU). Santa Barbara Co.: *Torrey s.n.* (NY). Santiago Canyon, *Bush s.n.* (GH). Ventura Co.: For.Ser. Rd, Wheelers to Nordhoff Peak, *Pollard s.n.* (CAS). Above Fillmore, *Lamb 1290* (CAN). Below Foster Park, *Pollard s.n.* (TEX); near Foster Park, *Pollard s.n.* (CAS); S of Foster Park, *Pollard s.n.* (RSA(2)), *Pollard s.n.* (CAS). Matilija Hot Springs Rd, *Semple & Chmielewski 8969* (MT, UC, WAT). Oak View, *Pollard s.n.* (CAS), *Pollard s.n.* (WTU); near Oak View, *Pollard s.n.* (RSA). Ojai Valley, *Pollard s.n.* (CAS); Lyons Hot Springs, *Pollard s.n.* (CAS). San Joaquin Cyn, *Pollard s.n.* (CAS). Sespe Creek, *Munz 9371* (RSA). South Pierpont Bay, *Pollard s.n.* (CAS). Ventura, *Pollard s.n.* (GH, WS); near Ventura, *Pollard s.n.* (CAS).

aff. var. *fastigiata*

U.S.A. CALIFORNIA. Los Angeles Co.: San Gabriel Mts., San Gabriel Canyon, *Wheeler 2134* (GH, LL). Ventura Co.: between Casitas Springs and Foster Park, *Pollard s.n.* (CAS, NY). Fillmore, *Semple & Chmielewski 8971* (WAT). Lockwood Valley, *Hall 6700* (UC).

1.2.2 *Heterotheca sessiliflora* (Nutt.) Shinnars var. *sanjacintensis* Semple, *Phytologia* 73: 452.

1992. TYPE: U.S.A. CALIFORNIA. Riverside Co.: CA-243 just S of Idyllwild Park at Manzanita Drive, 30 Sep 1987, $2n = 9_{II}$, *Semple & Chmielewski 8982* (Holotype: WAT!; isotopes (all shoots from same plant): CAS!, MT!, NY!, RSA!, UC!). PARATYPES: U.S.A. CALIFORNIA. Riverside Co.: Riverside Co.: CA-243 just S of Idyllwild Park at Manzanita Drive, 30 Sep 1987, $2n = 9_{II}$, *Semple & Chmielewski 8981* (Each shoot from a separate plant: CAN, CAS, DAO, JCS-personal herbarium, MO, OBI, RM, RSA, SD, UC, WAT).

Perennial from stout woody taproots, STEMS several to many, ascending-erect, (34)-47-67-87-(106) cm tall, moderately hispid-strigose, longer spreading hairs many, becoming more glandular above; (25)-34-53-71-(90) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (12)-19-25-30-(38) mm long, (3)-4.7-5.9-7.1-(8) mm wide, subsessile, cuneate, acute, moderately hispid-strigose on both surfaces; margins entire, strigose, longer spreading hairs near base, undulate. UPPER STEM LEAVES lanceolate, sessile, reduced upward, (11)-12-14.5-17-(20) mm long, (3.5)-4-4.7-5.5-(6.5) mm wide, moderately to densely glandular (5)-7-17-28-(42) glands/mm², moderately to densely short hispid-strigose (27)-51-79-107-(147) hairs/mm², margins very undulate. HEADS (7)-10-25-40-(58); peduncles densely glandular, bracts few, reduced upward, (1.9)-2.1-3.2-4.3-(6) mm long, 0.3-0.7-1.0-(1.5) mm wide. INVOLUCRES (7.5)-8-9.5-11-(12) mm high; mid series phyllaries moderately glandular, sparsely strigose. RAY FLORETS (5)-7-10-12-(14), strap 3.5-4.8-6-(8.8) mm long, (0.7)-1.1-1.3-1.6-(1.8) mm wide. DISC FLORETS (22)-30-36-41-(43), corolla (5.2)-5.9-6.5-7-(7.5) mm long, lobes (0.4)-0.48-0.54-0.6-(0.65) mm long, sparsely pilose, hairs 0.25-0.3-0.4-(0.6) mm long. ACHENES 2-2.6-3.4-(4) mm long, moderately strigose; inner pappus whorl of 25-40 barbellate bristles, (5.2)-6.2-6.7-7.2 mm long. Chromosome number: $2n = 18$; several reports.

Distribution and habitat: Endemic to the San Jacinto Mountains and Mt. Palomar areas of southern California (Fig. 14A); gravelly washes, road sides, open areas in *Pinus jeffreyi* woods; sandy and rocky soils; (750-) 1400-1600 m elevation.

Discussion: Variety *sanjacintensis* has a capitulescence form and very undulate stem leaves that are similar to var. *fastigiata*, but the formers leaves are far less densely strigose than those of var. *fastigiata* and the hairs are somewhat longer (Fig. 16B). Individuals with less undulate leaves are similar to var. *camphorata* of ssp. *echioides*, which occurs much farther north in California in the Coastal Range from San Mateo to San Luis Obispo Counties. Variety *sanjacintensis* has slightly larger involucre with more rays and disc florets than var. *fastigiata*, but the sample size on which these observations were made was small. This may bias the means for these traits.

Specimens Examined: U.S.A. CALIFORNIA. Los Angeles Co.: Monrovia, *Rusby s.n.* (NY). Riverside Co.: Hemet Valley, San Jacinto Mts., CA-74 5 mi E of Keen Camp, *Breedlove 950* (DS). S of Lake Hemet, *Semple & Chmielewski 8985* (JCS, RSA, UC, WAT), *Elias, Boyd & Tan 10160* (NY). Idyllwild, *Semple & Chmielewski 8981* (CAS, DAO, JCS, MO, NY, OBI, RSA, SD, UC, WAT), *Semple &*

Chmielewski 8982 (CAN, MT, NY, RSA, UC, WAT), *Spencer* 1278 (NY). Temescal Canyon, *Munz & Johnston* 11249 (LL, RSA). San Diego Co.: Palomar Mt, near observatory, *Roos* 4587 (RSA), *Tilforth & Dourley* 439 (RSA).

aff. var. *sanjacintensis*

U.S.A. CALIFORNIA. Los Angeles Co.: San Gabriel Cyn, mile above dam, *Clokey & Templeton* 5666 (CAN, KANU, NY(2), WTU). Riverside Co.: Forest Falls at Forest Home Conference Center, *White* s.n. (TEX, close to var. *echioides*). Hemet Valley, San Jacinto Mts., *Munz & Balls* 17990 (WTU).

1.3 *Heterotheca sessiliflora* (Nutt.) Shinnery ssp. *echioides* (Benth.) Semple, *Phytologia* 73: 450. 1992. *Chrysopsis echioides* Benth., *Bot. Voy. Sulphur* 25. 1844. *Chrysopsis villosa* (Pursh) Nutt. var. *echioides* (Benth.) A.Gray, *Syn. Fl. N. Amer.* 1 (2): 123. 1884. *Heterotheca echioides* (Benth.) Shinnery, *Field & Lab.* 19: 71. 1951. TYPE: U.S.A. CALIFORNIA. Bodegas, 1841, *Hinds* s.n. (Holotype: K!)

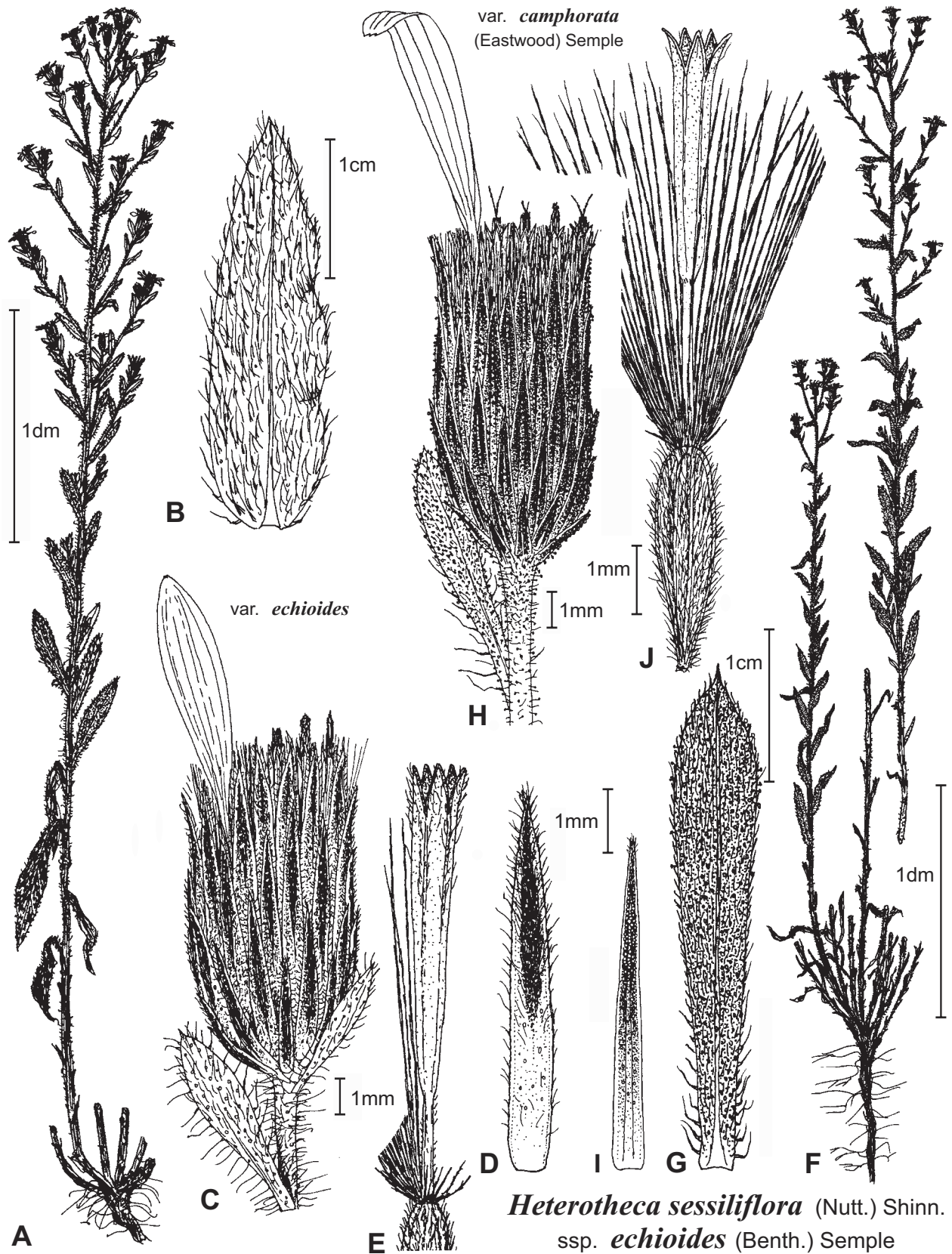
Perennial from stout woody taproots, STEMS several to many, ascending-erect, (10)-22-43-63-(98) cm tall, moderately sparsely to densely strigose-hispid, longer spreading hairs many, sometimes becoming densely glandular and sparsely pubescent above; (9)-22-43-62-(90) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (8)-15-25-35-(47) mm long, (2.4)-3.6-5.3-7-(10) mm wide, subsessile, cuneate, acute, moderately to densely hispid-strigose on both surfaces, very sparsely to moderately glandular; margins entire, strigose, longer spreading hairs near base, flat to somewhat undulate. UPPER STEM LEAVES lanceolate, sessile, reduced upward, (6.5)-8.3-16.2-24-(40) mm long, (1.5)-2.7-4.4-6.2-(7.7) mm wide, bases rounded, sparsely to densely glandular (5)-11-19-29-(50) glands/mm², sparsely to densely hispid-strigose, (5)-17-77-136-(200) hairs/mm², margins flat to somewhat undulate, spreading hairs numerous. CAPITULESCENCE corymbiform to paniculiform, branches ascending, heads (2)-4-16-27-(50); peduncles moderately glandular and sparsely to densely hispid-strigose, bracts few, usually reduced upward, (2)-3.1-5.5-7.8-(12) mm long, (0.6)-0.7-1.2-1.8-(4) mm wide, sometimes foliaceous. INVOLUCRES cylindrical when fresh, cylindrical to campanulate upon drying, (6.3)-7.2-8.6-10-(12) mm high; phyllaries in 5-6 imbricate series, outer 1/5 length of inner, mid series lanceolate, usually sparsely glandular and strigose. RAY FLORETS (6)-8-11-14-(17), strap (4.5)-5.8-7.8-9.8-(13) mm long, (0.7)-1.0-1.3-1.7-(2.4) mm wide. DISC FLORETS (9)-15-28-41-(61), corolla ampliate, (5)-5.6-6.3-7-(7.9) mm long, lobes (0.4)-0.44-0.6-0.76-(1) mm long, sparsely pilose, hairs (0.2)-0.27-0.4-0.5-(0.9) mm long. ACHENES (1.3)-2-2.6-3.3-(4) mm long, moderately to densely strigose; inner pappus whorl of 25-45 barbellate bristles, (4.9)-5.7-6.7-7.7-(9.3) mm long. Chromosome numbers: $2n = 18, 36$; many reports.

Flowering time: (May)-JULY-OCTOBER-(December); generally blooming earlier in northern California than southern California.

Distribution and habitat: Most of central and southern California west of the Sierra Nevadas and deserts; (Fig. 14A); chaparral scrub, arid prairies, pastures and fields, near washes, roadsides, disturbed areas, sandstone outcrops; sandy, gravelly soils; 10-2100 m (30-6880 ft.) elevation.

Discussion: Subspecies *echioides* is the most common and widely distributed taxon in the species. It is characterized by a coarse hispid-strigose indument on the stem and leaves, at least on the lower portion of the plant (Fig. 17). This is the only subspecies known to include tetraploids as well as diploids, with the result that there is considerable variation in involucre size. Three varieties are recognized on the basis of leaf indument features and to a lesser degree the waviness of leaf margins, stem height and the numbers of heads per shoot.

Figure 17. Morphology of *Heterotheca sessiliflora* ssp. *echioides*. A-E. **Var. *echioides*.** A. Habit of mid size plant. B. Upper stem leaf, adaxial surface; non-undulate form on left, undulate form on right. C. Head with only some florets drawn. D. Mid series phyllary with chlorophyllous zone dark. E. Disc floret with some pappus bristles and upper portion of achene. F-J. **Var. *camphorata*.** F. Habit; scale as in A. G. Mid stem leaf. H. Head with only some florets drawn. I. Mid series phyllary with chlorophyllous zone dark. J. Mature achene with disc corolla attached. ➔



The type specimen is a fragment that has mostly fruiting heads. Its stage of development makes assigning it definitively to either var. *echioides* or var. *bolanderioides* difficult. Its distribution and some leaf shape features place it with specimens of var. *bolanderioides* (Fig. 18), but its indument features place it with specimens treated here as var. *echioides*. If the type specimen can unequivocally be placed with the serpentine endemic tetraploid race, then nomenclatural changes will be necessitated since the epithet *echioides* would have to be applied to the tetraploids and a new name proposed for the common widely distributed diploid race. I do not think that this is justified with the data available.

1.3.1 *Heterotheca sessiliflora* (Nutt.) Shinnery var. *echioides*

Chrysopsis californica Elmer, Bot. Gaz. 39: 48. 1905. TYPE: U.S.A. CALIFORNIA. Santa Barbara Co., Graviota, sandy soil near beach, May 1902, *Elmer 4148* (Holotype: DS!; isotopes: MIN!, US!)

Perennial from stout woody taproots, STEMS several to many, ascending-erect, (10)-26-~~46~~-65-(76) cm tall, moderately to densely hispid-strigose, longer spreading hairs many, becoming more glandular above; (19)-26-~~44~~-62-(83) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (8)-13-~~24~~-36-(47) mm long, (2.4)-3-~~4.7~~-6.5-(7.7) mm wide, subsessile, cuneate, acute, moderately to densely hispid-strigose on both surfaces, sparsely to moderately glandular; margins entire, strigose, longer spreading hairs near base, sometimes somewhat undulate. UPPER STEM LEAVES narrowly ovate to lanceolate, sessile, reduced upward, (6.5)-8.1-~~13.5~~-19-(25) mm long, (1.5)-1.9-~~3.5~~-5.1-(6.5) mm wide, moderately to densely glandular (10)-12-~~19~~-27-(42) glands/mm², densely to very densely hispid-strigose (100)-120-~~147~~-173-(200) hairs/mm², margins very undulate. CAPITULESCENCE corymbiform to paniculiform; heads (3)-7.4-~~19~~-31-(50); peduncles moderately glandular, bracts few, reduced upward, (3.5)-3.7-~~4.4~~-5.1-(6) mm long, 0.6-0.7-~~1.0~~-1.3-(1.5) mm wide, rarely foliaceous. INVOLUCRES (6.3)-7-~~8.1~~-9.3-(10) mm high; mid series phyllaries moderately glandular, sparsely to moderately strigose. RAY FLORETS 7-~~10~~-12-(14), strap 5.2-5.9-~~7.6~~-9.3-(11) mm long, (0.8)-1.0-~~1.2~~-1.5-(1.8) mm wide. DISC FLORETS (9)-10-~~23~~-37-(61), corolla (5)-5.4-~~6.0~~-6.5-(6.9) mm long, lobes (0.4)-0.44-~~0.52~~-0.6-(0.75) mm long, moderately pilose, hairs 0.18-0.25-~~0.35~~-0.47-(0.63) mm long. ACHENES 1.8-2.5-~~3.1~~-3.7-(4) mm long, moderately strigose; inner pappus whorl of 25-45 barbellate bristles, (4.9)-5.5-~~6.3~~-7.1-(7.7) mm long. Chromosome number: $2n = 18$; many reports.

Distribution and habitat: Coastal ranges from Marin Co. to southern San Diego Co., California, east around the central valleys, Tehachapi Mts. and lower elevations in the Transverse Mts. (Fig. 14A); grassy slopes, chaparral scrub, arid prairies, pastures and fields, near washes, dry stream beds, roadsides, disturbed areas, sandstone outcrops; sandy, gravelly soils; 10-2100 m (30-6880 ft.) elevation.

Discussion: Variety *echioides* is the “weedy” race of the species. It is distinguished by its indument of coarse spreading hairs on the upper stem, peduncles, leaves and bracts (Figs. 17A-C). The capitulescence in larger plants is generally elongate paniculiform. Stems can be more than a meter tall, although plants half that height are more common. It is difficult to distinguish from less typical individuals of var. *camphorata*, which is much less hispid and more glandular in the upper portions of the shoots, and var. *bolanderioides*, which has larger heads and longer hairs on the corolla lobes and is usually much shorter in stature. In the southern part of the range and in the Tehachapi Mts. the upper stem leaves of var. *echioides* are somewhat undulate (solid triangles, Fig. 14A), but this is not the case further north in its range.

Where the range of var. *echioides* is sympatric with ssp. *fastigiata*, individuals that are most likely hybrids have been collected a number of times. These have a more appressed indument that usual for var. *echioides*, but not the tightly appressed indument of var. *fastigiata*. The waviness of the leaf margins is also intermediate in hybrids between the two taxa.

Specimens examined: U.S.A. CALIFORNIA. Warner's Ranch, *Hayes s.n.* (NY). San Joaquin Plains, *Greene s.n.* (GH). Kings Mt., dry ground San Joaquin Valley, *Rose s.n.* (LL, WIS). Calif. O.F.F. For. San Joaquin, west side and Valley Floor, *Short & Johnson S-168* (RM). Alameda Co.: Tesla Rd. 8 mi from Livermore, *Howell 10837* (CAS). Contra Costa Co.: Antioch, *Munz 12189* (NY, RSA,

WTU). Mt. Diablo, *Schreiber* 940 (UC). Fresno Co.: *Bioletti s.n.* (UC). N of Priest Valley, *Semple et al.* 5653 (MO, NY, SFS, USF, WAT). Kern Co.: NE of Bakersfield, *Munz* 12245 (CAS, NY, RSA, WTU). N of Choice Valley School, *Twisselmann* 5983 (CAS(2)), *Twisselmann* 11617 (CAS(2), DS, JEPS, RSA, TEX). near Ft. Tigon, *Rothrock* 197 (GH), *Rothrock* 272 (GH). NW of Frazier Park, *Ferren* 1713 (UC, WAT). Kelso Valley, *Twisselmann* 3066 (CAS(2)). just above Kernville, *Twisselmann* 9033 (CAN, CAS, TEX). W of Lorraine, *Hardham* 2578 (CAS). Lynns Valley, *Farnsworth* 241 (TEX). N end Lynns Valley, *Farnsworth* 308 (CAS, TEX), *Twisselmann* 12743 (CAN, CAS). N of Panama, *Twisselman* 4764 (CAS(2)). W of Rock Corral, *Twisselmann* 12749 (CAN, CAS, TEX). Rosedale, *Abrams* 477 (DS), *Davy* 2920 (UC). San Emigdio Range, Cuddy Valley, *Twisselmann* 12778 (CAS(2), JEPS, RM, RSA), *Twisselmann* 12779 (CAS, JEPS, RSA), *Twisselman* 2304 (CAS), *Twisselmann* 2305 (CAS). South Piute Mts., *Shevock* 8860 (CAS). Tehachapi, *Brandegees s.n.* (UC), *Curran s.n.* (WS). S of Tehachapi, Tehachapi Mt. Park, *Semple & Chmielewski* 8959 (FSU, RSA, TUFTS, UAC, WAT), *Semple* 10483 (WAT). Tehachapi Mts., *Minthorn s.n.* (RM), *Twisselmann* 3999 (CAS(2)). Walker Basin, *Semple & Chmielewski* 8961 (MO, MT, UC, WAT). S of Walker Basin, *Semple & Chmielewski* 8960 (WAT). SE of Weldon, *Twisselmann* 10213 (CAN, CAS(2)). W of Woody, *Semple & Chmielewski* 8946 (WAT). Los Angeles Co.: Chilao, *Ewan* 8334 (GH(2), ND). E of Chatsworth Park, *Peirson* 2219 (RSA). El Segundo Dunes, *Sanders* 7396 (TEX, WAT). Fairmont, *Hall* 6713 (UC). E of Gorman, *Cross* 14 (TEX). Los Angeles, *Hosse s.n.* (DS), *Hasse* 48101 (NY). Newhall, *Munz* 7786 (NY, RSA, UC), *Peirson* 4163 (DS, RSA). N of Newhall, *Henrickson* 8078 (ASU, RSA). Pasadena, *McClatchie s.n.* (DS). Peace Valley Meadow, *Hodgson* 160 (RM). Pomona, *Davy* 2878 (UC). San Antonio Cyn, *Shields s.n.* (UT). Santa Monica Mts., *Moxley* 819 (DS). Saugus, *Wolf* 4081 (DS, RSA, WTU). San Gabriel Mts., *Ewan* 8334 (LL); Chiles Flat, *Grimmell s.n.* (DS). Tejon Dist, Peace Valley Meadow, *Hodgson* 65125 (CAS). Madera Co.: Chowchilla, *Hoover* 687 (CAN), *Hoover* 1608 (CAN). Mariposa Co.: Hennessey Trail, *Congdon s.n.* (MIN). Merced Co.: Livingston, *Hoover* 1592 (CAN). N of Livingston, *Crampton* 490 (UC). Monterey Co.: Carmel Highlands, opp. Yankee Pt., *Balls* 12106 (RSA). W of Greenfield, *Howell* 11559 (CAS, NY, RSA), *Semple & Heard* 8597 (ASU, MO, OBI, RM, RSA, UAC, WAT). E of Jamesburg, *Howell* 11569 (CAS). NE of Jamesburg, F.S.H. Nat. Hist. Res., *Cook & Cook* 387 (CAS), *Durham* 658 (DS). Between Jamesburg and Tassajara Hotsprings, *Thomas* 1209 (DS, RSA). Jolon, *Vasey* 257 (NY), below Jolon, *Mason* 8153 (UC). King City, *Samontacchi* 638 (UC(2)). NE of King City, *Rose* 35612 (CAS, DS, GH, NY, RSA, UC). Hills between Jolon and King City, *McMurphy s.n.* (DS, RSA). Partuipitar Ridge, *Howitt* 1831 (CAS). Priest Valley, *Howell* 40098 (CAS). W of Priest Valley, *Semple & Chmielewski* 8943 (WAT). San Lucas, *Degener* 4678 (NY). Santa Lucia Mts., E of "The Indians", *Howell* 5638 (CAS); Jolon Rd to sea, *Hardham* 5230 (CAS); E of Twin Peaks, *Dudley s.n.* (DS); Upper Big Creek, Anila Trail, *Dudley s.n.* (DS). Near Soledad, *Howell & True* 49109 (CAS). Tassahara Hot Springs, *Cox s.n.* (DS). Orange Co.: N of Balboa, *Johnston s.n.* (RSA). inland from Balboa Beach, *Peirson* 5086 (RSA). Newport Bay, *Booth s.n.* (CAN). Newport Lagoon, *Booth s.n.* (RSA, UC), *Ewan* 7737 (LL). Rancho Santa Ana, Botany Garden, *Howell* 744 (RSA). Sulphur Hill, *Reed* 5502 (NY, RSA). Santa Ana Canyon, *Howell* 3109 (CAS, DS, GH), *Howell* 3113 (CAS, LL). Riverside Co.: *Grant* 4429 (NY). Banning, *Gilman* 33 (UC), *Peebles* 111 (LL). Hemet, *Roos s.n.* (ASU). Idyllwild, *Semple & Chmielewski* 8983 (ALTA, CAN, MT, RSA, WAT). NW of Murrietta, *Keck* 265 (UC). Radec, *Jaeger s.n.* (DS, RSA). Ramona, *Brandagee s.n.* UC(2). San Jacinto, *Gregory* 38839 (CAN). San Jacinto Mts., Tranquility Trail, *Spencer* 2368 (GH). Between Temescal and Elsinore, *Baker s.n.* (RSA). Whitewater, *Parish* 746 (DS). San Benito Co.: N of Bitterwater on rd to New Idria, *Raven* 8813 (CAS). Hernandez, *Howell* 11557 (CAS). ENE of Hernandez, Clear Cr Rd., *Solbrig, Sharmsmith & Chisaki* 2831 (GH). between Hollister and Vinyard School, *Ferris & Ernst* 13069 (DS, CAN, NY). Paicines, *Rose* T 58 (WIS). S of Paicines, *Howell* 8040 (CAS). Priest Valley, *Abrams* 7678 (DS). Coalinga Rd 0.5 km SE of CA-25, *Semple & Chmielewski* 8940 (WAT). San Bernardino Co.: Bloomington Plains, *Wilder* 896 (UC). Cajon Pass, *Wheeler* 83 (DS). N of Crestline town limit, *Semple & Chmielewski* 8975 (DAO, MO, MT, NY, RSA, WAT). Near Cucamonga, *Walder* 896 (RSA). Horsethief Cyn, *Ewan* 5187 (LL). Mentone, *Abrams* 2934 (DS, NY). Mohave Desert, *Spencer* 628 (GH(2), NY). San Bernardino, *Parish s.n.* (NDG), *Parish s.n.* (NY), *Parish* 570 (GH, PH). Near San Bernardino, *Parish* 2015 (DS), *Parish* 5122 (NY). San Bernardino Valley, *Parish & Parish* 2015 (CAN). San Diego Co.: *Alderson s.n.* (GH). CA-76 W of CA-79, *Semple & Chmielewski* 8986 (JCS, RSA, WAT). Warners Springs, *Coombe s.n.* (CAS), *Stokes s.n.* (DS). Witch Creek, *Alderson* 247 (UC), *Alderson* 721 (UC). San Luis Obispo Co.: *Miles s.n.* (GH). S of Arroyo Grande, Black Lake Cyn, *Keil* 17902 (ASU, OBI). Atascadero, *Hardham* 1176 (RSA). Atascadero, *Semple et al.* 5639 (JCS, MO, TUFTS, UC, WAT). Avenales Wildlife Area, Shell Cr. Rd, *Keil* K14191 (ASU, OBI). Calf Cyn., *Hoover* 9587 (CAS, OBI). Carrisa Plains, Carrisa Plain School, *Semple & Chmielewski* 8962 (KANU, RSA, UAC, WAT), *Twisselmann* 7914 (TEX); Lewis Ranch, *Twisselmann* 7912 (JEPS, RSA), *Twisselmann* 7914 (CAS(2), IND, KANU). Creston, *Hoover* 10066 (CAS, OBI, UC). N of LaPanza, *Hoover* 6313 (CAS, OBI, UC). Summit of Palo Prieta Cr., *Twisselmann* 536 (CAS), *Twisselmann* 793 (CAS). Paradise Valley, *Hardham* 1296 (CAS). W of Paso Robles, Oak Flat, *Harham* 1432 (RSA). San Luis Obispo, *Cobb s.n.* (WTU). San Miguel, *Knoche* 2425 (DS). Santa Lucia Mts, York Mt., *Hardham* 1354 (CAS). Templeton, *Howell* 643 (RSA), *Abrams* 5050 (DS, NY, RSA). S of Templeton, *Howell* 3004 (CAS, JEPS, UC). Tremblor Range, near summit of Gillis Cyn, *Twisselmann* 2352 (CAS(2)). CA-58 (MP 0.75) just E of CA-229, *Semple & Chmielewski* 8963 (CAS, FSU, MT, TEX, WAT). San Mateo Co.: Menlo Park, *Dudley s.n.* (DS). Santa Barbara Co.: *Torrey s.n.* (NY(2)). Cuyama Cyn just below Buckhorn Canyon, *Hoover* 11636 (OBI). Ellwood, *Eastwood* 222 (CAS, GH, NY, UC). Gaviota, *Brandegees s.n.* (UC). NE of Lompoc, behind La Purisima Mission, *Breedlove* 4158 (CAS, DS), *Pollard s.n.* (CAS). Orcutt, *Abrams* 7646 (DS). San Marcos Pass, *Greyerson s.n.* (DS). Santa Ynez Mts., *Cooper s.n.* (NY). SE of Venticopa, *Semple et al.* 5635 (ALTA, MO, JCS, UC, WAT). Santa Clara Co.: NW of Agule Spring, Calif. O.F.F. For., *Sindel* 366 (RM, UC). Menlo Park, *Abrams* 2228 (DS). Mt. Hamilton, W slope, *Sharmsmith* 1348 (WTU), *Sharmsmith* 1357 (LL), *Sharmsmith* 1411 (UC), *Smith s.n.* (CAN). Los Altos, *Campbell s.n.* (CAS). Palo Alto, Stanford University, *Elmer* 1753 (NY). Saratoga, *Abrams s.n.* (RSA, WTU). E of San Jose, rd to Mt. Hamilton, *Howell* 11511 (GH). Santa Cruz Mts., Page Mill Rd., *Blake* 11759 L (LL), *Smith* 1126 (GH). Solano Co.: near Vacaville, *Jepson s.n.* (UC), *Jepson* 14682 (CAN). Vaca Mts., Weldon Canyon, *Jepson s.n.* (PH, WTU), *Jepson* 14681 (JEPS, UC). Stanislaus Co.: Gobin Ranch. *Hoover* 696 (JEPS, UC). Near Modesto, *Bioletti s.n.* (CAN). Salida Stat., *Congdon s.n.* (WS). Tulare Co.: Bea Cr., *Purpus* 4069 (UC). below Three Rivers, *Abrams* 7721 (DS, NY). Visalia,

Congdon s.n. (DS), *Congdon s.n.* (DS). Ventura Co.: Oak View, *Pollard s.n.* (CAS). Ojai, *Fauntleroy s.n.* (CAS), *Pollard s.n.* (CAS). Oxnard, *Davy 7802* (UC). SE of Venticopa, *Semple et al. 5634* (CAN, MO, MT, NY(2), OBI, UAC, USF, WAT).

aff. var. *echioides* (approaching var. *camphorata* or var. *fastigiata*)

U.S.A. CALIFORNIA. Kern Co.: N of Choice Valley School, *Twisselmann 1537* (CAS(2), CAN). Los Angeles Co.: near Redondo, *McClatchie s.n.* (NY). Saugus, *Munz & Johnston 11135* (RSA). Upland, *Johnston s.n.* (RSA). Monterey Co.: Carmel Highlands, opposite Yankee Pt., *Balls 12165* (CAS, DS, RSA). Santa Lucia Mts., above Posts, *Jepson 2589* (CAN, WS). San Benito Co.: 15.2 mi SW of Paicines, rd to Panoche, *Keck 1827* (CAS, DS). San Bernardino Co.: Horsethief Cyn, 1 mi below summit, *Ewan 5187* (DS). San Bernardino Valley, *Parish s.n.* (UC). Vicinity of San Bernardino, *Parish 5121* (DS, NY, RSA). San Luis Obispo Co.: San Luis Obispo, *Palmer 204* (NY(3, two on same sheet)). Santa Barbara Co.: Ellwood, *Eastwood 222* (CAS, GH, NY, UC). Santa Clara Co.: Mt. Hamilton, *Sharsmith 1354* (UC). Saratoga, *Davy 337* (UC). Santa Cruz Co.: top of Jamison Crk Rd., *Hesse 1387* (CAN). Ventura Co.: Fillmore, *Semple & Chmielewski 8971* (WAT). Oak View, *Pollard s.n.* (CAS).

1.3.2 *Heterotheca sessiliflora* (Nutt.) Shinnery var. *camphorata* (Eastw.) Semple, Phytologia 73:

451. 1992. *Chrysopsis camphorata* Eastw., Zöe 5: 81. 1900. *Chrysopsis villosa* (Pursh) Nutt. var. *camphorata* (Eastw.) Jepson, Man. Fl. Pl. Calif. 1036. 1925. *Heterotheca camphorata* (Eastw.) Semple, Canad. J. Bot. 58: 148. 1980. TYPE: U.S.A. CALIFORNIA. Santa Cruz Co.; Glenwood, Jul 1900, *Davis s.n.* (Holotype: CAS!; isotopes: DS!, GH(2)!, NY(2)!, RM(3)!, UC!, US!)

Chrysopsis vestita E.L. Greene in Baker, West. Amer. Plants 1: 8. 1902. TYPE: U.S.A. CALIFORNIA. Santa Clara Co.: Palo Alto, occasional near the marshes, 1-2 ft., 15 Sep 1902, *Baker 1670* (Holotype: NDG, not seen; isotype: LL!)

Perennial from stout woody taproots, STEMS several to many, ascending-erect, (29)-35-55-75-(98) cm tall, moderately hispid-strigose below becoming densely glandular above and less hispid-strigose; (30)-44-58-72-(90) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (12)-14-21-29-(37) mm long, (3.5)-3.7-5.5-7.3-(10) mm wide, subsessile, cuneate, acute, moderately hispid-strigose on both surfaces; margins entire, strigose, longer spreading hairs near base, undulate. UPPER STEM LEAVES lanceolate, sessile, reduced upward, (7)-8.9-11.6-14.2-(16) mm long, (1.5)-2.7-3.9-5.2-(6) mm wide, moderately to densely glandular, (5)-7-19-31-(50) glands/mm², sparsely to moderately hispid-strigose (5)-11-29-47-(70) hairs/mm², margins flat. CAPITULESCENCE corymbiform to paniculiform; heads (5)-9-20-31-(46); peduncles densely glandular, bracts few, reduced upward, (2)-2.9-4.1-5.3-(6) mm long, 0.8-1.1-1.5-1.8-(2.1) mm wide. INVOLUCRES (6.5)-7-8.0-8.9-(10) mm high; mid series phyllaries moderately to densely glandular, very sparsely strigose. RAY FLORETS (6)-7-10-13-(15), strap (5)-5.7-7.0-8.4-(9) mm long, (0.8)-1.1-1.5-1.8-(2.1) mm wide. DISC FLORETS (12)-16-28-40-(55), corolla 5.5-6.1-6.6-(7.1) mm long, lobes 0.4-0.5-0.6-(0.7) mm long, very sparsely pilose, hairs 0.4-0.5-0.6-(0.65) mm long. ACHENES (1.3)-1.5-2.1-2.7-(3.1) mm long, sparsely to moderately strigose; inner pappus whorl of 25-40 barbellate bristles, (5.2)-5.7-6.4-7.1-(7.7) mm long. Chromosome number: $2n = 18$, many reports; 36, several reports.

Distribution and habitat: Coastal ranges of central California from Santa Clara to northern San Luis Obispo Counties (Fig. 14B); chaparral mixed with *Pinus sabiniana*, dry open hills with oaks, grassy sandy flats, fields, grassy roadsides, washes; sand, gravelly soils; 550-1300 m (1800-4300 ft.) elevation.

Discussion: Variety *camphorata* is distinguished on the basis of having usually densely glandular and sparsely hispid upper stems, leaves and capitulescence parts (Fig. 17F-I). The lower stem and leaves are essentially similar to those plants from northern populations of var. *echioides* being moderately to densely hispid-strigose. There is a great range in involucre size in var. *camphorata*. Some plants with larger heads are diploids and some are tetraploids.

The variety appears to have been much more common in the past in areas of San Mateo and Santa Clara Counties that were cleared of forest leaving extensive areas of disturbed sandy soil. Now that these areas have reforested to some extent, the habitat for the variety is no longer as common.

Specimens examined: U.S.A. CALIFORNIA. "California," *Coulter 349* (GH). Monterey Co.: Arroyo Seco, *Hardham 1409* (CAS). Arroyo Seco Rd 10.6 km SW of Co.Rd-G16, *Semple & Chmielewski 8934* (WAT), 29.6 km SW of Co.Rd-G16, *Semple & Chmielewski*

8937 (WAT). Big Sur, *Baker* 7889 (LL, UC); Mount Manuel, *Kelly s.n.* (UC). Cachagua Valley, *Plowman* 7916 (CAS). SW Camp Stephani, *Wheeler* 4315 (LL, ND, RSA, WTU). S of Carmel, *Schallert* 1507 (NY). E of Carmel Valley village, *Semple & Chmielewski* 8932 (WAT). SE of Carmel Valley, *Keil* 11949 (ASU, OBI). Carmel Valley Rd, MP 26.7, *Semple & Chmielewski* 8933 (WAT). Chima Camp, Pine Ridge trail, *Baker* 7858 (LL). F.S.Simes Hastings Nat.Hist.Res., *Cook & Cook* 286 (CAS), *Cook & Cook* 404 (WS), *Durham s.n.* (DS), *Durham s.n.* (WIS ex POM). W of Greenfield, *Semple & Heard* 8603 (WAT); *Semple & Heard* 8606 (WAT). E of Jamesburg, *Howell* 11583 (CAS, LL). N of Liggett-Hunter Military Base, *Semple & Chmielewski* 8938 (WAT). Los Padres For & Range Expt. Station, *Samontacchi* 671 (RM, UC). Near public campground on Nacimiento Cr., *Rodin* 5985 (OBI). Pacific Grove, *Lemmon s.n.* (UC). Behind Posts, *Heckard* 2830 (NY). Santa Lucia Mts., *Howitt* 1394 (CAS), *Howitt* 1398 (CAS), *Vortriede s.n.* (UC); upper Chachagua Creek, *Dudley s.n.* (DS); Cone Peak Trail, *Hardham* 2631 (CAS), *Twisslemann* 4095 (CAS(2)); above Jolon Valley, *Ewan* 8979 (CAS, UC, WTU); Bald Mt., *Hardham* 2488 (RSA); Rooster Creek, *Hardham* 3895 (RSA); Santa Lucia Camp, *Howell* 651 (RSA), *Howell* 3013 (JEPS, LL, RSA, UC); Tassajara, *Dudley s.n.* (DS). San Benito Co.: Harlan Pk., *Ferris & Wiggins* 9808 (CAS, DS, GH, UC, WTU). Hwy-25 NW of HWY-246, *Keil* 17929 (ASU, OBI, TEX). SE of Paicinese, *Keck* 1827 (DS). above Picacho, *Twisslemann* 12833 (CAN, CAS(2)). Pinnacles, *Eastwood* 6744 (CAS), *Ehlers* 1118 (CAN), *Howell* 11534 (CAS, DS), *Raven* 8808 (CAN, CAS, WS), *Rose* 33328 (IN, LL, WIS), *Rose* 35621 (CAS, DS, NY, RSA, UC, WTU). San Luis Obispo Co.: Upper Arroyo Grande, 5 mi above County Park, *Hoover* 6293 (OBI). San Luis Obispo, *Palmer s.n.* (PH). Santa Clara Co.: Loma Prieta Peak, *Elmer* 4981 (NY). Mt. Hamilton region, San Antonia Valley Rd, *Semple & Chmielewski* 8923 (WAT). Mt. Hamilton, *Rose* 37655 (WTU), *Semple & Chmielewski* 8924 (WAT), *Semple & Chmielewski* 8926 (WAT), *Sharsmith* 3889 (LL, UC); Madrone Springs Rd, *Abrams* 6696 (DS, NY). New Almaden, *Sindel* 404A (UC), *Belshaw* 2229 (UC(2)). Palo Alto, *Baker* 1670 (GH, NY, UC); Stanford University, *Dudley s.n.* (DS), Page Mill Rd NE of CA-35, *Semple & Chmielewski* 8916 (WAT). San Lorenzo R Cyn, *Hesse* 1381 (CAN, WS). Saratoga, *Davy* 335 (UC(2)), *Spencer* {319} (GH, NY, RSA). N of Scotts Valley, *Semple & Chmielewski* 8922 (WAT). Stevens Creek Rd., *Randall s.n.* (DS(2), RSA). Santa Cruz Co.: Ben Lomond, *Hesse* 358 (CAN), *Hesse* 1201 (CAN). Boulder Crk, *Hesse* 1382 (CAN), *Hesse* 1390 (CAN), *Hesse* 2685a (CAN), *Walker* 817 (RM, UC). Brookdale, *Freile s.n.* (CAS). Clear Crk, *Elhers* 1010 (CAN). Below Eccles, *Dudley s.n.* (DS(2)). Glenwood, *Davis s.n.* (CAS, DS(2), GH), *Davis s.n.* (CAS, GH), *Davis s.n.* (CAS, UC). S of Glenwood, *Rose* 35576 (CAS, RM). W of Glenwood, summit of Mt. Charlie Ridge, *Bacigalupi & Ferris* 2703 (GH, UC). Mt. Hermon, *Cox s.n.* (DS), *Howell* 11614 (GH, RSA), *Reed* 9045 (RSA). S of Mt. Hermon, *Mason* 3999 (UC). near Lexington, *Dudley s.n.* (DS). S of Los Gatos, *Semple & Chmielewski* 8920 (WAT). Montezuma, *Spencer* {319} GH(2). Rd. from Santa Cruz to Los Gatos, *Howell* 4382 (CAS). Santa Cruz, *Hartweg* 1773 (NY(2)). Scotts Valley, *Semple & Chmielewski* 8921 (WAT). W of Scott Valley, *Semple et al.* 5668 (CAN, JEPS, JCS, MT, MO, NY, OBI, UAC, WAT), *Yates* 4047 (RM, UC(2)). Santa Cruz Mts., *Anderson s.n.* (JEPS, RM, UNCC, UT), *Davis* 88 (UC), *Davis* 123 (UC). Stanislaus Co.: Del Puerto Canyon, *Hoover* 3835 (LL, UC).

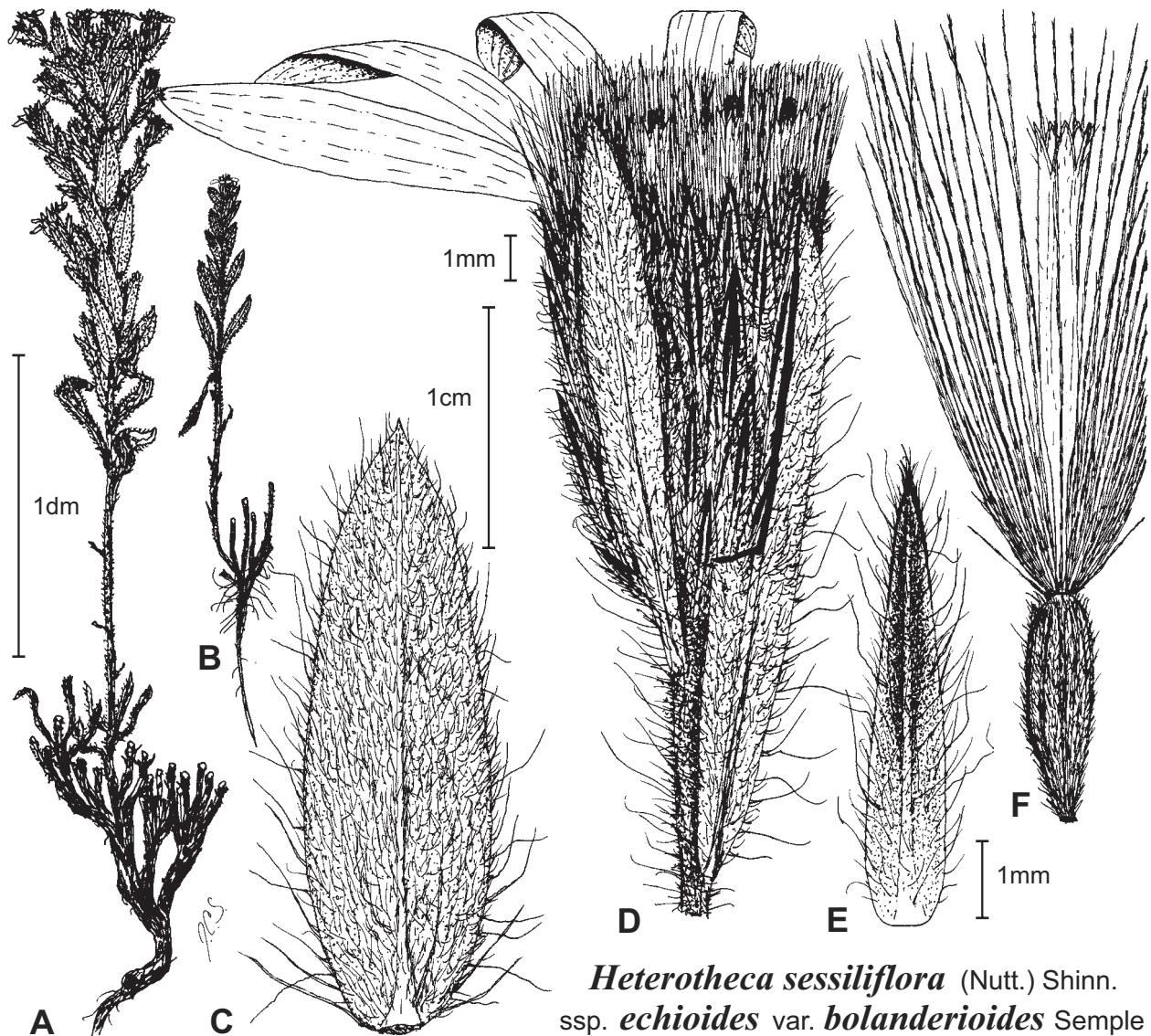
aff. *camphorata* (either close to var. *echioides* or odd growth form.)

U.S.A. CALIFORNIA. Contra Costa Co.: Antioch, *Lee & Carter* 1624 (CAN). Fresno Co.: W of Priest Valley, *Semple & Chmielewski* 8944 (WAT). western part of county, Los Gatos Cyn, *Twisslemann* 12814 (CAN). Monterey Co.: Big Sur, *Eastwood* 14030 (CAS). Chews Ridge, *Clausen* 891 (DS). Between Jamesburg and Tassajara Hot Springs, *Robbins, Dawson & Ornduff* 3791 (CAN). SW of King City, *Hardham* 10467 (CAS). San Benito Co.: SE of Paicines, *Keck* 1827 (RSA). Santa Cruz Co.: Bear Creek Cyn, *Hesse* 1385 (CAN). Head of Aplos Creek, *Abrams* 3073 (RSA). San Luis Obispo Co.: along road from Arroyo Grande & Huasna, *Eastwood* 14995 (CAS, LL). CA-58 at Shell, Camatti, Navajo and San Juan Crks, *McLeod* 1340 (OBI).

1.3.3 *Heterotheca sessiliflora* (Nutt.) Shinnery var. *bolanderioides* Semple, Phytologia 73: 450.

1992. TYPE: U.S.A. CALIFORNIA. Contra Costa Co., Charles Tilden Reg. Park, Vollmer Peak. Scattered population along ridge top, in rocks and loose gravel in grassy area between shrubs, 16 Aug 1990, 2n = 36, *Semple, Suario & Ahmed* 9339 (Holotype: UC!; isotypes: CAN!, CAS!, MO!, NY!, RSA!, WAT!). PARATYPES: U.S.A. CALIFORNIA. Santa Clara Co.: Page Mill Rd. NE of CA-35, 21 Sep 1987, *Semple & Chmielewski* 8915 (WAT). Marin Co.: San Geronimo, grass covered rocky ridge N. of golf course, common on slope above and below Nicasio valley road, large number of plants, 15 Aug 1990, *Semple, Suario & Ahmed* 9333 (WAT). Santa Cruz Co.: W of Palo Alto, CA-35 17.5 km SE of CA-84, *Semple & Chmielewski* 8918 (WAT); CA-35 NW of Saratoga, high elevation, *Semple & Semple* 5670 (JCS, MO, MT, UC, USF, WAT).

Perennial from stout woody taproots, STEMS several to many, ascending-erect, (17)-20-27-33-(44) cm tall, moderately to densely hispid-strigose, long spreading hairs many, becoming more glandular above; (9)-13-25-36-(46) nodes below capitulescence. LOWER STEM LEAVES lanceolate, (15)-20-30-39-(46) mm long, (4.5)-4.7-5.9-7.0-(8.3) mm wide, subsessile, cuneate, acute, moderately to densely hispid-strigose on both surfaces; margins entire, strigose, longer spreading hairs near base, flat. UPPER STEM LEAVES (ob)lanceolate, sessile, little reduced upward, (11)-15-23.6-33-(40) mm long, (3.5)-4.6-5.9-7.2-(7.7) mm wide, moderately to densely glandular (7)-10-20-27-(40) glands/mm², moderately to densely long hispid-strigose (8)-15-38-62-(80) hairs/mm², margins flat. CAPITULESCENCE corymbiform; heads (1)-3-7-11-(13); peduncles sparsely to moderately glandular and moderately to densely hispid-strigose, bracts few, sometimes little reduced upward,



Heterotheca sessiliflora (Nutt.) Shinn.
ssp. *echioides* var. *bolanderioides* Semple

Figure 18. Morphology of *Heterotheca sessiliflora* ssp. *echioides* var. *bolanderioides*. A. Shoot and rootstock of mid-size plant. B. Shoot of depauperate plant. C. Mid-upper stem leaf; leaves can be narrower or more densely hairy. D. Head and subtending bracts and leaves, upper portion of the lower leaf has been removed; only some florets shown. E. Mid series phyllary with chlorophyllous zone dark. F. Mature achene with disc corolla attached; pappus bristles not fully shown on right side.

(4)-5.7-8.1-10.4-(12) mm long, 0.8-1.6-2.4-(4) mm wide. INVOLUCRES (7)-8.6-9.9-11.1-(12) mm high; mid series phyllaries moderately glandular, sparsely to densely strigose. RAY FLORETS (7)-10-13-16-(17), strap (4.5)-6.2-8.7-11.1-(13) mm long, (0.7)-1.0-1.4-1.9-(2.4) mm wide. DISC FLORETS (23)-26-35-44-(55), corolla (5.6)-6.3-6.9-7.5-(7.9) mm long, lobes (0.4)-0.6-0.75-0.9-(1) mm long, moderately pilose, hairs 0.4-0.5-0.7-(1.0) mm long. ACHENES (1.9)-2-2.6-3.1-(3.8) mm long, moderately to densely strigose; inner pappus whorl of 25-40 barbellate bristles, (5.4)-6.6-7.6-8.6-(9.3) mm long. Chromosome number: $2n = 36$; many reports.

Distribution and habitat: Endemic to serpentine soils mostly on hill and mountain tops surrounding San

Francisco Bay (Fig. 14B); grassy slopes, rocky hilltops and hillsides, 150-675 m (500-2200 ft.) elevation.

Discussion: Variety *bolanderioides* is the only predominantly or exclusively tetraploid member of the species (Fig. 18). As the name indicates, it is similar to ssp. *bolanderi* in which most collections of the taxon have been placed in the past (Fig. 19). Individuals of var. *bolanderioides* can be similar in indument to diploids (rarely tetraploids) of var. *camphorata*, which has relatively few hairs (for the subspecies) on its upper stem and branch leaves, and to diploids of var. *echioides*, which usually has a leaf indument of dense spreading to appressed hairs obscuring the underlying glands and smaller involucre. It is uncertain whether var. *bolanderioides* is a tetraploid derivative of var. *echioides* or whether it may be an allopolyploid involving ssp. *echioides* and ssp. *bolanderi*. As noted above in the discussion of var. *echioides*, there is a possibility that the type specimen of the subspecies is actually a member of this tetraploid race. If this is ever confirmed, then the name *bolanderioides* would go into synonymy under the name *echioides* and another name would have to be adopted for the common diploid race of the subspecies.

Specimens examined: U.S.A. CALIFORNIA. Alameda Co.: *Tinsley s.n.* (UBC). Contra Costa Co.: Berkeley, Grizzly Peak, *Jepson 4173* (CAN), *Tracy 1950* (WTU); hill rear of Blind. Inst., *Walker 164* (UC); hills back of Berkeley, *Copeland 1121* (WIS); Strawberry Cyn., *Jepson 9826* (CAN). Berkeley Hills, Charles Tilden Reg. Park, *Semple, Suario & Ahmed 9339* (WAT); summit of Sugar Loaf, *Jepson 19013* (CAN), Upper Telegraph Cyn., *Ewan 7975* (UC). North Berkeley Hills, *Howell 5416* (CAS, RSA). Oakland Hills, *Howell 1432* (CAS), *Mann s.n.* (GH). SE of Redwood Ridge, *Constance 429* (UC). Marin Co.: *Edwards s.n.* (NY). Bolinas Ridge, *Morley 83* (GH, NY, RM, UC). Fairfax, *Howell 21304* (CAS, GH); W of Fairfax, *Semple, Suario & Ahmed 9336* (WAT). Mill Valley, *Howell 14802* (CAS, RSA), *Walker 1376* (UC). Mt. Tamalpais, *Eastwood 1524* (CAS, GH, NY). San Geronimo, *Semple, Suario & Ahmed 9333* (WAT). Tamalpais, *Brandege s.n.* (UC), *Michener & Bioletti s.n.* (NDG). Tiburon Pen., *Penalosa 1977* (CAS). W Tiburon, *Howell s.n.* (CAS). San Francisco Co.: San Francisco, *Wilkes Expedition s.n.* (NY); Bayview Park, *Rose 33288* (WTU); at summit of San Miguel Hills, *Raven 11313* (TEX). South San Francisco, *Suksdorf 340* (WS). Hills S of Visitacion Valley, *Howell 11435* (CAS, RSA, WIS). San Mateo Co.: *Baker 56* (Holotype: NDG!; TYPE: "neglecta", name on sheet annotated E.L. Greene), *Congdon sn.* (MIN). Alpine Rd SW of CA-35, *Semple & Chmielewski 8917* (WAT). Page Mill Rd NE of CA-35, *Semple & Chmielewski 8915* (WAT). Salada, *Rose 264* (LL, WIS). San Bruno Mt, Sierra Pt., *Wheeler s.n.* (CAS), summit, *Rose 66087* (CAS, JEPS, RSA). Santa Clara Co.: Black Mt. on Palo Alto Rd., *Baker 2418* (LL). Saratoga Summit, *Rose 41459* (CAN, CAS, GH(2), LL, NDG, NY, PH, RSA, UBC, UC, UNCC, WIS). Santa Cruz Co.: Castle Rock Ridge, *Rose 37666* (PH, UC). NW of Saratoga, *Semple et al. 5670* (ASU, JCS, JEPS, MO, MT, UCSB, USF). Sonoma Co.: *Congdon sn.* (MIN).

aff. var. *bolanderioides*

U.S.A. CALIFORNIA. Contra Costa Co.: Oakland Hills, *Jepson 14683* (WS).

1.4 *Heterotheca sessiliflora* (Nutt.) Shinnery ssp. *bolanderi* (A. Gray) Semple, Phytologia 73: 449.

1992. *Chrysopsis bolanderi* A.Gray, Proc. Amer. Acad. Arts 6: 543. 1866. *Chrysopsis villosa* (Pursh) Nutt. var. *bolanderi* (A.Gray) A.Gray, Synopt. Fl. N. Amer. 1 (2): 123. 1884. *Heterotheca bolanderi* (A.Gray) Harms, Brittonia 26: 61. 1974. TYPE: U.S.A. CALIFORNIA. Oakland Hills near San Francisco, 1863, *Bolander 2466* (Holotype: GH!; isotypes: K!, US!)

Chrysopsis arenaria Elmer, Bot. Gaz. 41: 321-322. 1906. TYPE: U.S.A. CALIFORNIA. Marin Co., Jul 1903, *Elmer 4556* (Holotype: US!; isotypes: MIN!, NY!, WIS!). *Elmer 4456* (NY, possible misnumbered 4556)

Perennial from stout woody taproots, herbaceous, STEMS several to many, ascending-erect, (10)-15-25-33-(40) cm tall, moderately strigose-hispid, long spreading hairs few to many, becoming glandular and moderately pubescent above; (10)-12-19-25-(35) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (20)-27-39-51-(60) mm long, (5)-6.6-9.3-11-(13) mm wide, subsessile, cuneate, acute, moderately (rarely densely) hispid-strigose on both surfaces; margins entire, strigose, longer spreading hairs near base, flat to very weakly undulate. UPPER STEM LEAVES (ob)-lanceolate, sessile, reduced upward, (13)-21-28-35-(40) mm long, (4)-5.3-6.3-7.3-(8) mm wide, glabrate to moderately glandular (0)-2-8-14-(20) glands/mm², moderately to densely long strigose, 15-41-67-(120) hairs/mm², margins not undulate. CAPITULESCENCE cymose-corymbiform, branches ascending, solitary in dwarf plants, heads (1)-2-5-8-(13); peduncles moderately hispid and glandular, bracts few, lower ones lanceolate, leaf-like, reduced upward, sometimes head subtended by one or more foliar bracts exceeding involucre. INVOLUCRES cylindrical to turbinate when fresh, campanulate upon drying, (9)-9.8-11.2-12.6-(15) mm high; phyllaries in 4-5 imbricate

series, outer 1/4-1/3 length of inner, mid series lanceolate, sparsely to moderately glandular, moderately long strigose, margins hyaline, fimbriate-ciliate apically. RAY FLORETS (9)-12-15-18-(21), strap yellow 9-12-15-(20) mm long, (1.1)-1.3-1.7-2-(2.5) mm wide. DISC FLORETS (25)-32-47-63-(81), yellow, corolla somewhat ampliate, (6)-6.3-7.3-8.2-(9.5) mm long, lobes 0.6-0.8-0.9-(1.1) mm long, sparsely pilose, hairs (0.2)-0.3-0.5-0.7-(1) mm long. ACHENES 2-3-(4.5) mm long, moderately strigose; pappus off-white, double, outer whorl of a few linear scales 0.25-1.0 mm long, inner whorl of 35-45 barbellate bristles 6-9-(10) mm long, shorter than to exceeding the corolla. Chromosome numbers: $2n = 18$.

Distribution and habitat: Medecino Co. to San Mateo Co., California, lower elevations in around San Francisco Bay (Fig. 14C); dunes and headlands, roadsides; 10-150 m elevation. In the San Francisco Bay area, older collections come from lower elevation habitats that no longer exist due to expansion of metropolitan areas. Along the coast north of the Bay area, the species can be found in very large populations in sand dunes. Smaller populations occur on headlands and sandy roadside margins.

Discussion: Subsp. *bolanderi* is distinguished by its few-flowered capitulescence with large heads, non-undulate leaves, long hairs, and large achenes (Fig. 19). Corolla lobe hairs are often very few in number and sometimes difficult to find, especially in older heads. Plants from more upland habitats can be confused with plants of ssp. *echioides* var. *bolanderioides* (Fig. 18), which tends to have easily-seen, very long hairs attached to the corolla lobes and corolla tube (Fig. 11A). Plants from Medecino often have long peduncles (Fig. 19A), while those from around San Francisco Bay tend to have shorter peduncles and a more congested compact capitulescence (Fig. 19B).

The four collections listed below from northwestern Washington State require comment. These were collected in 1896, 1897, 1921 and 1990 from sandy sites near the ocean. While none are typical for ssp. *bolanderi*, they also would be aberrant in *H. villosa*, the alternative taxon in which to place the specimens. They may be chance introductions from northern California that survived long enough to be noticed by observant botanists. The most recent collection *Naas & Naas 5579* (WTU) is similar to collections from Mendecino Co., California, e.g. *Semple et al. 5685* (WAT), but lacks obvious corolla lobe hairs.

Robust plants with large heads and long rays form very attractive colonies of wild flowers.

Representative Specimens: U.S.A. CALIFORNIA. *Bolander s.n.* (GH). *Gibbons s.n.* (PH). Highland Station, *Greene s.n.* (NY). Alameda Co.: Botanic Garden, University Cal., *Parish 19124* (WIS). San Leandro, *Edwards s.n.* (NY). Marin Co.: *Michener & Bioletti 1114a* (MIN). *Michener & Bioletti s.n.* (NY). NW of Inverness, *Rose 46270* (GH, NY). Olema, *Walker 1167* (UC). N of Rodeo Lagoon, *Robbins 3881* (CAN, OBI). Point Reyes P.O., *Elmer 4456* (RSA, WS). Pt. Reyes Pen., Pierce Pt. Rd., *Howell 22890* (CAS, DAO). Sausalito, *Eastwood 296* (CAS, GH, NY). Sausalito, *Howell s.n.* (CAS, NY). Tomales, Lone Pine Beach, *Schreiber 676* (UC). Mendecino Co.: *McMinn 1967* (UC). N of Albion, *Heller 15313* (CAS, NY, UC). S of Albion, *Peirson 6417* (RSA). Anchor Bay, 3 mi N of Gualala, *Bacigalupi 1801* (DS). N of Anchor Bay, *Semple & Heard 8547* (WAT). NW from Anchor Bay, *Everett & Balls 23993* (RSA, UC, UNCC). S of Anchor Cove, *Wolf 1345* (DS, RSA). Between Arena and Anchor Bay, *Baker 5256* (CAS). Big River, *McMurphy 345* (DS, NY). Caspar Pt., *Heckard & Chang 1997* (CAN). N of Cleone, *Semple et al. 5685* (WAT), *Semple & Heard 8540* (WAT). S of Elk, *Keck 5957* (DS, DS ex Carneg. Wash.). Ft. Bragg, *Jepson 14686* (CAN), *Million s.n.* (CAS). *Eastwood 1641* (CAS, GH). above Ft. Bragg, *Congdon s.n.* (MIN). Ft. Bragg, *Jepson 17739* (CAN). N of Fort Bragg, *Keck 2676* (DS, DS ex Carneg. Wash.), *Howell 5477* (CAS), *Breedlove 5365* (UBC), *Mason 5405* (UC(2)); W of Grange Hall, *Thorne & Everett 34153* (GH, RSA). Little River, near coast, *Peirson 3891* (CAS, RSA). Mendecino, *Jones 29140* (CAS, DS(2), RM, RSA, UC). N of Mendecino, *Munz 22727* (DS, RSA, UC). Noyo, *Bolander 6490* (GH, UC), *Duncan 270* (DS, RM). Point Arena Lighthouse, *Ferris 9381* (CAS, DS, GH, LL, RSA, UC, WS). Point Arena Rd., *Congdon s.n.* (MIN). Punta Cabrillo, *Dudley s.n.* (DS). S of Mendecino, *Semple et al. 5681* (WAT). Ten Mile dunes, *Smith 7210* (RSA). Ten Mile River, *Cooper 99* (CAN). S of Westport, *Semple & Heard 8533* (WAT), *Semple & Heard 8535* (WAT). San Francisco Co.: Potrero, *Kellogg & Hartford 417* (NY). San Francisco, hills S of Visitacion Valley, *Howell 11435* (LL). San Mateo Co.: near Redwood City, along Bayshore Rd., *Demaree 10461* (WTU). Santa Cruz Co.: NW of Davenport, *Buck & West 111* (CAN). Sonoma Co.: *Kellogg & Hartford 407* (NY).

aff. ssp. bolanderi, probably adventive from California

U.S.A. WASHINGTON. Clallam Co.: E shore of Washington Harbour, 14 Sep 1921, *St. John 5869* (GH, UC, WS). Island Co.: Whidb[e]y Island, Jul 1896, *Gardner s.n.* (UC), 1 Aug 1897, *Gardner 153* (WS); W of Coupeville, 7 Jul 1990, *Naas & Naas 5579* (WTU).

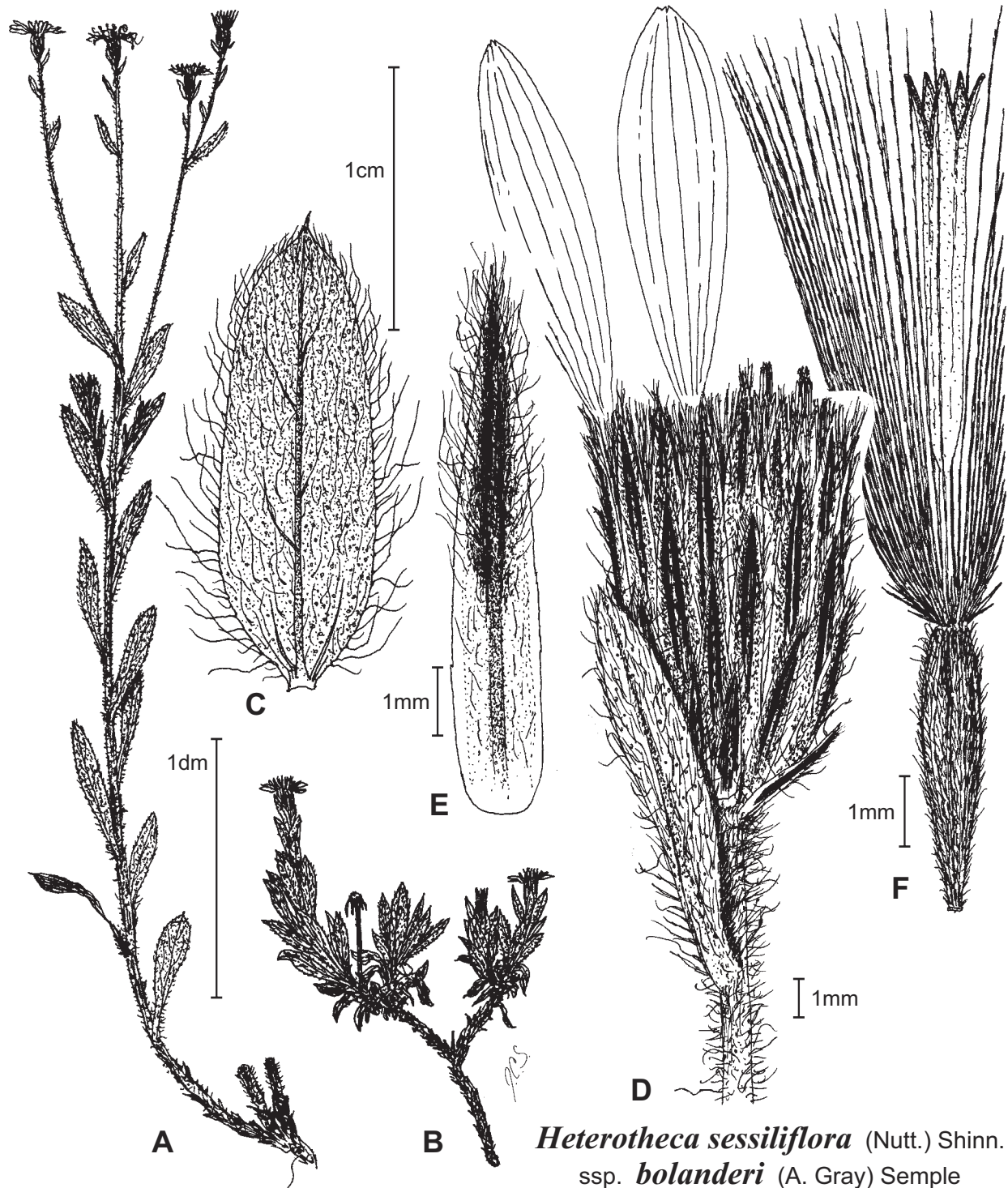


Figure 19. Morphology of *Heterotheca sessiliflora* ssp. *bolanderi*. A. Shoot of a robust plant with long peduncles. B. Branch of a small plant with subsessile heads. C. Mid stem leaf, abaxial surface; leaves can be more densely long-pubescent. D. Head with only some florets drawn. E. Mid series phyllary with chlorophyllous zone dark, margins may be anthocyanotic. F. Mature achene with disc corolla attached.

2. *Heterotheca monarchensis* York, Shevock & Semple, sp. nov.

TYPE: U.S.A. CALIFORNIA. Fresno Co.: ca. 86 km E of Fresno, Sequoia N.F., Monarch Wilderness, 2000 m NW of Boyden Cave on N side of Kings River canyon, rocky outcrops, T13S R29E S4 NE¼, 1800m, 31 Jul 1995, York & Shevock 109 (Holotype: CAS; isotypes: FSC, JEPS, MO, RSA, US, WAT).

Heterothecae sessiliflorae var. *echioidi accedens sed foliis oblanceolatis anguste cuneatis, vix deminutis distaliter, bracteis subter capitulis grandibus foliiformibus, caulibus multinodibus minus quam 20 cm altibus*; *Heterothecae villosae* var. *villosae accedens sed foliis glandulosis et lobis corollarum discorum pilis anguste osteoformibus ad 0.7 mm longis*.

Perennials from stout woody taproots, herbaceous, STEMS several to many, ascending-erect, (9)-10.8-12.5-13.8-(17.5) cm tall, moderately to densely hispid, hairs long; (11)-19-22.5-26-(32) nodes below capitulescence. LOWER STEM LEAVES oblanceolate to obovate, (11)-13.7-15.5-17.2-(25) mm long, (2)-2.6-3.2-3.7-(5) mm wide, petiolate, cuneate, acute, moderately-densely hispid-strigose on both surfaces, sparsely glandular; margins entire, strigose, longer spreading hairs near base, somewhat undulate. UPPER STEM LEAVES similar to lower, little reduced upward, (9)-11.2-13-14.9-(19) mm long, (2.5)-3-3.2-3.4-(4) mm wide, sparsely glandular 8-13-18-(21) glands/mm², moderately to densely hispid-strigose, (39)-47-65-83-(85) hairs/mm², margins usually slightly undulate. CAPITULESCENCE solitary to cymose-corymbiform, branches ascending, heads 1-2(-5); peduncles 2-5-(10) mm long, densely hispid, sparsely glandular, bracts foliar and sometimes exceeding the involucre in length, bracts subtending heads narrower than leaves, (8)-9.5-11.4-13.3-(14) mm long, 1-1.4-1.8-(2.2) mm wide. INVOLUCRES cylindrical to turbinate when fresh, campanulate upon drying, (6)-6.5-7.1-7.8-(8.5) mm high; phyllaries in 3-4 imbricate series, outer 1/4-1/24 length of inner, mid series narrowly triangular, sparsely glandular, moderately strigose, margins hyaline, fimbriate-ciliate apically. RAY FLORETS (8)-12-14.5-16-(19), strap yellow, (10)-11-12.1-13-(14) mm long, (1.1)-1.3-1.6-1.8-(2.2) mm wide. DISC FLORETS (30)-33-39-43-(45), yellow, corolla somewhat ampliate, (5)-5.6-5.8-6-(6.2) mm long, lobes 0.45-0.5-0.6-(0.75) mm long, sparsely pilose, hairs (0.2)-0.3-4-0.5-(0.6) mm long. ACHENES 2-3 mm long, moderately strigose; pappus off-white, double, outer whorl of a few linear scales 0.25-0.5 mm long, inner whorl of 25-40 barbellate bristles 5-6.5 mm long. Chromosome number: $2n = 18$, first report, progeny of WAT isotype.

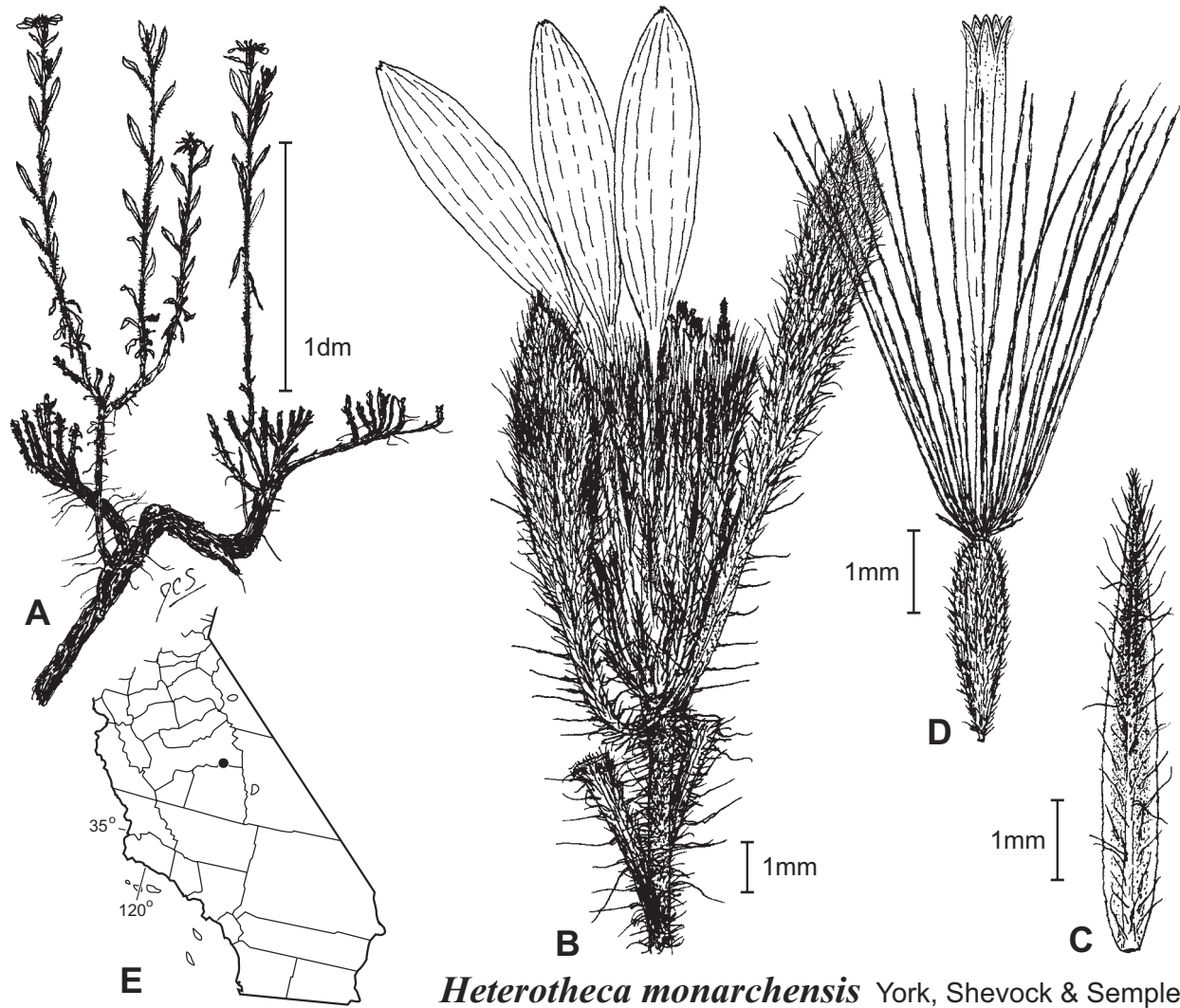
Flowering Period: (May) JUNE-OCTOBER

Distribution and habitat: Rare in northeastern Fresno Co., very locally common (Fig. 20E); scattered on limestone in cracks, ledges and flats, higher densities of plants occur in coarse sandy flats at the base of cliffs; 1095-1829 m (5700-6000 ft.) elevation; associated limestone community dominated by *Bromus madritensis* L. ssp. *rubens* (L.) Husnot, *Cercocarpus intricatus* S. Wats., *C. betuloides* Torr. & Gray var. *betuloides*, *C. ledifolius* Nutt. var. *intermontanus* N. Holmgren, *Garrya flavescens* S. Wats., *Pinus monophylla* Torr. & Fremont and *Yucca whipplei* Torr.; other associated species include *Agryrochosma jonesii* (Maxon) M.D. Windham, *Asclepias fascicularis* Decne., *Astragalus congdonii* S. Wats., *Avena sativa* L. *Cheilanthes cooperae* D. Eaton, *Cirsium occidentale* (Nutt.) Jeps. var. *californicum* (A. Gray) Keil & C. Turner, *Clarkia rhomboidea* Douglas, *Eriogonum nudum* Benth. (s.l.) *Eysimum capitatum* (Douglas) E.L. Greene, *Mentzelia laevicaulis* (Hook.) Torr. & Gray, *Mimulus floribundus* Lindl., *Nemacladus interior* (Munz) G. Robb., *Rhamnus tomentella* Benth. *Selaginella asprella* Maxon, *S. hansenii* Hieron., *Streptanthus fenestratus* (E.L. Greene) J. Howell, and *Umbellularia californica* (Hook. & Arn.) Nutt.

Discussion: *Heterotheca monarchensis* is distinguished by its small, oblanceolate densely long-villose leaves, its long thin hairs on the corolla lobes, and its small stature (Fig. 20). The type material has features similar to aspects of *H. sessiliflora* var. *echioides* (Fig. 17) and *H. villosa* var. *villosa* (Fig. 41). The slightly undulate leaf margins and corolla lobe hairs indicated a relationship with *H. sessiliflora* var. *echioides*, which usually is much taller and has more spreading hairs on the stem and upper stem leaves that are sessile and

oblong. Some densely hairy specimens of *H. sessiliflora* var. *bolanderioides* and individuals of ssp. *sessiliflora* that are silvery-white look superficially similar to the type material of *H. monarchensis*, but the former two usually have ovate-lanceolate upper stem leaves while *H. monarchensis* has oblanceolate leaves. All three can have heads partially surrounded by upper stem leaves and long foliar bracts subtending the heads. The leaf shape is more typical for members of *H. villosa* that occur in the Sierra Nevada further north and east. It would be easy to misidentify specimens of *H. monarchensis* as *H. villosa* if the long thin corolla hairs were very few or broken off.

Recent explorations on the xeric limestones (marbles) of the southern Sierra Nevada in the Kings River watershed yielded this new goldenaster, named for its location in the Monarch Wilderness. The species is scattered over the southwest and southeast exposures of a large, north-south trending, limestone ridge. This sheer-walled limestone formation rises more than 1000 m above the Kings River and is located just northeast of Horseshoe Bend along the north side of Kings River. The limestone is a spur of a larger metamorphic and



Heterotheca monarchensis York, Shevock & Semple

Figure 20. Morphology and distribution of *Heterotheca monarchensis*. A. Habit, only some shoots illustrated. B. Upper portion of shoot and head; only some florets drawn, lower leaves shown cut away. C. Mid series phyllary with chlorophyllous zone dark. D. Mature achene with disc corolla attached. E. Distribution in southern California.

granitic rock formation that forms Monarch Divide (a.k.a Junction Ridge) separating the Middle from the South Forks of Kings River. This area is more than 100 km from the nearest known population of *H. sessiliflora* to the west and south and some 80 km from the nearest known population of *H. villosa* var. *minor* to the north at 3050 m (10,000 ft.) elevation. An additional population was located in 1996 on the south side of the canyon in this area of limited access and rugged terrain. Further exploration potentially will yield more sites in the area of the three known populations.

Specimens examined: U.S.A. CALIFORNIA. Fresno Co.: Monarch Wilderness, 1200 m NW of Boyden Cave, *York 198* (CAS). 1370 m S of Boyden Cave on S side of Kings R. Cyn., T13S R29E S10 SW¼ of SW¼, 1580 m, *York 678* (FSC).

3. ***Heterotheca thiniicola* (Rzedowski & Ezcurra) B.L. Turner**, *Phytologia* 63: 128. 1987. *Haplopappus thiniicola* Rzedowski & Ezcurra, *Ciencia Interamericana* 26: 16. 1986. TYPE: MÉXICO. SONORA. Municipio Puerto Peñasco, Gran Desierto de Alta, 8 km NE de la estacion Gustavo Sotelo, 17 Dec 1984, *Ezcurra 84001* (Holotype: MEXU, not seen; isotype: TEX!).

[Description based on limited material.] Perennial subshrubs to shrubs from stout woody taproots, STEMS several to many, ascending-erect, to 1.5 m tall, sometimes profusely branched, moderately to densely strigose-hispid, long spreading hairs few; many nodes below capitulescence. LOWER-MID STEM LEAVES oblanceolate, 6-15 mm long, 2-4 mm wide, acute, mucronate, cuneate, margins usually slightly undulate. UPPER STEM AND RAMEAL LEAVES, lanceolate to ovate or oblong, sometimes rameal leaves orbiculate, much reduced upward, moderately to densely glandular 10-40 small glands/mm², moderately to densely short-strigose 80-90 hairs/mm², margins usually undulate, long spreading hairs few or absent. CAPITULESCENCE solitary to cymose-corymbiform, branches ascending, heads 1(-4) per branch, stem branches below primary capitulescence elongating on older shoots and capitulescence becoming paniculiform; peduncles densely short hispid-strigose, very sparsely glandular, bracts few, lower ones lanceolate, leaf-like, reduced upward, 2-4 mm long, 0.5-1 mm wide, sometimes phyllary-like. INVOLUCRES cylindrical to campanulate when fresh, campanulate upon drying, 6-7 mm high; phyllaries in 5-6 imbricate series, outer 1/5-1/4 length of inner, mid series narrowly triangular, eglandular, moderately strigose, margins hyaline, fimbriate-ciliate apically. RAY FLORETS 7-13, strap yellow, 6-7 mm long, 0.9-1.5 mm wide. DISC FLORETS 20-30, yellow, corolla slightly ampliate, 4-5 mm long, lobes 0.5-0.7 mm long, hairs few, 0.1-0.2 mm long. ACHENES 2.5-3.5 mm long, moderately strigose; pappus off-white, double, outer whorl of a few linear scales 0.25-0.5 mm long, inner whorl of 25-35 barbellate bristles 3.5-4.5 mm long, shorter than corolla tube. Chromosome number: $2n =$ unknown.

Flowering Period: (May)-SEPTEMBER

Distribution and habitat: Sand dunes of Desierto de Altar, northwestern Sonora, México (Fig. 21F); 110 m (360 ft.) elevation.

Discussion: *Heterotheca thiniicola* is distinguished by its small branch leaves and shrubby habit (Fig. 21). It is similar to *H. sessiliflora* var. *fastigiata*; both have leaves with short appressed hairs and undulate margins (Fig. 21). The shrubby habit is shared with *H. sessiliflora* ssp. *sessiliflora* (Fig. 15). This may be the evolutionary result of the subtropical dune environment not killing the shoots seasonally back to ground level. Such is the case with the usually annual *H. subaxillaris* of sect. *Heterotheca* growing in the southern part of its range in northeastern México.

Rzedowski and Ezcurra (1986) noted a superficial similarity of *H. thiniicola* to *Haplopappus* (*Hazardia*) *berberis* A. Gray or *Haplopappus detonsus* (Greene) Raven. Turner (1987) placed it near *Heterotheca sessiliflora*. Nesom (pers. comm.) treated it as part of *H. sessiliflora* var. *fastigiata*. While similar to var. *fastigiata*, *H. thiniicola* is sufficiently different to warrant recognition as a separate taxon. Its unique habitat indicates that it is more than just a disjunct population of the montane var. *fastigiata*.

Specimens examined: MÉXICO. SONORA. Mun. Puerto Peñasco, Gran Desierto de Alta, 10 km NE of Estacion Gustavo Sotelo, *Ezcurra s.n.* (MEXU(2)). MEX-8 13.8 mi ENE of Puerto Peñasco then 7.6 mi NW, *Felger & Zimmerman 88-227* (TEX(3)), *Zimmerman & Felger s.n.* (TEX).

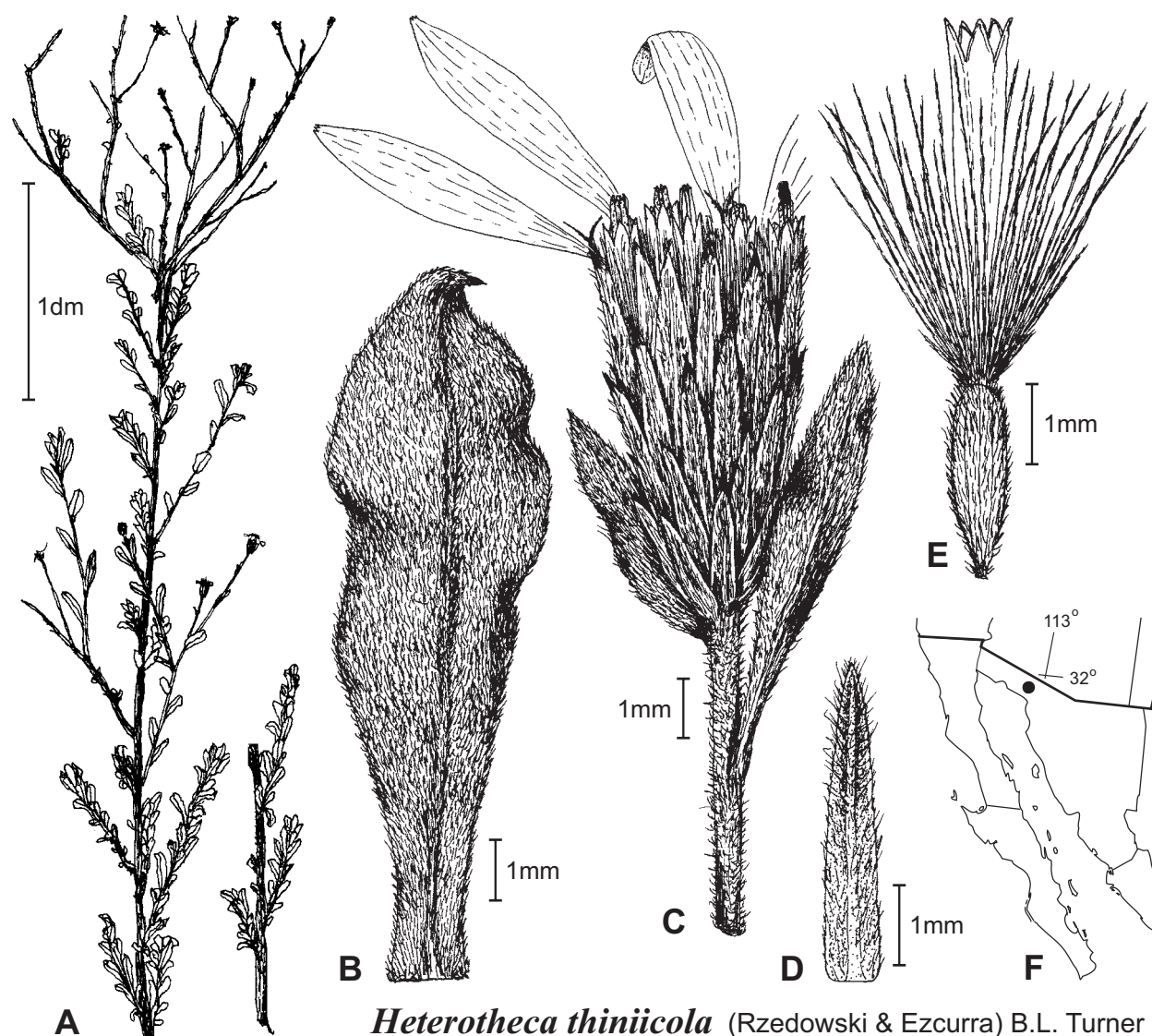


Figure 21. Morphology and distribution of *Heterotheca thiniicola*. **A.** Habit, lower portions of shoots are sometimes buried in loose sand. **B.** Lower-mid stem leaf. **C.** Upper portion of shoot with two leaves and head with only some florets drawn. **D.** Mid series phyllary with chlorophyllous zone dark. **E.** Mature achene with disc corolla attached. **F.** Distribution; northwestern México and the adjacent United States.

4. *Heterotheca mexicana* Harms in Turner, Phytologia 55: 204. 1984. *Heterotheca mexicana* Harms, Brittonia 26: 66. 1974. nom. nud. TYPE: MÉXICO. DURANGO. Fields along route 40, ca. 31 mi SW of Durango, 16 Aug 1960, King 3748 (Holotype: TEX!).

Perennial from stout woody taproots, STEMS several to many, ascending-erect, 13-18-22-(26) cm tall, strigose, long spreading hairs mostly near base; 15-20-25-(26) nodes below capitulescence. LOWER STEM LEAVES ovate to oblanceolate, 13-18.5-23.5-(26) cm long, (2.5)-2.9-4.5-5.9-(7) mm wide, petiolate, cuneate, mucronate, densely strigose-canescens on both surfaces; margins entire, strigose, a few longer spreading hairs near base. UPPER STEM LEAVES (ob)lanceolate to oblong, (10)-11.5-14.5-17.5-(18) mm long, 3-3.9-5.1-(6) mm wide, sessile, little upward, indument similar to lower, 0-(1) glands/mm², 55-89-130-(180) hairs/mm², margins flat or only remotely undulate. CAPITULESCENCE open cymose-corymbiform, heads 1-2-3-(5); peduncles moderately to densely strigose-canescens, eglandular, usually elongating just before anthesis, (10)-20-40-60 mm long; bracts none or few, linear-oblanceolate, usually greatly reduced. INVOLUCRES cylindrical to turbinate when fresh, campanulate-hemispheric upon drying, (7)-7.4-8.3-9.2-(9.5) mm high; phyllaries in 4-5 imbricate series, outer and mid series narrowly triangular, eglandular, moderately strigose, margins hyaline narrow, fimbriate-ciliate and anthocyanotic apically; inner ones similar. RAY FLORETS (9)-10-13-15-(17), strap yellow, (10)-12-13.9-15.8-(16.5) mm long, 1-1.8-2.5-(3.0) mm wide, tube glabrate. DISC FLORETS 15-21-27-(33), yellow, corolla barely ampliate, (5)-5.6-6.3-7-(7.2) mm long, lobes 0.5-0.7-0.8-(1) mm long, hairs few, 0.1-0.3-0.4-(0.5) mm long. ACHENES 2-2.5-3.1-(3.9) mm long, moderately strigose; pappus off-white, double, outer whorl of a few linear scales 0.2-1 mm long, inner whorl of 30-40 barbellate bristles (5.5)-6-7.1-8 mm long. Chromosome number: $2n = 18$, several reports.

Flowering Period: MAY-JUNE-JULY.

Distribution and habitat: Near and west of Durango, Durango, México (Fig. 22G); semi-desert scrub, open pine-oak-madrone woodlands, *Yucca-Acacia-Opuntia* hills; rocky grassy flats, rocky slopes, road banks, volcanic soils, sandy gravel; 2000-2600 m (6800-8500 ft.) elevation.

Discussion: *Heterotheca mexicana* is distinguished by its capitulescence of one to several long-peduncled heads, leaves with a dense strigose indument, and achenes with an outer whorl of only a few short linear scales (Fig. 22). This is the only species of sect. *Phyllotheca* native to west-central México. It is most similar to *H. mucronata* var. *mucronata* (Fig. 23) and *H. gypsophila* (Fig. 25), and less so to *H. villosa* var. *pedunculata* (Fig. 45), and *H. canescens* (Fig. 36). The capitulescence buds of plants, which were cultivated in the experimental greenhouse in Waterloo, Ontario, were observed to be nodding early in development. Shortly before anthesis the short peduncles rapidly elongated and the heads became erect. Thus, peduncle length is a function of the stage of development, and short and long peduncles are to be expected.

Specimens examined: MÉXICO. DURANGO. Gibson & Gibson 2711 (NY). Durango, King 3725 (DS, MEXU, NY, TEX(2), UC); vicinity, Palmer 221 (F, UC), Palmer 923 (UC). E of Durango, Lane & Longstreth 2720 (TEX). N of Durango, Sundberg 2867 (TEX(2), WAT). N of Durango (Glorieta), Pinkava, McGill, Reeves & Nash P13432 (ASU). N of Durango, S of Morillo, McGill, Brown & Pinkava 9415 (ASU). W of Durango, Anderson & Anderson 5192 (OS, TEX), Cronquist 9546 (MEXU, TEX), Bollwinkel & Wunderlin 232 (WIS), Breedlove 14309 (CAS), Breedlove & Almeda 45798 (CAS), Jackson 7194 (TEX), Roberts & Keil 10337 (NY, OS); E of El Pino, Sundberg 2898 (TEX, WAT). Near Rio Tunal, Hendricks 412 (WIS).

5. *Heterotheca mucronata* Harms in Turner, Phytologia 55: 205. *Heterotheca mucronata* Harms in Turner & Flyr, Amer. J. Bot. 53: 26. 1966. nom. nud. *Heterotheca mucronata* Harms, Brittonia 26: 66. 1974. nom. nud. TYPE: MÉXICO. NUEVO LEON. Sierra Madre Oriental, Puerto de Santa Ana, about 15 mi SW of Galeana, 28 Jun 1934, Mueller & Mueller 934 (Holotype: TEX!; isotype: GH!).

Perennial from stout woody taproots, STEMS several to many, ascending-erect, (5)-13-21-30-(45) cm tall, appressed strigose, long spreading hairs numerous; (9)-11-21-30-(46) nodes below capitulescence. LOWER STEM LEAVES ovate to oblanceolate, (14)-18-28-38-(48) cm long, (4)-5.2-8.2-11.2-(15) mm wide, petiolate,

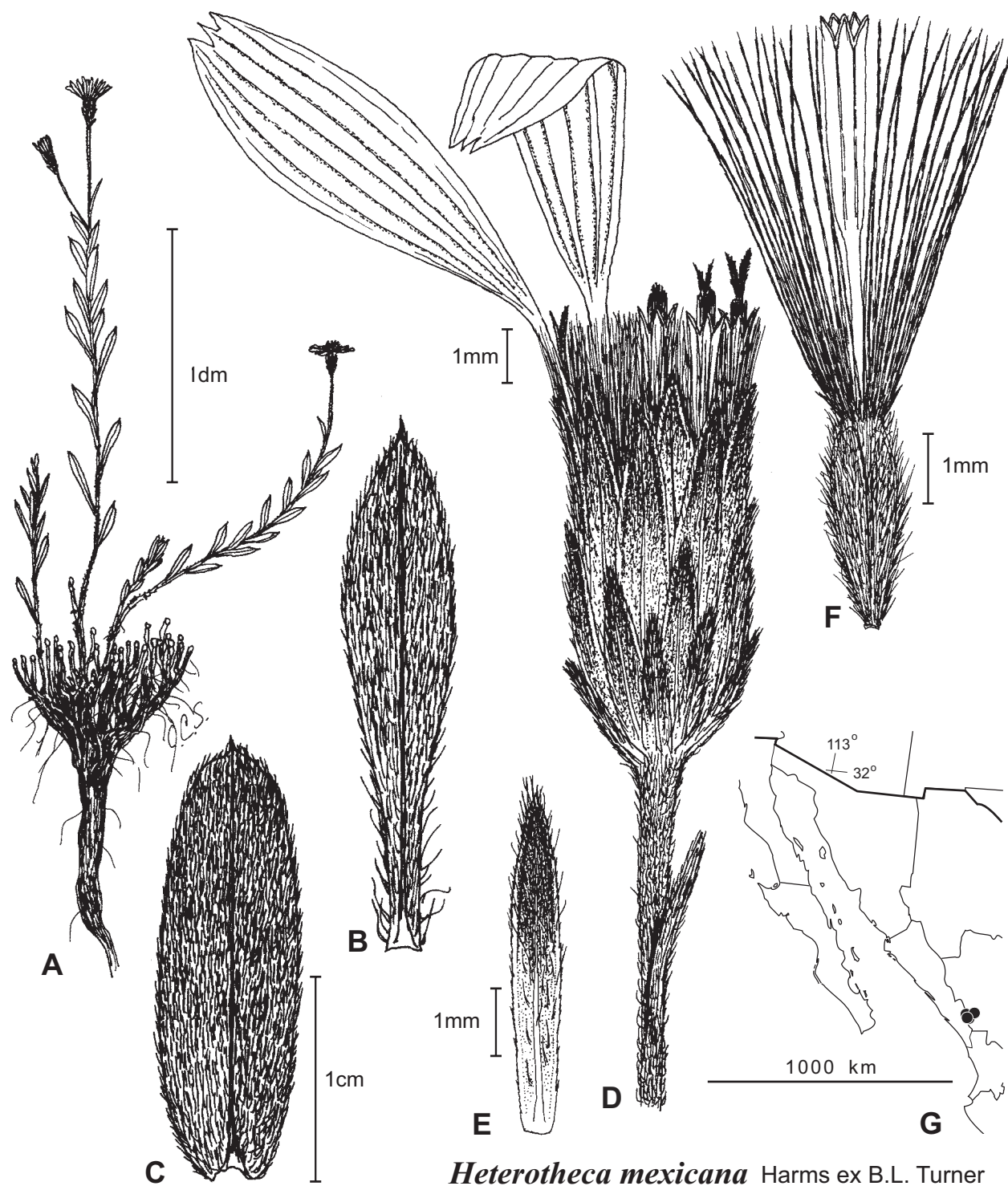


Figure 22. Morphology of *Heterotheca mexicana*. **A.** Habit; only some shoots shown. **B-C.** Lower and upper stem leaves, respectively; upper leaves can be similar to lower ones. **D.** Head with only some florets drawn. **E.** Mid series phyllary with chlorophyllous zone dark. **F.** Mature achene with disc corolla attached. **G.** Distribution; western México.

cuneate, mucronate, sparsely to moderately glandular, sparsely to densely strigose-canescens, glandular on both surfaces; margins entire, strigose, some longer spreading hairs near base. UPPER STEM LEAVES obovate to oblanceolate, rarely oblong, (11)-14.5-**20**-25.6-(34) mm long, (3)-4.2-**5.9**-7.6-(10) mm wide, sessile, usually little reduced upward, obtuse to rarely acute, mucronate tip 0.2-**0.4**-0.5-(1) mm long, indument similar to lower, (0)-1-**8**-15-(25) glands/mm², (12)-23-**62**-101-(145) hairs/mm², margins flat or only remotely undulate; branch leaves reduced upward. CAPITULESCENCE open cymose-corymbiform, heads 1-**2**-3-(4); peduncles moderately to densely hispid-strigose and sparsely to moderately glandular, usually elongating before anthesis, (0.5)-3-**12.7**-23-(48) mm long; bracts none or few, linear-oblanceolate, usually greatly reduced, rarely foliar and linear-oblanceolate, indument like leaves; when lateral branches elongate then the capitulescence pattern is repeated on secondary or higher level branches. INVOLUCRES narrowly campanulate when fresh, campanulate-hemispheric upon drying, (5)-7.5-**8.3**-9.2-(10) mm high; phyllaries in 4-5 imbricate series, outer ones about 1/3 the length of the inner, lanceolate, sparsely to moderately strigose, eglandular to densely glandular, margins hyaline narrow, fimbriate-ciliate and anthocyanotic apically; inner ones similar. RAY FLORETS (13)-15-**20**-24-(29), strap yellow, (8.5)-10-**12.3**-14.5-(19) mm long, 1-**1.6**-2.1-(2.8) mm wide. DISC FLORETS (15)-21-**36**-50-(72), yellow, glabrate, corolla barely ampliate, (4.3)-5.4-**6.1**-6.7-(7.5) mm long, lobes 0.5-**0.65**-0.74-(0.8) mm long, hairs few, 0.1-**0.2**-0.3 mm long. ACHENES 1.5-**2.0**-35 mm long, moderately strigose; pappus off-white, double, outer whorl of linear scales 0.25-1 mm long, sometimes scales broad, inner whorl of 35-45 barbellate bristles (4.6)-5.3-**6**-6.6-(7.5) mm long. Chromosome numbers: $2n = 18, 36$; several reports.

Flowering Period: MAY-JULY (-October)

Distribution and habitat: Southern half of Nuevo Leon and adjacent states in México (Figs. 23F and 24E). Limestone, extensive chaparral and oaks and pine forests; lower slopes *Yucca*, *Dasyllirion*; upper slopes *Pinus ponderosa*; 750-3500 m (2450 - 11600 ft.) elevation.

Discussion: *Heterotheca mucronata* is distinguished by its capitulescence of one to several often long-peduncled heads, leaves with a moderately dense long-strigose indument and often distinctly mucronate tips (Fig. 23). It is the member of the *Mexicana* group closest to *H. mexicana* (Fig. 22). It occurs at both the diploid and tetraploid level. It is not much more mucronate than *H. gypsophila* and *H. mexicana*, which lacks a well developed short outer pappus whorl. Two varieties are distinguished on the basis of indument features. The typical variety has moderately to densely pubescent and sparsely glandular leaves. Variety *harmisana* has sparsely pubescent and moderately glandular leaves (Fig. 24). The difference is readily apparent in the color of the leaves due to the surfaces being more obscured by white hairs in var. *mucronata*.

5.1 *Heterotheca mucronata* Harms in Turner var. *mucronata*

STEMS several to many, ascending-erect, (5)-11.6-**25.4**-28.5-(29) cm tall, appressed strigose, long hispid hairs numerous; (10)-13-**23**-25-(29) nodes below capitulescence. LOWER STEM LEAVES ovate to oblanceolate, (14)-16.4-**26.3**-36.2-(48) cm long, (3.5)-4.7-**7.4**-10.2-(13) mm wide, petiolate, cuneate, mucronate, moderately to densely strigose-canescens and usually sparsely glandular on both surfaces; margins entire, strigose, some longer hispid hairs near base. UPPER STEM LEAVES oblanceolate, (12)-14.1-**19.1**-24-(27.7) mm long, (4)-4.6-**5.7**-6.8-(8) mm wide, sessile, little reduced upward, acute to obtuse, mucronate tip 0.2-**0.4**-0.5-(1) mm long, indument similar to lower, 0-**4**-8-(14) glands/mm², (20)-45-**81**-117-(145) hairs/mm², margins flat or only remotely undulate. CAPITULESCENCE open cymose-corymbiform, heads 1-**2**-3-(4); peduncles moderately to densely hispid and sparsely to moderately glandular, usually elongating before anthesis, 3-**16.6**-30.5-(48) mm long; bracts none or few, linear-oblanceolate, usually greatly reduced, rarely foliar and linear-oblanceolate, indument like leaves. INVOLUCRES narrowly campanulate when fresh, campanulate-hemispheric upon drying, (7)-7.5-**8.2**-8.9-(9.5) mm high; phyllaries in 4-5 imbricate series, outer ones about 1/2 the length of the inner, lanceolate, narrowly triangular-lanceolate, sparsely to moderately

strigose, eglandular to sparsely glandular, margins hyaline narrow, fimbriate-ciliate and anthocyanotic apically; inner ones similar. RAY FLORETS (11)-14-19-24-(29), strap yellow, (8.8)-10.2-11.7-13.1-(14.4) mm long, 1.2-1.6-2-(2.6) mm wide, tube glabrate. DISC FLORETS (13)-22-37-52-(66), yellow, glabrate, corolla barely ampliate, (5.2)-5.5-6-6.5-(7) mm long, lobes 0.5-0.6-0.8 mm long, hairs few, 0.1-0.2-0.3 mm long. ACHENES 1.5-1.8-2.2-(2.6) mm long, moderately strigose; pappus off-white, double, outer whorl of linear scales 0.5-1 mm long, sometimes fused into broader scales, inner whorl of 35-45 barbellate bristle (5.2)-5.4-6-6.6-(7.3) mm long. Chromosome numbers $2n=36$, several counts.

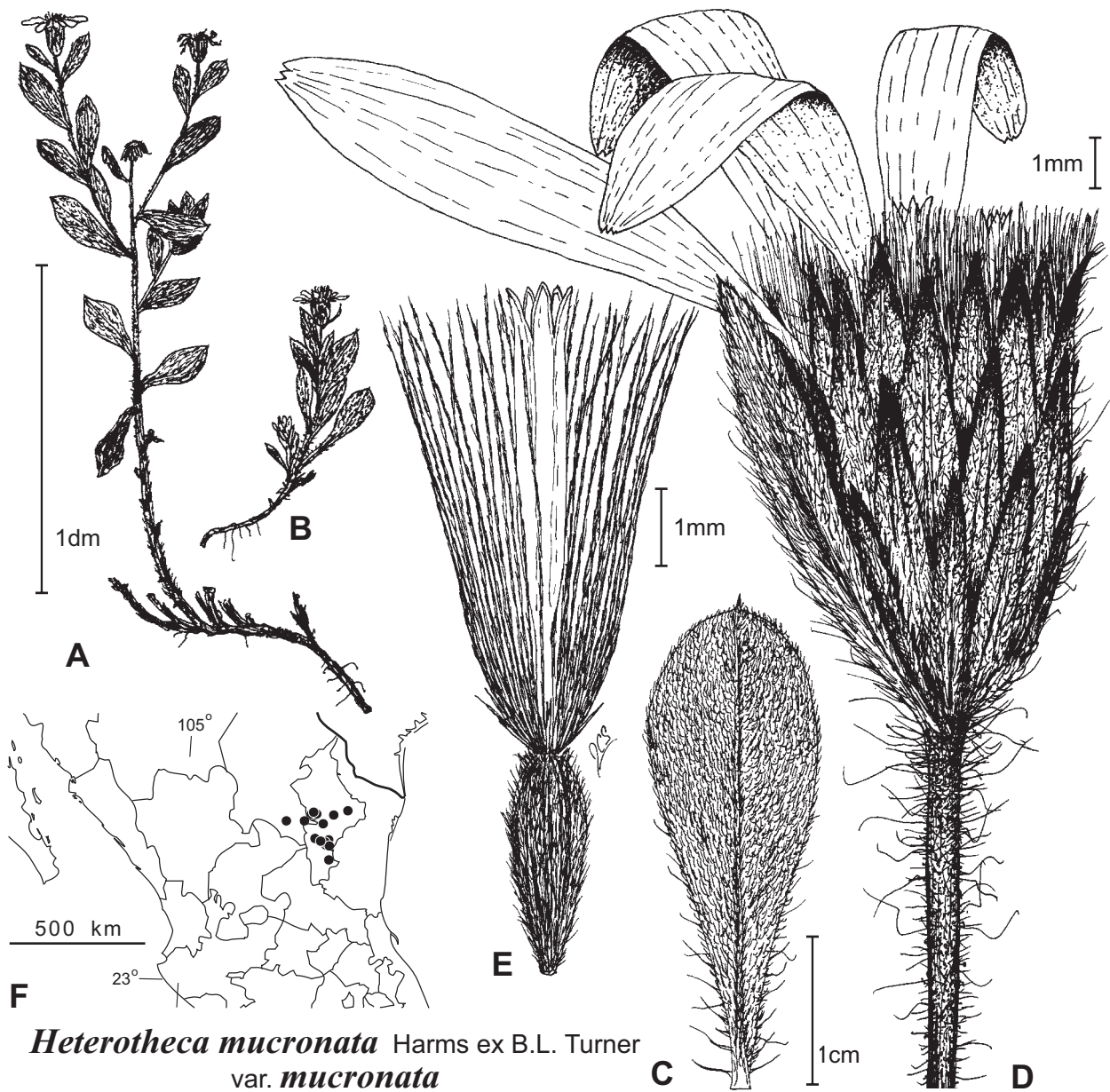


Figure 23. Morphology and distribution of *Heterotheca mucronata* var. *mucronata*. A. Habit of robust shoot. B. Shoot from small plant. C. Mid stem leaf. D. Head with only some florets drawn, the bract subtending the head is usually not present. E. Mature achene with disc corolla attached. F. Distribution; northeastern México.

Flowering Period: (May)- JUNE-OCTOBER-(November in south).

Distribution and habitat: Central and southern Nuevo Leon and adjacent Mexican states (Fig. 23F); cliff faces, limestone bluffs, stream banks, gypsum hills, rocky hillside, open rocky bed of dry river, riparian forests of *Quercus*, *Juglans* and *Carya*, pioneer vegetation of burned coniferous forests, along road; 750-3500 m (2450 - 11600 ft.) elevation.

Discussion: Variety *mucronata* is distinguished by its moderately pilose-canescens leaves (Fig. 23) that are usually not so densely pubescent that the surface is fully obscured from view. Its leaves have more hairs and fewer glands than those of var. *harmsiana* (Fig. 24). Solitary-headed, more densely pubescent individuals are similar to some individuals of *H. mexicana* (Fig. 22). Plants in Coahuila may have narrow oblanceolate leaves and a more compact capitulescence than found in plants in Nuevo Leon. Plants in riparian habitats can branch repeatedly producing smaller leaves.

Specimens examined: MÉXICO. COAHUILA. Mun. Arteaga, Sierra Zapaliname, *Hinton 22074* (TEX). E of Jame, Sierra de Viga, *Henrickson et al. 16137* (TEX). General Cepida, *Nelson 6727* (GH). S of La Cuchilla, Sierra Guadalupe, *Pennell 17380* (GH). E of Saltillo, *Palmer 480* (F, GH, NY). SW of Saltillo, Cañon de San Lorenzo, *Martinez, Hernandez, Bogler & Bogler 1861* (NY, TEX). Sierra La Marta, E of Cerro Moro, *Ginzburg, Whittemore & Gomez 155* (TEX). SE de Saltillo, Sierra La Marta, *McDonald 2148* (TEX). NUEVO LEON. Monterrey, above Chipinque motel, *Peterson 1254* (TEX). Rio Ramos near Los Adjuntas in the Sierra Madre, *Soule, Patterson & LeDuc 3277* (TEX). Mun. Aramberri, N of Aramberri, *Hinton 19993* (MEXU, TEX). E of Dulces Nombres, *Meyer & Rogers 2650* (GH). SE of Dulces Nombres, *Nesom, Mayfield & Hinton 7469* (TEX, WAT). Chippinque Mesa, between toll gate and mesa, *Phipps 37* (TEX). Mun. Galeana: Agua Blanca, *Hinton 22297* (TEX). El Gallo, *Hinton 19139* (TEX). El Sauce, *Hinton 19244* (MEXU, TEX). Galena, 5 km along rd to Rayones, *Hinton 24484* (TEX). Sierra La Marta, *Hinton 18307* (F, MEXU, TEX). SW of Galena, Taray-Santa Barbara Divida, *Mueller & Mueller 419* (GH). Hacienda La Jolla, *Schneider 1098* (UC, F). Las Canoas on Cerro Potosi, *Mueller 2191* (GH, F). Mun. Iturbide, S of Iturbide, Loma le Banderra, *Sundberg, Nixon, Grimes & Dorr 1850* (TEX); below Iturbide, *Grimes, Nixon, Dorr & Sundberg 2340* (MEXU, TEX). W of Linares, *McGregor, Harms, Robinson, del Rosario & Segal 155* (KANU, NY), *Roberts & Keil 10468* (NY, OS), *Turner & Powell 1058* (TEX), *Urbatsch 2450* (OS), *Whalen 316* (TEX), *Whalen 318* (TEX). Mun. Montemorelos, 5 km SE of La Trinidad, Cañon Cebolla, *Patterson 6326* (TEX). Monterrey, *Kenoyer A104* (F), *Mueller & Mueller 281* (F, GH, TEX); Cerro de la Silla, *White & Chatters 28* (MEXU), *White 1471* (ARIZ, GH). Villa de Santiago, Las Adjuntas, *Leavenworth 172* (GH, F). TAMAULIPAS. Cerro Barrie, vicin San Jose, *Barlett 10492* (TEX). Mun. Hidalgo, road from Stat. Engracia toward Dulces Nombres, 3.0 rd mi NE of Paraje de Los Caballos, *Nesom, Mayfield & Hinton 7507* (TEX, WAT). Mun. San Carlos: *Martinez 01100* (TEX); Sierra de San Carlos, Cerro del Diente, 17 km al Sur de San Carlos, *Hernandez 02275* (TEX). ZACATECAS. Sierrro del Astillero, NW Tanque El Alto, *Johnston, Wendt & Chiang 11571* (ASU, TEX).

aff. var. mucronata (approaching var. *harmsiana* and mixed collections of both varieties)

MÉXICO. COAHUILA. El Morro, limites con Nuevo León, Sierra De Arteaga, *Villarreal & Carranza 6293* (MEXU). Sierra de la Paila, *Villarreal 5341* (KANU, TEX(2)). TAMAULIPAS. S of San Carlos, Sierra de San Carlos, N side of Bufo El Diente, *Nesom, Norris, Martinez & Woodruff 6099* (MEXU, TEX(2)).

aff. var. mucronata (approaching *H. gypsophila*)

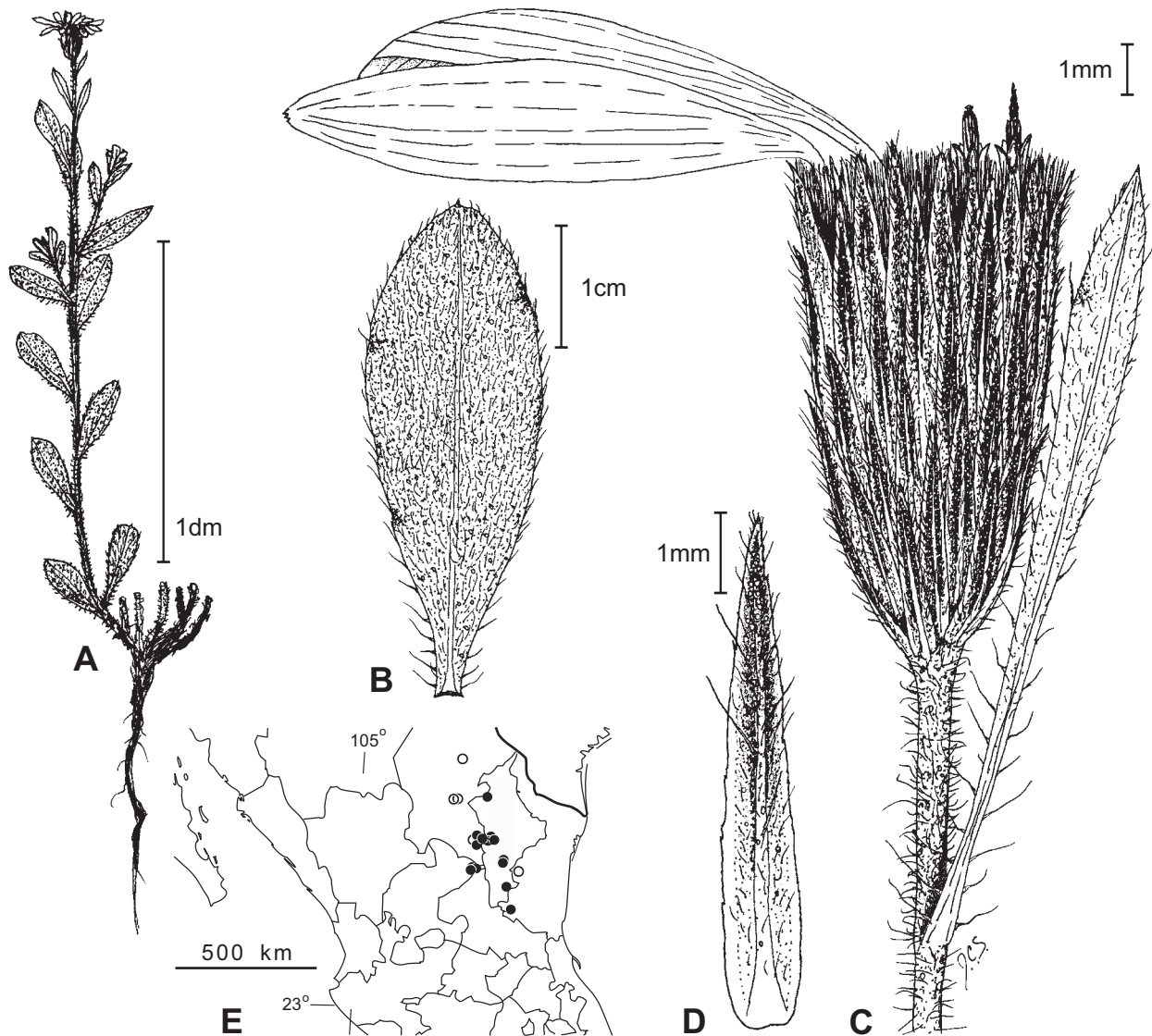
MÉXICO. NUEVO LEON. 20 mi WSW of Linares on Hwy 60 7 mi E of Iturbide, *Nesom s.n.* (TEX).

5.2 *Heterotheca mucronata* Harms in Turner var. *harmsiana* Semple, var. nov. TYPE: MÉXICO.

ZACATECAS. Rd above Concepcion del Oro, ca. 8 mi W of jct Rte 54, rocky cactus hillsides, ca. 8300 ft., 18 Jun 1976, $2n = 9_{II}$, *Pinkava, McGill, Reeves & Nash P13486* (Holotype: ASU!; isotype: WAT ex JCS!).

Heterothecae mucronatae var. *mucronatae accedens sed foliis utrinque sparsim strigosis et modice dense glandulosis.*

STEMS several to many, ascending-erect, (3)-12.8-**21.1**-29.5-(32) cm tall, appressed strigose, long hispid hairs numerous; (9)-10-**19**-28-(32) nodes below capitulescence. LOWER STEM LEAVES ovate to oblanceolate, (14)-17.8-**29**-40.3-(45) cm long, (5.3)-6.2-**9.7**-13.2-(15) mm wide, petiolate, cuneate, mucronate, moderately strigose and moderately glandular on both surfaces; margins entire, strigose, some longer hispid hairs near base. UPPER STEM LEAVES oblanceolate, (12)-14.1-**21.5**-29-(33) mm long, (3)-3.7-**6.5**-9.3-(10) mm wide, sessile, usually little reduced upward, acute to obtuse, mucronate tip 0.2-**0.4**-0.6-(0.8) mm long, indument similar to lower, (1)-5-**13**-20-(25) glands/mm², (12)-18-**29**-40-(50) hairs/mm², margins flat. CAPITULESCENCE



Heterotheca mucronata Harms ex B.L. Turner var. *harmsiana* Semple

Figure 24. Morphology and distribution of *Heterotheca mucronata* var. *harmsiana*. A. Habit of mid-size plant, only one shoot drawn. B. Mid stem leaf. C. Upper stem and head with only some florets drawn. D. Mid series phyllary with chlorophyllous zone dark. E. Distribution in northeastern México (aff. var. *harmsiana*).

open cymose-corymbiform, heads 1-1.3-2; peduncles moderately hispid-strigose and moderately glandular, elongating little before anthesis, 3-9.9-18-(26) mm long; bracts none or few, linear-oblongate, usually greatly reduced, rarely foliar and linear-oblongate, indument like leaves. INVOLUCRES narrowly campanulate when fresh, campanulate-hemispheric upon drying, (7.5)-7.9-8.8-9.8-(10) mm high; phyllaries in 4-5 imbricate series, 1/4-1/3 the length of the inner, narrowly triangular-lanceolate, sparsely strigose, sparsely to moderately glandular, margins hyaline narrow, fimbriate-ciliate and anthocyanotic apically; inner ones similar. RAY FLORETS (14)-15-19-23-(24), strap yellow, (9.8)-10.4-13.7-17-(18.8) mm long, 1.2-1.8-2.4-(2.8) mm wide. DISC FLORETS (15)-19-25.5-32-(38), yellow, corolla barely ampliate, (5.7)-5.8-6.5-7.2-(7.5) mm long, lobes (0.5)-0.6-0.7-0.8 mm long, hairs few, 0.1-0.2-0.2.5 mm long. ACHENES 1.6-2-2.4-(2.6)

mm long, moderately strigose; pappus off-white, double, outer whorl of linear scales 0.25-1 mm long, sometimes fused into broader scales, inner whorl of 35-45 barbellate bristle (5.2)-5.4-**6.1**-6.8-(7.1) mm long. Chromosome number: $2n = 18$, one report.

Flowering Period: (May-) JUNE-OCTOBER-(November in south).

Distribution and habitat: Southern Coahuila, Nuevo Leon and Zacatecas, México (Fig. 24E); dry rocky river beds, rocky cactus hillsides, douglas fir and oak forests, mountain pine and chaparral limestone slopes; 1020-2900 m (3350 -9500 ft.) elevation.

Discussion: Variety *harmsiana* is named in honor of Vernon L. Harms who first determined that members of section *Phyllothea* in México were distinct from *H. villosa* (Fig. 41). The variety is distinguished by its sparsely pubescent and moderately glandular leaves and phyllaries. It is distinct from the typical variety of the species in the same way var. *camphorata* differs from var. *echioides* within *H. sessiliflora* spp. *echioides* and var. *minor* differs from var. *villosa* within *H. villosa*. The type material is very short for the species, but otherwise is representative. Like var. *mucronata*, var. *harmsiana* can become repeatedly branched in more favorable habitats.

Specimens from Coahuila can be morphologically similar to narrow-leaved forms of *H. fulcrata* var. *fulcrata*, but the former lack the distinctive foliar bracts typically subtending the heads of the latter. The Coahuilan material may represent a separate variety within *H. mucronata*. Data on these plants is insufficient at this time to justify describing a new taxon. The sample size is too small to determine whether or not differences in phyllary indument, leaf shape and capitulescence form are significantly different. The narrow leaved forms look somewhat similar to the lateral branches that can sometimes develop on damaged or older plants from other parts of the range, e.g., *Henrickson 6284* (LL) and *Henrickson 13302c* (LL).

Specimens examined: MÉXICO. COAHUILA. Mun. Arteaga, Cerro de la Viga, 5 mi SE of Jame, *Sundberg, Nixon, Grimes & Dorr 1771* (NY, TEX). E of Saltillo, Los Alpes and vicinity, *Gentry, Barclay & Arguelles 20128* (ARIZ). S of Saltillo, Cañon San Lorenzo, *Jackson 4097* (TEX). Sierra de Parras N slope and top approached from Ejido Cerro Colorado, *Chiang, Wendt & Johnston 10070B* (LL). NUEVO LEON. 12 km NE of San Antonio Pena Nevada, area of Cero Pene Nevada, *Wells & Nesom 389* (TEX). Chipinque Mesa, between mesa and top, *Phipps 87* (TEX). Chipinque Park SW of Monterrey, *Poole & Watson 1365* (TEX). Chipinque mesa and motel on Mt. SW of Monterrey, *Turner, Ayers & Scott 15616* (TEX). Mun. Galeana: La Becerra *Hinton 19609* (TEX), *Hinton 19667* (TEX), *Hinton 19782* (TEX), *Hinton 19920* (MEXU, TEX), *Hinton 20245* (TEX). Monterrey, near Olinala, *Smith M394* (TEX). Mun. Villaldama, Sierra Gomas, Cañon El Alamo, *Patterson 6698* (TEX), *Patterson 6705* (TEX), *Patterson 6715* (TEX). ZACATECAS. 15 air mi E of Concepcion del Oro, *Henrickson 13302c* (TEX). 3.1 mi above Concepcion del Oro, *Henrickson 6284* (TEX). 1 km E of Aranzazu and 6 km W of Concepcion del Oro, *Johnston, Wendt & Chiang 10476* (TEX).

aff. var. *harmsiana* (most have narrower more acute leaves than typical for the taxon)

MÉXICO. COAHUILA. 29 air mi WNW of Cuatro Ciénegas, N slope of Sierra de la Madera, *Henrickson & Prigge 15341* (TEX). ca. 35 air mi W of Cuatro Ciénegas, *Henrickson 12005* (ASU, TEX). Sierra de la Madera, vicinity of La Cueva, Corte Blanco fork of Charretera, *Johnston 8897* (TEX). Mun. Las Vigas: Canyon de la Carbonera, sierra de Arteaga, *Villarreal & Carranza 3791* (MEXU, TEX). Mun. Muzquiz: 140 km NW of Muzquiz on Coa Hwy 2A, Cuesta del Plomo, *Nesom & Mayfield 7432* (MEXU, TEX). Mun. de Villa Acuna, Serranias del Burro, Rancho El Bonito, Cañon El Toro, *Riskind 2158b* (TEX). K-884 S of Saltillo, *Runyon 1324* (TEX). NUEVO LEON. N of Galeana, Cerro Potosi, *Norris 17744* (CAS).

6. *Heterotheca gypsophila* Turner, *Phytologia* 55: 206. 1984. TYPE: MÉXICO. NUEVO LEON. 4 mi N of Pablillo, on bank of gypsum arroyo in pinyon forest, 21 Jul 1958, *Correll & Johnston 19919* (Holotype: LL!; isotypes: LL!, NY!, TEX!).

Perennial from stout woody taproots, STEMS several to many, ascending-erect, 13-**16.5**-22 cm tall, hispid-strigose, longer spreading hairs scattered along stem; 14-**18**-20-(22) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (15)-18.8-**23.6**-28.5 mm long, (4)-4.8-**6.1**-7.3 mm wide, petiolate, cuneate, mucronate, densely strigose-canescens on both surfaces; margins entire, strigose, a few longer hispid hairs near base. UPPER STEM LEAVES (ob)lanceolate to oblong, (14)-15.2-**17.5**-20 mm long, (3.7)-4-**4.7**-5.4-(6) mm wide, sessile, little upward, indument similar to lower, eglandular, 120-**135**-152-(160) hairs/mm²,

margins flat or only remotely undulate. CAPITULESCENCE open cymose-corymbiform, heads 1-2-3-(5); peduncles densely strigose-canescens, eglandular, (19)-22-32-43 mm long; bracts none or few, linear-oblongate, usually greatly reduced. INVOLUCRES cylindrical to turbinate when fresh, campanulate-hemispheric upon drying, 7-7.7-8.4-(9) mm high; phyllaries in 4-5 imbricate series, outer ones 1/4 to 1/3 length of inner, narrowly triangular, eglandular, densely strigose, margins hyaline narrow, fimbriate-ciliate and sometimes anthocyanotic apically; inner ones similar. RAY FLORETS (11)-12-14-16-(17), strap yellow, (9)-10-11.1-12-(13) mm long, 0.9-1.1-1.2 mm wide. DISC FLORETS 15-20-25, yellow, glabrate, corolla barely ampliate, 5-5.6-6.4-(7) mm long, lobes 0.5-0.6-0.7-(0.8) mm long, hairs few, 0.1-0.2-0.3 mm long. ACHENES 1.5-1.8-2.5-(2.9) mm long, moderate densely strigose; pappus off-white, double, outer whorl of linear scales

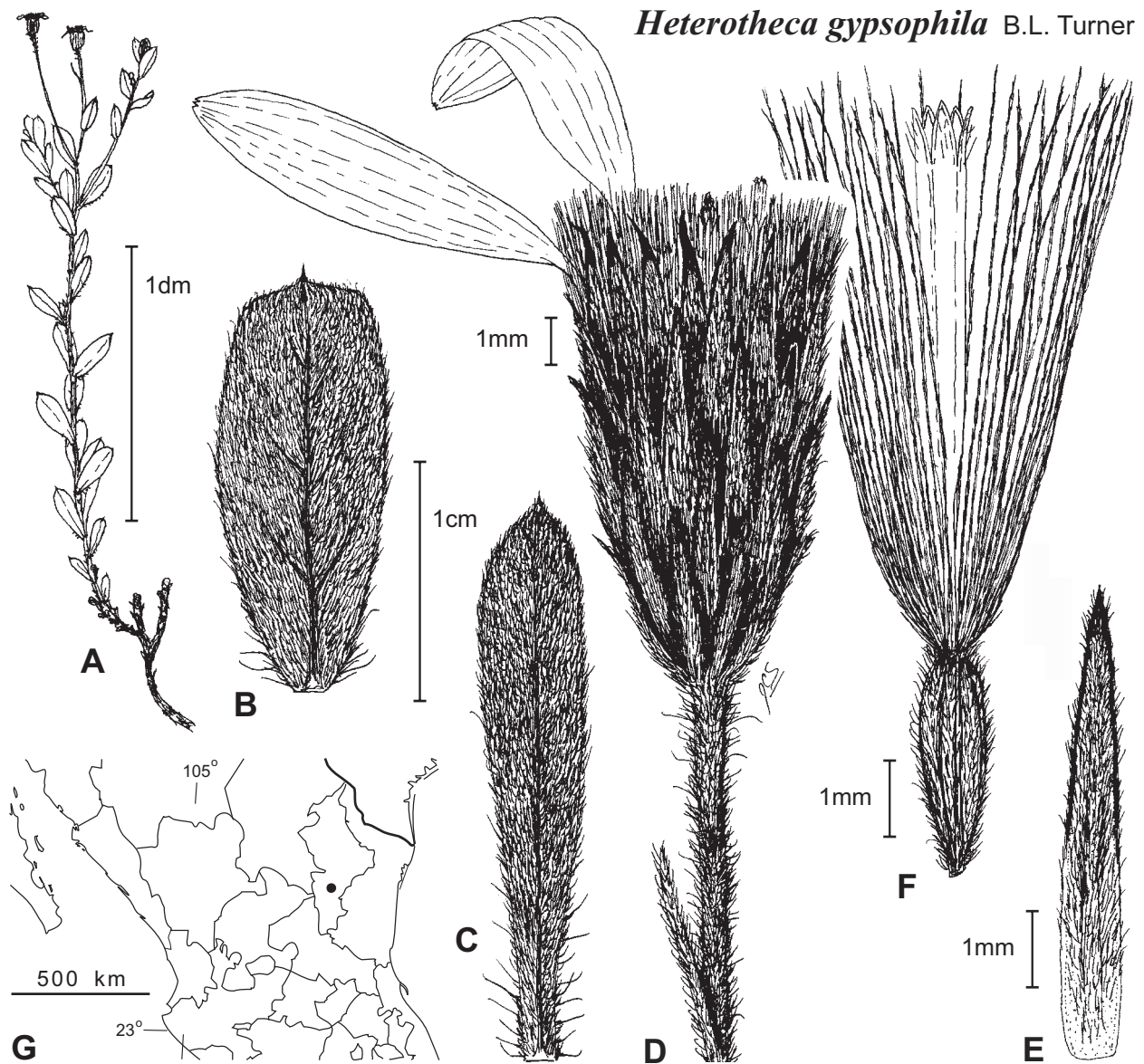


Figure 25. Morphology and distribution of *Heterotheca gypsophila*. A. Habit. B-C. Upper stem leaves, adaxial surface. D. Head with only some florets drawn. E. Mid series phyllary with anthocyanotic margins. F. Mature achene with disc corolla attached. G. Distribution; northeastern México.

0.25-0.75 mm long, inner whorl of 30-40 barbellate bristles 5.1-**6.3**-7.5-(8.6) mm long. Chromosome number: $2n = 36$, one report.

Flowering Period: MAY-JUNE-JULY

Distribution and habitat: Endemic to gypsum soils near Galeana, Nuevo Leon, México (Fig. 25G); 1700-2000 m (5500-6500 ft.) elevation.

Discussion: *Heterotheca gypsophila* (Fig. 25) is similar to *H. mucronata* var. *mucronata* (Fig. 23) except the phyllaries are more densely strigose. The species is endemic to a small area within the range of *H. mucronata* and is clearly closely related to var. *mucronata*. A case could be made to include *H. gypsophila* within *H. mucronata* at the variety or subspecies level. I have deferred here to the delimitation of the Mexican species as originally proposed by B.L. Turner (1984), except for the addition of var. *harmsiana*. More data on within-population variability should be obtained before the existing nomenclature is revised.

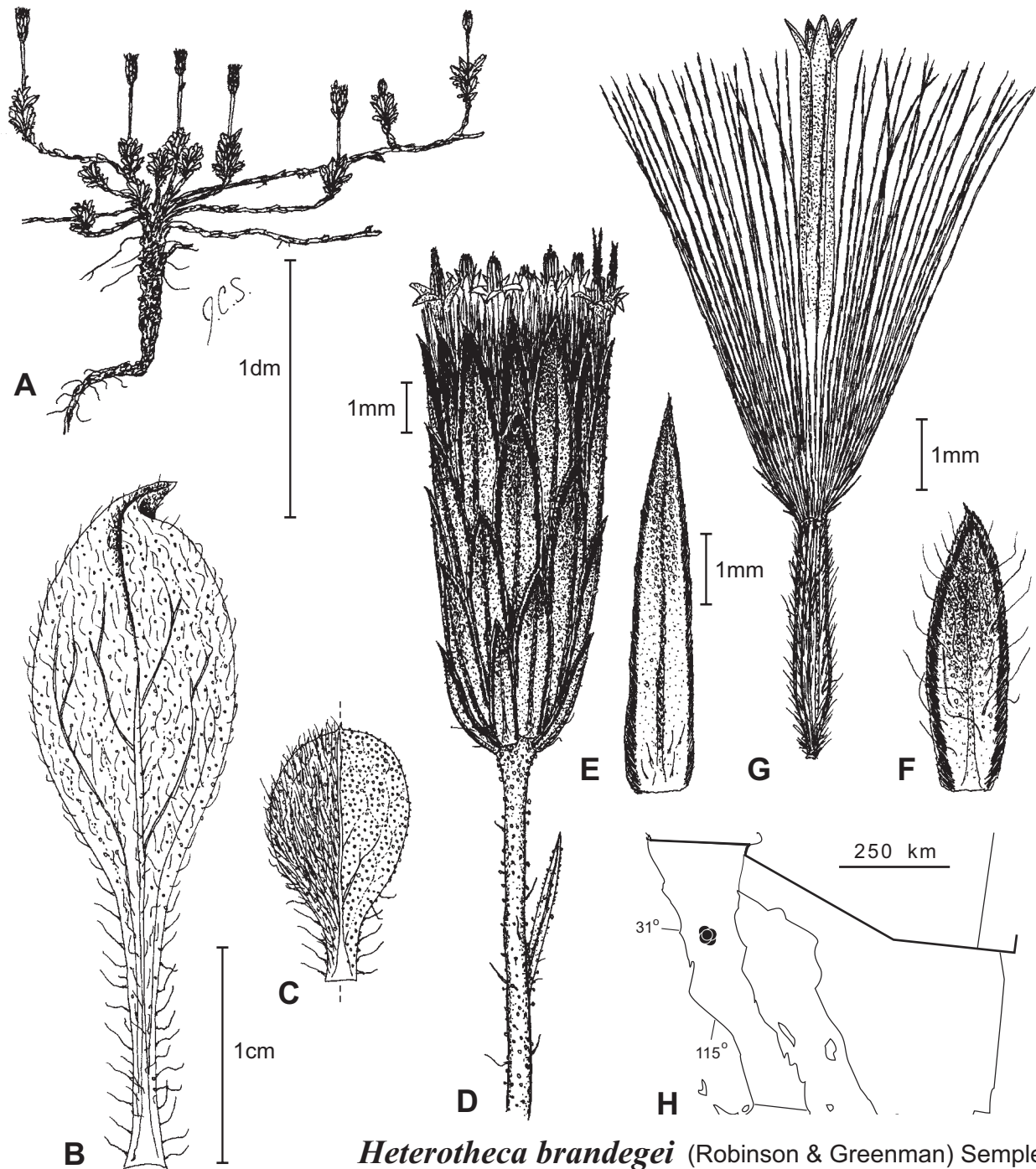
Specimens examined: MÉXICO. NUEVO LEON. S of jct of San Roberto-Linares Hwy and Galeana-Dr. Arroyo Hwy, *Funk, Sanders & Whalen 2750* (OS). Mun. Galeana, El Carrizo, *Hinton 18471* (TEX). S of Galeana, *Turner, Clary & Patterson 93-157* (TEX). SW of Pueblo Galeana, San Francisco Cañon, *Mueller & Mueller 344* (GH). Pabllillo, *Hinton 18476* (TEX). N of Pabllillo, Hwy-51, *Gieschen s.n.* (TEX). S of Pabllillo, *Hinton 18634* (TEX).

7. *Heterotheca brandegei* (Robinson & Greenman) Semple, Syst. Bot. 13: 557 1988. *Chrysopsis brandegei* Robinson & Greenman, Proc. Amer. Acad. 32: 43. 1896. TYPE: MÉXICO. Lower California, San Pedro Martir, May 1893 [not 1883; see Moran (1952), Mexican itineraries of T. S. Brandegee. Madroño 11: 253-262.] (Holotype: *Brandegee s.n* GH!; isotypes: MIN(2!), RM!, UC!)

Heterotheca martirensis Moran, Trans. San Diego Soc. Nat. Hist. 15: 289. 1969. TYPE: MÉXICO. BAHIA CALIFORNIA NORTE. Sierra San Pedro Martir, east rim, north slope of Cerro "2828", common in crevices on flat granitic surfaces at 2800 m el., near 31°02'N, 115°27'W, 14 September 1968, *Moran 15612* (Holotype: SD!; isotypes: CAS!, GH!, K!, MEXU, NY!, RSA!, UC!, UC ex Brandegee!, US!)

Mat-forming perennial from stout woody rootstock to 1 cm thick; rhizomes to 15 cm long, scale-leaves triangular-ovate, obtuse, purple becoming brown, ciliate, grading into foliage leaves. STEMS decumbent to erect, 3.5-**6.7**-9.8-(13.3) cm long including peduncle, sparsely to densely hispid-strigose, hairs 0.5-1.0 mm long, very sparsely to moderately stipitate-glandular; 8-**16**-23 nodes below capitulescence. LOWER STEM LEAVES spatulate to obovate-oblongate, (9)-10.1-**14.9**-19.8-(25) mm long, 3-**4.1**-5.4-(6) mm wide, petiolate, cuneate, mucronate, sparsely to densely hispid-strigose on both surfaces, sparsely to densely stipitate-glandular on both surfaces; margins entire, long hispid hairs below, ciliate above. UPPER STEM LEAVES similar to lower, (9)-10.5-**13.2**-15.9-(16.5) mm long, (2.3)-2.9-**3.8**-4.7-(5) mm wide, little upward, indument similar to lower, 0-**3.5**-14-(17) glands/mm², (2)-3-**11**-18-(25) hairs/mm², margins flat or only remotely undulate, apex sometimes falcate. CAPITULESCENCE of solitary heads; peduncles glabrate to either densely hispid and sparsely glandular or sparsely hispid and densely glandular, (14)-15.2-**27.3**-39.5-(46) mm long, bracts 0-3, linear, 2-3 mm long. INVOLUCRES narrowly campanulate when fresh to hemispheric when dried, (7)-7.4-**8.3**-9.2-(9.8) mm high; phyllaries in 4-5 imbricate series, outer ones 1/4-1/3 the length of the inner ones, narrowly lanceolate-triangular, glabrate to moderately stipitate-glandular or strigose or both, tinted reddish purple, margins hyaline, increasingly fimbriate-ciliate apically; inner ones similar. RAY FLORETS absent. DISC FLORETS 11-**16**-21-(25), yellow becoming red with age, corolla narrowly funnellform, slightly ampliate, 5.6-**6.5**-7.4-(8.3) mm long, lobes 0.5-**0.6**-0.7-(0.8) mm long, glabrous or hairs very few, 0.1-**0.2**-0.3 mm long. ACHENES narrowly obconic to fusiform, (1.3)-1.8-**2.4**-3 mm long, about 10 low ribs, moderately strigose; pappus off-white, double, outer whorl of many linear scales 0.25-1.5 mm long, inner whorl of 35-55 barbellate bristles, 5.8-**6.6**-7.2-(7.8) mm long. Chromosome number: $2n = 18$, two reports.

Flowering Period: MAY-SEPTEMBER.



Heterotheca brandegei (Robinson & Greenman) Semple

Figure 26. Morphology of *Heterotheca brandegei*. A. Habit; aerial shoots can be longer. B-C. Lower stem leaves of robust and diminutive shoots, respectively; pubescent form on left, non-pubescent form on right in C. D. Head with only some florets drawn; peduncle indument can be either more pubescent or less glandular. E-F. Phyllaries with chlorophyllous zone stippled and marginal anthocyanotic region darkened. E. Outer phyllary from pubescent plant. F. Mid series phyllary from sparsely pubescent plant. G. Mature achene with disc corolla attached. H. Distribution; Baja California and adjacent México.

Distribution and habitat: Higher elevations of Sierra San Pedro Martir, Baha California Norte, México (Fig. 26H); rock crevices, granitic outcrops, and decomposing granite in Jeffrey and Sugar Pine forests; sandy loam soil on tonalite; 2000-2900 m (6500-9600 ft.) elevation.

Discussion: *Heterotheca brandegei* is distinguished by its eradiate heads on long peduncles and its small stature (Fig. 26). The species is one of several discoid members of the genus. Its scapose habit and anthocyanotic phyllaries suggest a relationship to members of the *H. mexicana* species group; Moran (1969) noted a similarity to *H. jonesii*. Some individuals are similar to members of *H. mucronata* var. *mucronata* of northeastern México; hispid-villous and glandular leaves (Thorne et al. 61974 RSA). Some individuals are similar to *H. viscida* of southern Arizona and *H. mucronata* var. *harmsiana* of northeastern México; moderately (leaves, phyllaries) to densely glandular (peduncles) and only sparsely hispid-strigose (Moran & Thorne 14257 RSA, TEX).

The implications of this range of variation in indument features in the genus are several. Even in a species with a limited distribution and a relatively few number of populations the full range in indument variation can be encountered. In other species with a greater range in distribution than *H. brandegei* (e.g. *H. sessiliflora*, *H. fulcrata*, *H. mucronata* and *H. villosa*), past periods of isolation apparently have allowed fixation of different alleles controlling indument features in different portions of the range resulting in morphologically more well defined races (generally labelled in this treatment as varieties). In some species, it appears that only a single indument form has persisted; e.g., *H. canescens*, *H. jonesii* and *H. mexicana*.

Specimens examined: MÉXICO. BAHIA CALIFORNIA NORTE. Sierra San Pedro Martir, Almeda & Sauer 2590 (CAS, NY); El Alto de Corona, Moran 17902 (SD); Arroyo Copal., Moran 15435 (SD); Cerro "2828", Helen V. Witham 408 (SD), Moran 15053 (SD); Cerro Botella Azul, Moran 21078 (LL, POM, SD); Cerro Venado Blanco, Boyd, Ross & McCulloh 2321 (F), Moran 15634 (KANU, SD); near E crest, Thorne et al. 57281 (RSA); N of La Corona, Frank Vasek & Oscar Clarke s.n. (SD); E of La Encantada, Meling s.n. (DS); La Grulla, Moran 19172 (SD); Los Llanitos, Moran & Thorne 14257 (DS, RSA, SD, TEX); above Observatory living quarters, Thorne, Elias & Rojas 61974 (RSA), near observatory tower, Thorne et al. 61472 (RSA); road to observatory, Anderson, Moran & Nelson 4696 (NY); El Picacho del Diablo, Moran 25595 (SD); Cañon del Diablo, Moran 25569 (SD); rim overlooking El Picacho de la Providencia, Wiggins 16641A (DS); E of Sam's Corral, Moran 16531 (SD), Moran & Thorne 16537 (SD, RSA); Vallecitos, Thorne et al. 60870 (RSA(2)); above Yerba Buena, Moran & Thorne 14196 (RSA, SD), Morin 15067 (SD).

8. *Heterotheca viscida* (A. Gray) Harms, Rhodora 70: 302. 1968. *Chrysopsis villosa* (Pursh) Nutt. var. *viscida* A. Gray, Synopt. Fl. N. Amer. 1, 2: 123. 1884. *Chrysopsis viscida* (Gray) Greene, Erythea 2: 96. 1894. SYNTYPES: U.S.A. ARIZONA. [Santa Cruz Co.:] Santa Rita Mts., 7500 ft., clefts of dry ledges, 28 May 1881, Pringle s.n. (Lectotype: designated by Harms (1968): GH!; isolectotypes: NY(3)!, PH!). ARIZONA. Chiricahua Mts., Dos Cabezas, Lemmon 207 (GH!, possibly UC ex Lemmon Herb.(2)!). UTAH. American Forks Canyon, 1880, M.E. Jones s.n. (GH! = *Heterotheca fulcrata* var. *fulcrata*).

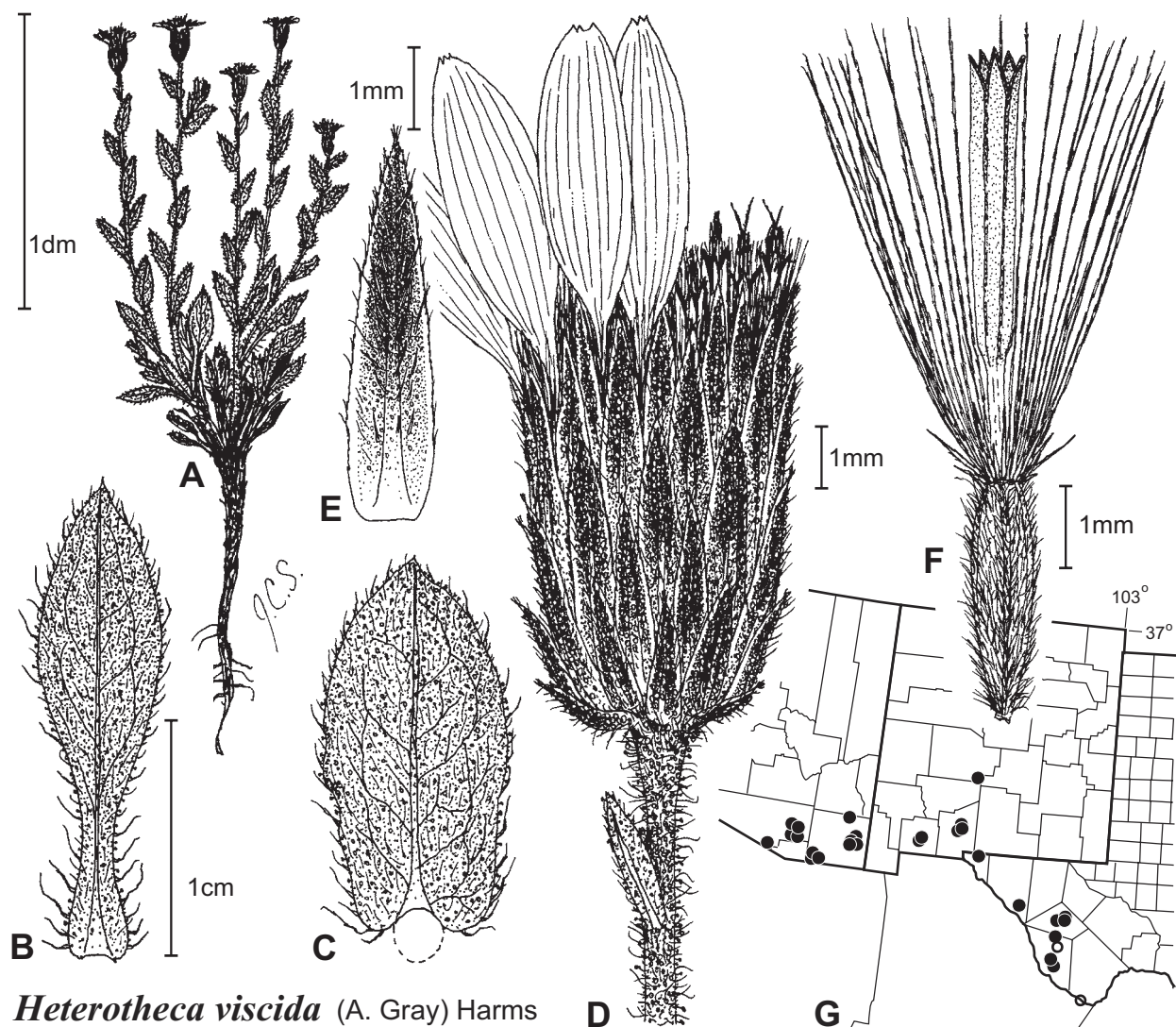
Perennial from stout woody taproots, STEMS several to many, ascending-erect, (13)-16-26-37-(42) cm tall, appressed strigose, long spreading hairs mostly near base; (8)-10-13-16-(20) nodes below capitulescence. LOWER STEM LEAVES ovate to oblanceolate, 23-35-47-(51) cm long, .5-9-12-(15) mm wide, petiolate, cuneate, mucronate, sparsely hispid-strigose on both surfaces; margins entire, hispid-strigose, a few much longer spreading hairs near base. UPPER STEM LEAVES lanceolate to ovate, (11)-16-21-26-(28) mm long, (5)-6.6-9.5-12.5 mm wide, sessile, obtuse to acute, sometimes slightly clasping, little upward, indument similar to lower, (3)-4-15-25-(35) glands/mm², 1-3-4-(6) hairs/mm², margins flat or only remotely undulate, a few much longer spreading hairs near base. CAPITULESCENCE solitary to open cymose-corymbiform, heads 1-4-6-(7); peduncles sparsely to moderately hispid, moderately to densely glandular, (10)-16-25-34-(36) mm long; bracts none or few, linear-oblanceolate, usually greatly reduced. INVOLUCRES campulate when fresh, campanulate-hemispheric upon drying, (7.5)-8-9-10.2-(11) mm high; phyllaries in 4-5 imbricate series, outer ones 1/5 to 1/4 the length of the inner, narrowly triangular, glandular, sparsely strigose, margins hyaline narrow to broad, fimbriate-ciliate and sometimes anthocyanotic apically; inner ones lanceolate. RAY FLORETS (9)-12-15-18-(20), strap yellow, (10)-11-11.8-12.5-(13) mm long, (0.7)-1-1.5-1.9-(2.5) mm wide. DISC

FLORETS 16-41-76-(98), yellow, glabrous, corolla somewhat ampliate, (5)-5.3-6-6.8-(7.5) mm long, lobes 0.5-0.6-0.7-(0.75) mm long, hairs few, 0-0.25 mm long. ACHENES 1.6-2-2.5 mm long, moderately strigose; pappus off-white, double, outer whorl of linear scales 0.2-1 mm long, inner whorl of 25-40 barbellate bristles 5-5.6-6.2-(7) mm long. Chromosome number: $2n = 18$.

Flowering Period: MAY-JUNE-JULY to October.

Distribution and habitat: Mountains of southeastern Arizona to Trans-Pecos Texas (Fig. 27G); clefts and crevices in cliffs and dry ledges, rocky slopes in oak-manzanita chaparral and ponderosa pine and gambel oak woods; on igneous rocks and igneous soils, rhyolite tuff; 1500-3000 m (4900-9560 ft.) elevation.

Discussion: *Heterotheca viscida* is distinguished by its (ob)ovate, moderately glandular and hispid-strigose leaves and its pedunculate heads without specialized subtending foliaceous bracts (Fig. 27). The plants from



Heterotheca viscida (A. Gray) Harms

Figure 27. Morphology and distribution of *Heterotheca viscida*. A. Habit. B-C. Lower and upper stem leaves, respectively, adaxial surface. D. Head with only some florets drawn. E. Mid series phyllary with chlorophyllous zone dark. F. Mature achene with disc corolla attached. G. Distribution in Arizona, New Mexico, Texas and adjacent México (○ aff. *viscida*).

Texas generally have oblanceolate leaves and smaller heads and can be similar to forms of *H. fulcata* var. *arizonica* and var. *senilis* (Fig. 30). The species typically blooms earlier in the season than related species.

Heterotheca viscida represents a morphological link between the *H. mucronata* complex of northeastern México and the *H. fulcrata* complex of northern México and the southwestern United States. The realization that the range of *H. fulcrata* var. *arizonica* extended into the Big Bend region of Texas and México solved the problem of how to treat the smaller leaved glandular plants that otherwise might have been included in *H. viscida*, but would have been very atypical in this species.

Specimens examined: U.S.A. ARIZONA. Cochise Co.: Chiricahua Mts., Cave Creek Cyn., *Kusche s.n.* (CAS); Chiricahua Pk., *Leithliter & Leithliter 468* (ASU); S of Chiricahua Saddle, *Leithliter & Leithliter 115* (ASU); Rucker Cyn., *Leithliter & Leithliter 753 & 758* (ASU); Saulsbury Tr., *Leithliter & Leithliter 410* (ASU); Winn Falls, *Wittmann 90* (WTU), *Wittmann 102* (WTU). Chiricahua N. Mon., *Rapson s.n.* (ASU); Bonita Cyn., *Reeves R1384* (ASU, NY). Bootlegger Saddle, *Gallagher 205* (ASU). Massai Pt. Tr. at Echo Cyn. Tr., *Reeves R2798* (ASU(2)). Sugarloaf Mt., *Reeves R982* (ASU), just past the "Arch," *Reeves R2* (ASU), near tunnel, *Reeves R2895* (ASU); Totem Cyn., *Reeves R1917* (ASU), *Reeves R2818* (NY); Rustler's Park, *Goodman & Hitchcock 1187* (CAS, GH, MIN, NY, RM, LL, UC). Dos Cabezas Mts., around "heads", *Bingham 2658* (ASU), below heads, *Bingham 2480* (ASU). Huachuca Mts., *Pringle s.n.* (NY); Millers Cyn., *Gooding 102* (NY). Santa Cruz Co.: Mt. Wrightson (Baldy), *Parker 5855* (UC). Santa Rita Mts., *Jones s.n.* (POM), *Pringle s.n.* (GH, NY, PH), *Kearney & Peebles 10570* (DS, LL). NEW MEXICO. Dona Ana Co.: Organ Mts., Filmore Canyon, *Wooton s.n.* (NMC), Organ Needle, *Spellenberg & Dunford 5432* (NMC). Rio Grande valley below Donana, *Parry 510c&d* (NY), White Rocks, Camp Bache, *Bigelow 510* (NY). Luna Co.: Florida Mts., *Worthington 11932* (NMC, NY, TEX); WNW top of Gym Pk., *Worthington 19594* (TEX). Socorro Co.: White Sands Missile Range, Mockingbird Mts., *Spellenberg, Brozka & Hoban 10597* (NMC). TEXAS. Culberson Co.: Guadalupe Mts., Smith Cyn., *Turner 1253* (SRSC). El Paso Co.: Franklin Mts., Canutillo, *Barlow s.n.* (UC). Hudspeth Co.: Eagle Mts., *Turner 7827* (SRSC). Jeff Davis Co.: Davis Mts., *Young s.n.* (UC). Ajuga Cyn., *Correll 33350* (NY). Little Aguja Cyn., *Palmer 34530* (GH, LL), *Moore & Steyermark 3071* (CAS, GH, NY, UC). Lower Madera Cyn., *Poole, Brown & Diamond 2584* (TEX). Mt. Livermore, *Correll 13540* (NY), *Correll 33760* (LL), *Ferris & Duncan 2595* (NY, POM), *Hinckley s.n.* (GH, SRSC, TEX), *Hinckley s.n.* (NY), *Hinckley 70* (NY). Sawtooth Mt., *Correll 34988* (GH, TEX). NW of Sawtooth Mt., *Hall s.n.* (SRSC). Timber Mt., *Hinckley 193-A* (SRSC), *Hinckley & Hinckley 196* (SRSC), *Warnock 6495* (SRSC). Presidio Co.: Chinati Mts., Chinati Pk., McVaugh 7463 (LL), *Powell & Powell 3099* (LL, SRSC). Horse Creek Cyn., *Hinckley 2563* (NY, SRSC, TEX). Tigna Cyn., *Warnock & Hinckley 46873* (SRSC).

aff. *viscida* (approaching *H. fulcrata* var. *arizonica* or var. *senilis*)

MÉXICO. CHIHUAHUA. Fern Canyon side canyon of Sta. Elena Cyn. of the Rio Grande, on S side of river, ca. 3 mi W of picnic area of Big Bend N.P., Texas, *Wendt & Lott 96* (TEX). U.S.A. TEXAS. Presidio Co.: S of Marfa, *Hinckley 698* (NY(2)). San Esteban Cyn., *Warnock, McBryde & Cox 14465* (LL, SRSC).

9. *Heterotheca fulcrata* (E.L. Greene) Shinnery, Field & Lab.29: 71. 1951. *Chrysopsis fulcrata* Greene, Bull. Torrey Bot. Club.25: 119. 1898. SYNTYPES: NEW MEXICO. Dona Ana Co.: Organ Mts., *Wooton 510*. Lectotype: NDG 053814!; isolectotypes: MIN!, NY!, US!. Lincoln Co.: White Mountains, 6300 ft, near Cherokee Bill's Spring, 21 Aug 1897, *Wooton 511* (NDG-053811!, NY!, US!); *Wooton 512* (NDG-053815!; NY!, US!) [See Semple (1987) for discussion of typification and opinions by Wooton and Standley (1913, 1915), Shinnery (1951), and Harms (1968).]

Perennial from stout woody taproots; STEMS several to many, ascending-erect, (17)-23-37-49-(79) cm tall, sparsely to densely hispid-strigose and sparsely to densely stipitate-glandular; (8)-13-26.5-40-(69) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (13)-22-34-46-(60) cm long, (3.5)-5.3-7.6-10-(14) mm wide, subpetiolate to merely cuneate, mucronate, very sparsely to moderately glandular and sparsely to densely strigose-canescenscent on both surfaces; margins entire, strigose, a few longer hispid hairs near base. UPPER STEM LEAVES ovate to lanceolate, (12)-16-24.9-34-(55) long, (4)-4.9-7.6-10.3-(15) wide sessile, little upward to larger, indument similar to lower leaves or more glandular, 0-12-23-(48) glands/mm², (2)-4-39-74-(150) hairs/mm²; margins with a few longer hairs from base to apex. CAPITULESCENCE open to compactly cymose-corymbiform, heads 1-7-15-(43); peduncles sparsely to densely strigose-canescenscent, sparsely to moderately stipitate-glandular; bracts few, foliar, ovate to narrowly lanceolate, usually the upper most subtending or just below head. INVOLUCRES cylindrical to turbinate when fresh, campanulate-hemispheric upon drying, (5.7)-6.6-7.9-9.1-(10.3) mm high; phyllaries in 4-5 imbricate series, outer ones 1/4 to 1/3 the length of the inner ones, narrowly triangular, sparsely stipitate-glandular, sparsely to moderately strigose, margins hyaline broad, fimbriate-ciliate apically; inner ones similar. RAY FLORETS (5)-11-16-21-(34), strap

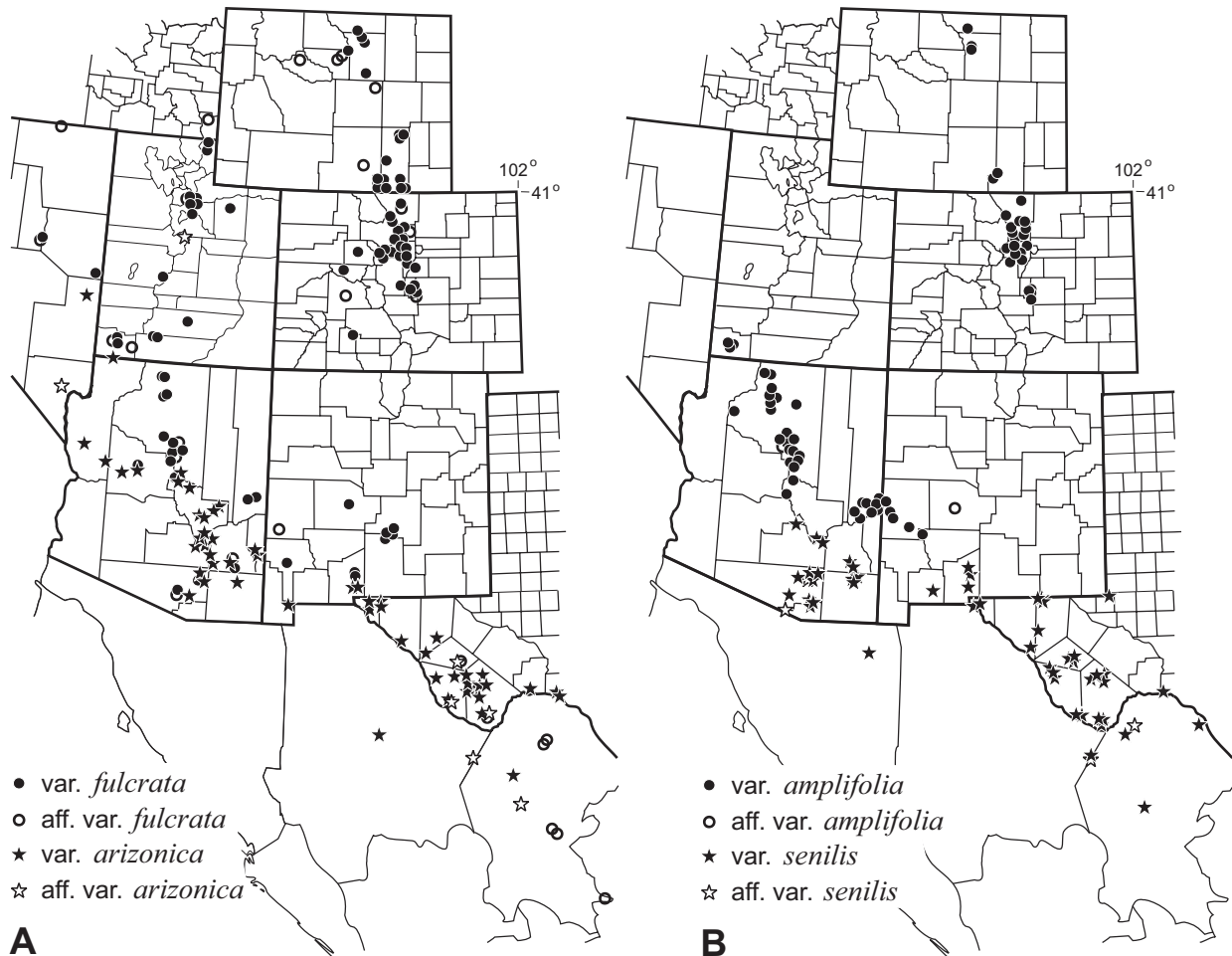


Figure 28. Distribution of *Heterotheca fulcrata* in the central and southern Rocky Mountain states of the United States and adjacent México. **A.** *Var. fulcrata* and *var. arizonica*. **B.** *Var. amplifolia* and *var. senilis*.

yellow, (7.3)-9.3-**11.2**-13.2-(15.8) mm long, (0.5)-1.1-**1.5**-2.0-(2.7) mm wide, tube glabrate. DISC FLORETS (12)-26-**46**-66-(110), yellow, glabrate, corolla barely ampliate, (4.3)-5.1-**5.7**-6.3-(7.5) mm long, lobes (0.4)-0.6-**0.7**-0.8-(0.9) mm long, hairs few, 0.05-**0.1**-0.2-0.3 mm long. ACHENES (1.5)-1.8-**2.4**-2.9-(4.0) mm long, sparsely to moderately strigose; pappus off-white, double, outer whorl of linear scales 0.25-1 mm long, inner whorl of 35-45 barbellate bristles (4.3)-5-**5.8**-6.5-(7.8) mm long. Chromosome numbers: $2n = 18$, numerous reports; 36, one unconfirmed report.

Flowering Period: (May)-JULY-SEPTEMBER-(November)

Distribution and habitat: Lower to mid elevations in the Front Range of Colorado and southern Wyoming and Big Horn Mts. of northern Wyoming; Lincoln Co., New Mexico; northern Wasatch Plateau of Utah; scattered forested locations in southern Utah and Arizona (Fig. 28); pine forests and adjacent open slopes and grasslands, chaparral transition at lower elevations; 600-3050 m (2000-10000 ft.) elevation.

Discussion: *Heterotheca fulcrata* is distinguished by the one to several modified bracts subtending the involucre on at least some heads of the capitulescences (Figs. 29 E, 30A-B). These bracts are usually ovate

lanceolate. In plants with large ovate upper stem leaves, the bracts are sometimes hidden by the leaves. In plants with small lanceolate upper stem leaves, the bracts may be larger than the upper most peduncular leaves and are usually more ovate or broadly lanceolate. Rarely, such bracts are missing below most heads making identification problematic. The numbers of hairs and glands per unit of leaf area, the size and shape of the leaves and the numbers of florets per head vary greatly within the species. Four varieties are recognized on the basis of differences in these traits and in the frequency of larger hairs along the leaf margins: var. *fulcrata*, var. *amplifolia*, var. *arizonica*, and var. *senilis*. All four are sympatric in southeastern Arizona and adjacent New Mexico (Fig. 28) along the Mogollon Rim and in the mountains south of the escarpment. Many intermediate forms occur throughout the range, and pure and mixed varietal populations occur in areas of sympatry. Forms of the typical variety occur throughout nearly all of the range of the species except for the southern most portion of the range in northern México. In northern Nevada, southern Idaho and northern Wyoming collections are atypical and easily misidentified as aberrant forms of *H. villosa*.

9.1 *Heterotheca fulcrata* (E.L. Greene) Shinnery var. *fulcrata*

Chrysopsis fulcrata Greene, Bull. Torr. Bot. Club. 25: 119. 1898. SYNTYPES: NEW MEXICO. Donna Ana Co.: Organ Mts., *Wooton 510* (Lectotype: NDG 053814!; isolectotypes: MIN!, NY!, US!). Lincoln Co.: White Mountains, 6300 ft, near Cherokee Bill's Spring, 21 Aug 1897, *Wooton 511* ("Lectoparatype": NDG-053811!; "isolectoparatypes": NY!, US!); *Wooton 512* ("Lectoparatype": NDG-053815!; "isolectoparatypes": NY!, US!). Harms (1968) noted that Wooton and Standley (1913, 1915) considered *Wooton 510* from the Organ Mts. as the lectotype. Shinnery (1951) designated *Wooton 511* (NDG) as "LECTOTYPE."

Chrysopsis cryptocephala Woot. & Standl., Contrib. U.S. Nat. Herb. 16: 179. 1913. TYPE: NEW MEXICO. sect. 23 of V Pasture, White Mts., 23 Jul 1905, *Wooton s.n.* (Holotype: US-563739!)

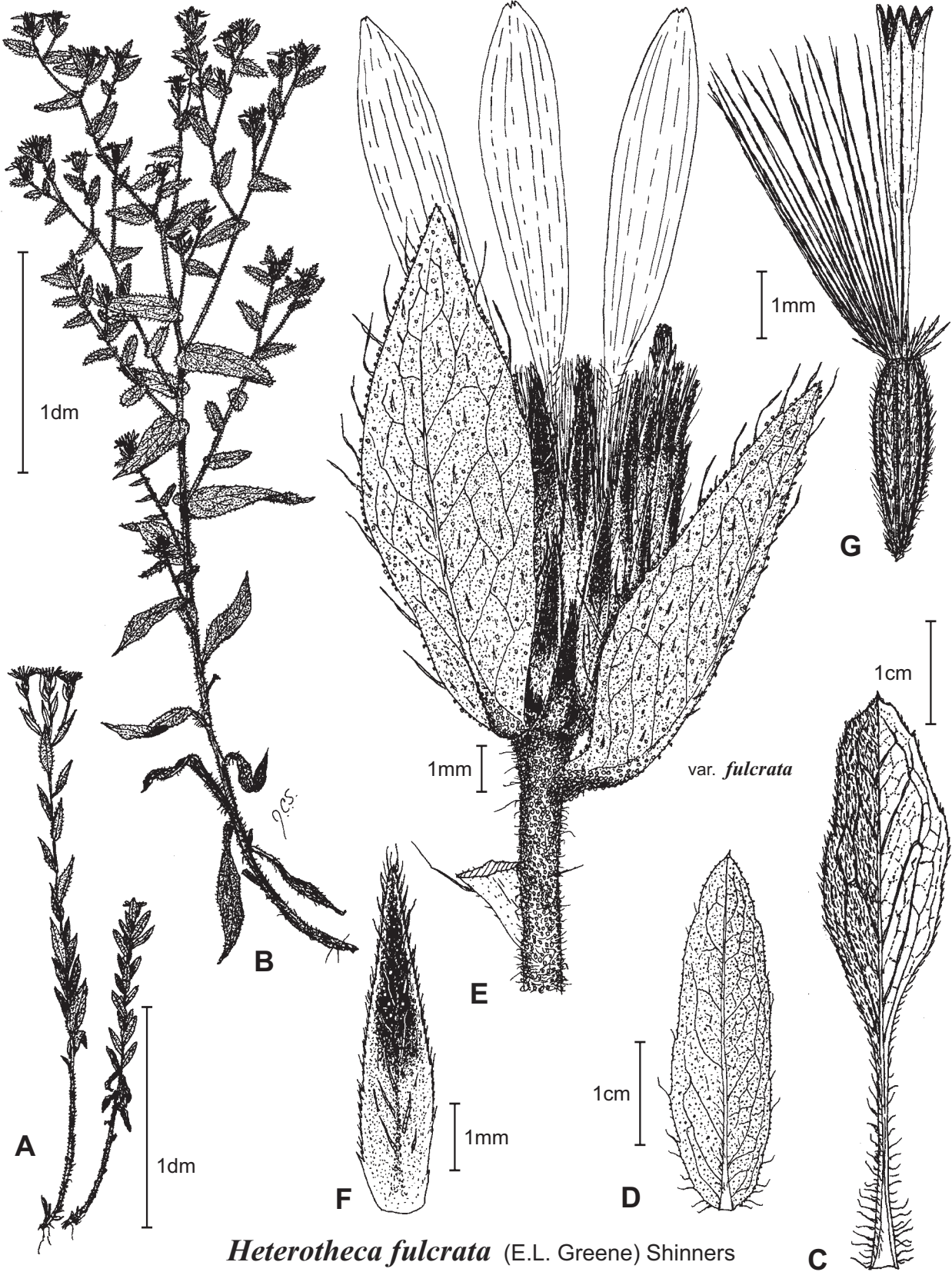
Chrysopsis resinolens A. Nels., Bull. Torrey Bot. Club 28: 232. 1901. TYPE: WYOMING. Albany Co., open slopes in the foothills of Laramie Peak, 13 Jul 1900, *Nelson 7583* (Holotype: RM!; isotypes: RM ex Osterhout!, GH!, MIN!, NY!(2), US!)

Chrysopsis resinolens var. *ciliata* A. Nels., Bull. Torr. Bot. Club. 28: 233. 1901. *Chrysopsis viscida ciliata* (A. Nels.) Blake in Tidestrom, Contrib. U.S. Nat. Herb. 25: 537. 1925. TYPE: WYOMING. Albany Co., on sandy river banks, Dunn's Ranch, 16 Jul 1900, *Nelson 7560* (Holotype: RM!; isotypes: NY!, US!)

Chrysopsis elata Osterhout., Bull. Torr. Bot. Club 57: 560. 1931. TYPE: COLORADO. Eagle Co., Red Cliff, 16 Aug 1906, *Osterhout 3359* [in error 3335] (Holotype: RM!; isotype: NY!)

STEMS several to many, ascending-erect, (17)-23-36-49-(79) cm tall, sparsely to moderately hispid-strigose and sparsely to moderately glandular; (8)-11-20-29-(44) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (19)-30-41-52-(60) cm long, (4.0)-5.8-8.2-10.5-(14) mm wide, subpetiolate to merely cuneate, very sparsely to moderately glandular and strigose-canescens on both surfaces. UPPER STEM LEAVES ovate to lanceolate, (12)-16-29.5-38.7-(55) mm long, (5)-5.6-8.4-11.2-(15) mm wide, sessile, very sparsely to moderately glandular and sparsely to moderately densely strigose, 0-3-13-23-(48) glands/mm², 2-4-29-58 hairs/mm². CAPITULESCENCE cymose-corymbiform, heads (1)-9-18-(43); peduncles sparsely to moderately strigose, sparsely to moderately stipitate-glandular; bracts few, sometimes nearly equal to upper leaves in size, indument like upper leaves. INVOLUCRES (6)-6.7-7.9-9.2-(10.3) mm high; phyllaries in 4-5 imbricate series, 1/4-1/3 the length of the inner, narrowly triangular, glandular, strigose, margins hyaline, wide, fimbriate-ciliate apically; inner ones similar to more lanceolate. RAY FLORETS (7)-11-15-19-(21), strap (7.8)-9.8-11.5-13.3-(14.5) mm long, (0.9)-1.1-1.5-1.9-(2.5) mm wide. DISC FLORETS (12)-25-38-54-(69), corolla (4.3)-5-5.6-6.3-(6.9) mm long, lobes (0.5)-0.6-0.7-0.8-(0.9) mm long. ACHENES (1.6)-1.9-2.4-2.9-(4.0) mm

Figure 29. Morphology of *Heterotheca fulcrata* var. *fulcrata*. A-B. Shoots; plants from dry and shaded moist soil, respectively. C. Basal stem leaf of seedling. D. Mid stem leaf of the *resinolens* morphotype; adaxial surface on left, abaxial surface on right. E. Head with only some florets drawn; subtending foliar bracts vary in size and shape. F. Mid series phyllary with chlorophyllous zone dark; indument varies. G. Mature achene with disc corolla attached. ➔



Heterotheca fulcrata (E.L. Greene) Shinnery

long, sparsely to moderately densely strigose; inner whorl of 35-45 barbellate bristles (4.3)-5-5.8-6.6-(7.6) mm long. Chromosome numbers: $2n = 18, 36$.

Flowering Period: (Late June)-AUGUST-SEPTEMBER(-October)

Distribution and habitat: Ponderosa Pine forests and open upper grass and sagebrush slopes of Front Range Rocky Mts. in Wyoming and Colorado with extensive disjunct populations in Utah, Arizona and New Mexico; very rare and atypical in adjacent México and Idaho, Nevada and Texas (Fig. 28A); riparian zones in ponderosa pine and Douglas-fir, grassy clearing in ponderosa pine forest, lower spruce-fir zone, sandy river banks, road sides; coarse sandy granitic soils with gravel, crushed lava gravelly soils, moist disturbed soils, shale slopes with sandstone outcrops; (1500m)-1800-3050 m ((5000)-6000-10000 ft.) elevation.

Discussion: Variety *fulcrata* is the most variable member of *H. fulcrata* (Fig. 29). It is characterized by having more hairs than glands per unit area of leaf surface with the numbers of hairs being few to moderate. The lectotype is rather pubescent for the variety, which also appears to be very plastic in leaf shape and size. Plants from wetter microhabitats in a population often have large leaves, while those from drier microhabitats have narrower, smaller leaves. In open higher elevation sites, plants tend to have narrow lanceolate rather than ovate leaves. This morph was described as *Chrysopsis resinolens*, which is treated here as a synonym because the two morphs are merely forms on a continuum of variation in leaf shape and size.

Many collections have been made that are morphologically intermediate in indument features with var. *amplifolia*. A few intermediates with the other two varieties have also been collected, as well as a number of possible hybrids with *H. pumila* (Fig. 33) and several varieties of *H. villosa*. Variety *fulcrata* is thus like var. *minor* in *H. villosa*; both are the matrix through which the other varieties are united. In the Laramie Hills east of Laramie, Wyoming, the variety is often difficult to separate from large-leaved intermediates between *H. villosa* var. *foliosa* and var. *minor*; a number of collections may be from hybrid swarms involving all three taxa. The few tetraploids found in the variety are aberrant and may be odd forms involving genes introgressed from *H. villosa*. At the extreme western limits of the range in Nevada and Idaho, plants tend to have reduced peduncular bracts that make the plants difficult to distinguish from forms of *villosa* var. *scabra*. Such plants could be treated as odd morphs of the latter taxon, but I believe that they are marginal population variants of var. *fulcrata*. Experimental work is needed to determine the extent of possible hybridization between marginal populations of var. *fulcrata* and the sympatric varieties of *H. villosa*.

Specimens examined: MÉXICO. COAHUILA. N of Campo Dos, trail to Campo Tres, *Wendt & Adamcewicz 526* (LL, MEXU). Sierra del Pino, vicinity of La Noria, *Johnston & Muller 506* (TEX). SONORA. SE of El Tigre, Cañon Internacional, *White 3493* (GH). U.S.A. "Rocky Mts.", *Thomas s.n.* (MIN). ARIZONA. E of Turkey Tanks, *Wooton s.n.* (NMC). Apache Co.: US-666 S of US-180, *Warnock 1677* (TEX). Coconino Co.: SW of Little Eden Spring, *Morefield, Roberts 2935* (RSA). S of Flagstaff, *Semple & Chmielewski 9007* (WAT); Oak Crk Cyn., *Russell, Smith & Walters 10843* (ASU), *Purpus 8245* (UC), *Semple & Chmielewski 9009* (WAT); S of Pine Flat Campground, *Semple & Chmielewski 9011* (WAT). Grand Cyn. N.P., N of Cape Royal, *Halvorson 205* (ASU). N of Sedona, Oak Cr., *Pinkava & Pinkava 14073* (ASU). Walnut Cyn., *Joyce 459* (WS). Gila Co.: Strawberry Hill, N of Pine, *Collom 418* (ASU). Graham Co.: Pinaleno Mts., above Arcadia Campground, *Keil, Pinkava & Lehto 10210* (ASU). Yavapai Co.: Stoneman L., *Pinkava & Pinkava 14071* (ASU). COLORADO. *Patterson s.n.* (WIS-27631), *Patterson s.n.* (WIS-13956). "Northern Colo.", *Kuntze 2984* (NY). Buffalo Creek Cyn., *Rusby s.n.* (NY). Cherokee Park, *Nelson 10007* (DS, RM). Shaffers Crossing, *Zobel s.n.* (CAS). Wagon Wheel Gap, *Griffin 173* (RM). Boulder Co.: Boulder, Mt. Alto, *Ramaley s.n.* (RM); near Boulder, *Tweedy 5848* (NY). W of Boulder, *Harms 2101-A* (KANU, SASK). Boulder Cyn., above Boulder Falls, *Weber & Barkley 14419* (BRY, MIN, NY, SD), W of Boulder Falls, *Semple et al. 6538* (JCS, MT, RM, WAT); Rogers Park, *Weber 8627* (CAS, MIN). Boulder Mt., Bear Cyn., *Hogan 1969* (WAT). Cole Creek Cyn., *Freeman 5* (ASU), *Freeman 9* (ASU). Eldora, *Clokey et al. 4318* (CAS, NY, UC, WIS). Eldorado Springs St.P., *Brewster 35* (BRY), *Brewster 47* (BRY). L. Eldora, *Clokey s.n.* (TEX), *Clokey 3199* (CAN, CAS(2), DS, GH, RM, UC, WTU). Pine Glade School, *Ramaley 3768* (NMC). E of Nederland, *Haber & Given 2004* (CAN), *Harms 2100* (KANU, SASK). N of Raymondville, *Wagenknecht 2988* (KANU, SASK). Between Sunshine and Ward, *Tweedy 4896* (NY). Ward, *Clokey et al. 4326* (NY, RM, UC). Clear Creek Co.: W of Bergen Park, *Higgins 8139* (ASU, NY). Clear Cr. Cyn., Forks Cr., *Moyer s.n.* (MIN). Near Echo L., *Ehlers 8303* (TEX). Near Empire, *Patterson 224* (GH, MIN, NY, PH). Idaho Springs, *Bates 7067* (TEX); near Idaho Springs, *Downing s.n.* (WIS); SW of Idaho Springs, *Semple & Zhang 10469* (RM, WAT). W of Idaho Springs, *Harms 2095* (KANU, SASK). Douglas Co.: SW of Sedalia, *Waterfall 14951* (GH, UC). El Paso Co.: SE of Crystola, *Anderson 2769* (DS). Colorado Springs, *Harms 2030* (KANU, SASK). Manitou, *Nelson 8614* (RM). Pikes Pk., Ruxton Dell, *Bacigalupi 831* (DS, GH, UC). Red Rock Cyn., *Bessey s.n.* (NY). Gilpin Co. *Ramaley & Robbins 3444* (NMC, RM). N of Blackhawk, *Harms 2097*

(KANU, SASK). Central City, *Orahoad s.n.* (USFS). N of Central City, *Pennell, Ewan & Schaeffer 24553* (GH). Headwaters of Clear Crk, *Parry 59* (GH, NY). E of Idaho Springs, *Harms 2096* (KANU, SASK), *Semple et al. 5804* (COLO, JCS, WAT). N of Rollinsville, *Harms 2099* (KANU, SASK). S of Rollinsville, *Semple et al. 5808* (CAN, COLO, JCS, MO, MT, WAT). Tolland, *Hall 10492* (UC), *Rankin s.n.* (NY(3)), *Rankin s.n.* (NY), *Zobel s.n.* (CAS(2), NY); Mammoth Gulch, *Munz 3187* (RSA). Jackson Co.: S of Rand, *Wagenknecht 3027* (KANU, SASK). Jefferson Co.: near Golden, *Ehlers 8266* (TEX). NW of Indian Hills, *Waterfall 3290* (GH). Pine Jct., Wandcrest Park, *Semple & Brammall 2707* (WAT). Larimer Co.: *Johnson 299* (RM). "Mountains" *Cowen s.n.* (NY), *Osterhout s.n.* (MIN, WTU). Beaver Cr., *Osterhout 5538* (RM). Bennett Camp Ground, *Lappin 199* (TEX). Chalmers L., *Wagenknecht 3040* (KANU, SASK). Dale Cr., *Osterhout 5541* (RM). W of Drake, *Sundberg 2548a* (TEX). Estes Park, *Cooper s.n.* (NMC), *Cooper s.n.* (MIN), *Cooper s.n.* (RM), *Cooper 184* (RM), *Osterhout 5153* (RM). S of Estes Park, Lily Mt., *Cooper s.n.* (MIN, NMC), *Stein 1944* (MO, RM); near Estes Park, *Johnston 699* (RM), *Moyer 3657* (MIN). Lone Pine Cr., *Osterhout 1792* (NY, RM, RSA). Moraine Park, Windy Gulch, *Osterhout 5553* (RM, RSA). Rocky Mt. N.P., *Harms 2110* (KANU, SASK), *Knowlton s.n.* (GH), *Meyer & Meyer 2471* (NY, UC), *Wagenknecht 3044* (KANU, SASK); Bear L., *Wagenknecht 2998* (KANU, SASK); Cub L. Trail 8, *Baker 4584a* (LL); below Fall R. Pass, *Rollins 1886* (LL, NY); near Glacier Basin, *Peirson 12548* (RSA); Hidden Valley Ranch, *Nelson & Nelson 4532* (DS, UC(2)); Mill Cr. Fish Pond, *Fullerton s.n.* (RM); Twin Sisters, *Baker 4620a* (LL). E of Rocky Mt. N.P., *Wagenknecht 3048* (KANU, SASK). Roosevelt N.F., Fish Crk Campground, *Ginter 596* (USFS). Thompson Cyn., below the Forks, *Osterhout 5423* (RM). Park Co.: W of Pine Junction, *K.Shea 355* (WAT). W of Wilkinson Pass, *Semple & Heard 7735* (WAT). Pitkin Co.: White R. N.F. between Marroon L. and Crater L., *Tomb 314* (TEX). Summit Co.: Breckenridge, *Shear 4569* (NY). E of Frisco, *Lowry 1303* (NY). Grays Peak, *Smith s.n.* (NY). Below Loveland Pass, *Harms 2092-A* (KANU, SASK). Teller Co.: near Crystola, Ute Pass, *Ehlers 7726* (GH). Divide, Cripple Cr., *Clokey 3886* (CAN, CAS, DS, GH, LL, MIN, NY, RSA, UC, WS, WTU). E of Florissant, *Semple & Brouillet 7248* (COLO, WAT); near Florissant, *Ramaley 1401* (RM). Pike N.F., Manitou Exp. Stat, *Gierisch 2649* (RM), *Jones & Sealander 100* (RM). Pikes Peak Rd., *Harms 2011* (KANU, SASK). Woodland Park, *Bogusch & Molby 4883* (LL). NEW MEXICO. Dona Ana Co.: Organ Mts., Old Tip Top, *Metcalfe s.n.* (NMC). Grant Co.: Silver City, *Greene s.n.* (GH, NY). Lincoln Co.: Capitan Mtns., E of Capitan Pass, *Baad 893* (WTU). Ruidoso, *Ward & Spellenberg 81-449* (NMC, NY). Otero Co.: SW of Ruidoso, N of Res. Rd-4, *Semple & Heard 8149* (WAT). NEVADA. Elko Co.: Ruby Range, Lamaille Cyn., *Maquire & Holmgren 22052* (GH). UTAH. Duchesne Co.: Boneta, *Brotherson 3356* (BRY). Garfield Co.: N of Escalante, *Higgins 11119* (BRY, NY). Kane Co.: N of Glendale, *Higgins 10922* (ASU, BRY, NY). Paunsagaunt Plateau, E fork of Sevier R., *Welsh & Taylor 14317* (BRY). Millard Co.: Pavant Range, Mine Camp Peak, *Greenwood s.n.* (BRY). Salt Lake Co.: Big Cottonwood Cyn., *Garrett 1585* (DS(2), GH, NY, RM); Lake Blanche, *Cottam 6284* (LL). Brighton, *Cooper s.n.* (MIN). Near Salt Lake City, *Moldenke & Moldenke 2106* (NY; mixed collection with *H. zionensis*). Summit Co.: East Cyn., *Garrett 5466* (LL). Wasatch Mts, Gogorza, Parley's Cyn., *Garrett 2304a* (LL, NY, RM). Utah Co.: Wasatch Mts., Mt. Timpanogos, *Garrett 3887* (LL), *Garrett 5712* (LL). Stewarts Cascade, *Welsh 633* (BRY, NY, RM). Wasatch Co.: American Fork, *Jones s.n.* (CAS, DS, RSA). Above Brighton, *Kortian 261* (RM). Washington Co.: USFS Work Centre, *Warrick 25* (BRY, RM). Zion N.P., Slickrock area, *Thorne & Chandler 5568* (NY). WYOMING. Albany Co.: Ames Monument, *Asplund 72-34* (RM). Centennial-Rambler Rd., *Gooding 2070* (DS, GH, NY, UC). Dry Park, near Fox Park, *Porter 2175* (RM). Dunn's Ranch, *Nelson s.n.* (RM). Jelm, *Nelson 8017* (NY). Laramie, *Pfadt 120* (RM). SSE of Laramie, *Macbride 2601* (RM). Medicine Bow Mts, Sheet Mt., *Gooding 2079* (DS, GH, NY, UC), *Nelson 972* (RM). Near Salem, *Nelson 1497* (GH, MIN, RM). Carbon Co.: W of Encampment, Sierra Madre, Haggarty Cr., *Williams 381* (RM). Johnson Co.: W of Kaycee, *Hartman 10098* (RM). Natrona Co.: Casper Mt., Garden Cr. Falls, *Jozwik 147* (RM). Seventeen Mile Well, *Gooding 215* (DS(2), GH, NY, RM, RSA(2), UC(2), WIS). Sheridan Co.: Big Horn Mts., SE of Big Horn, *Hartman 10655* (RM).

aff. var. *fulcrata*

MÉXICO. COAHUILA. Cuervo de la Viga, ca. 4 mi E of Jame, *Poole & Nixon 2274* (TEX). Sierra Maderas del Carmen, Pico de Centinela, Cyn. Hundido, *Johnston, Chiang, Wendt & Riskind 11818* (MEXU, TEX(2)). Sierra Maderas del Carmen, 0.25 mi N of Campo Dos along trail to Campo Tres, *Wendt & Adamcewicz 526* (LL, MEXU). U.S.A. ARIZONA. Alpine Co.: NE of Clifton, San Francisco Mts., *Greene s.n.* (GH, NY). Coconino Co.: *Schallert s.n.* (NY, WS). Oak Crk Cyn., Coconino N.F. Rec. Area, *Semple & Chmielewski 9013* (WAT). N of Parks, *Semple et al. 5546* (ASU, MO, WAT). COLORADO. Euchara Camps, *McAllister s.n.* (TEX). Boulder Co.: Eldora, *Jones 20408* (WTU). El Paso Co.: Cheyenne Mt., *Clarke s.n.* (NY). Pikes Pk., *Williams 2480* (LL, WAT). Gunnison Co.: N of Crested Butte, Gothic Mt., *Russell 28.6* (UC). Larimer Co.: Devils Gulch near Estes Park, *Eastwood s.n.* (CAS). Teller Co.: Woodland Park, *Iltis & Iltis 18723* (WIS). IDAHO. Bannock Co.: SE of Bancroft, *Foster 7134* (BRY, RM). Valley Co.: E of Lick Cr. Summit, *Atwood 13419* (NY). NEW MEXICO. Mogollon Mts., N of Gilita Campground, *Moir & Fitzhugh 713* (NMC). Lincoln Co.: Capitan Mts, E of Baca Ranger Stn., *Hendricks 2116* (USFS). MONTANA. *Anderson s.n.* (NY). Sand Coulee, *Anderson s.n.* (NY). TEXAS. Culberson Co.: Guadalupe Mts., S McKittrick Cyn., top of mts, J.C. Hunter ranch, *Warnock 12064* (LL, SRSC; approaching *H. viscida*). UTAH. Cache Co.: Bear R. Range, Tony Grove L., *Maguire 16107* (UC, WTU). Lake Co.: Alta, Wasatch Mts, *Jones 1271* (GH, NY, POM). Salt Lake Co.: Brighton, below Twin Lake, *Maguire 17340* (NY). Big Cottonwood Cyn, *Cooper 324* (RM). Salt Lake City, *Jones s.n.* (POM). Utah Co.: Aspen Grove, *Ream 9297* (UC). Washington Co.: Zion N.P., Hidden Cyn Tr, *Braem 898* (DS). WYOMING. Albany Co.: W of Centennial, *Semple & Chmielewski 8864* (WAT). Near Tie Siding, *Osterhout 1327* (NY, RM). Carbon Co.: Elk Mt., *Hammel & Hartman 634* (RM). Hot Springs Co.: Grass Cr. Cyn, *Hardy 439* (BRY). Johnson Co.: E of L. De Smet, *Dueholm 8674* (NY, RM). N side of L. De Smet, *Duelholm 8385* (RM). Natrona Co.: Salt Creek Oil Wells, *Gooding 251* (BRY, RM). Platte Co.: *Dorn 5376* (NY).

aff. var. *fulcrata* (indument approaching var. *amplifolia*)

U.S.A. ARIZONA. Coconino Co.: near Jacob Lake, *Howell & Eastwood 6411* (CAS). Oak Creek Cyn., *Keil K11760* (ASU, JCS). COLORADO. "Rocky Mountains" *Hall & Harbour 260* (NY, PH). Trail Glen, *Clements & Clements 39* (NY, RM). El Paso Co.: Manitou,

Bates 6439 (RM), *Bates 6509* (RM). Along the cog RR above Manitou, *Osterhout 5413* (RM), *Osterhout 5414* (RM). Gilpin Co.: Roosevelt N.F., *Wright B-3* (USFS). Tolland, *Overholts s.n.* (NY). Jefferson Co.: E of Conifer, *Shea 362* (WAT). Larimer Co.: Bald Mt., *Guthrie 71-G* (RM). Near Ft. Collins, *Baker s.n.* (RSA). S of Horsetooth, *Osterhout 6894* (RM). Long's Peak Inn, *Osterhout 5466* (RM), *Osterhout 5862* (RM(2)). Moraine Park, *Osterhout 7412* (RM), *Osterhout 7414* (RM). Stove Prairie, Bosworth's, *Osterhout 4774* (RM). Teller Co.: near Pikes Pk., *Clarke 207* (NY). **NEW MEXICO.** Catron Co.: Mogollan Mts., *Rusby 168* (MIN, NY(3), PH). **UTAH.** Salt Lake Co.: Little Cottonwood Cyn, *Cottam 14526* (RSA). Washington Co.: N of Enterprise Reservoir, Pine Cr., *Higgins 16040* (BRY) Pine Valley Mts., E of Pine Valley, *Gould 1950* (CAS, DS, GH, PH, UC, NY). **WYOMING.** Albany Co.: Centennial, *Nelson 8744* (BRY, DS, GH, NY, RM, RSA, UC(2)), *Nelson 8814* (UC). Johnson Co.: ESE of Buffalo, *Dueholm 8572* (RM). E side Lake De Smet, *Dueholm 8462* (RM). Sheridan Co.: Little Goose, *Willits 208* (RM).

aff. var. *fulcrata* (indument approaching var. *arizonica*)

U.S.A. ARIZONA. Coconino Co.: Oak Creek Cyn. across from East Pocket Knob, *Niles & Waer 110* (TEX).

aff. var. *fulcrata* (indument approaching var. *senilis*)

U.S.A. TEXAS. Brewster Co.: Chisos Mts., Big Rock Trail, *Cory 44873* (LL).

aff. var. *fulcrata* (approaching or introgressed with *H. pumila*)

U.S.A. COLORADO. Clear Creek Co.: near Empire, *Patterson 224* (CAS, F). El Paso Co.: Pikes Pk., *Brown 106* (NY).

aff. var. *fulcrata* (approaching or introgressed with *H. villosa* vars. *foliosa*, *nana* or *minor*)

U.S.A. ARIZONA. Coconino Co.: near Jacob Lake, *Howell & Eastwood 6411* (CAS). COLORADO. Arapahoe Co.: Denver, *Burk s.n.* (PH). El Paso Co.: Colorado Springs, *Clarke 209 & 206* (NY). Larimer Co.: Chambers L., *Osterhout 4183* (NY, RM). Dale Crk, *Osterhout 5542* (BRY, POM, RM). Thompson Cyn., *Baker 4751a* (LL). **UTAH.** "40th Parallel, N. Utah", *Watson 584* (GH, NY). Cache Co.: Cache N.F., Mt. Naomi, *Shaw 2645* (BRY). Salt Lake Co.: Parleys Cyn, *Garrett 8848* (RSA). **WYOMING.** Albany Co.: Bacon's Ranch, *Nelson 8921* (GH, NY(2), RM, UC). E of Laramie, Lincoln Monument, *Taylor & Taylor 20318* (KANU, NY). Tie City, *Nelson 7648* (BRY, GH, MIN, NY, POM, RM(2)). Washakie Co.: Big Horn Mts., NE of Ten Sleep, *B.E. Nelson 5178* (RM).

aff. var. *fulcrata* (approaching or introgressed with *H. villosa* var. *scabra*)

U.S.A. NEVADA. Elko Co.: Bull Run Mts., W of Bull Run Res., *Tiehm, Ertter & Williams 9050* (BRY, NY, RSA, TEX). Eureka Co.: Fish Cr. Range, SSW of Eureka, *Tiehm 11844* (KANU, NY, TEX, WTU). **UTAH.** Kane Co.: NW of Orderville, *Maguire 18858* (GH, NY, UC, WTU). Summit Co.: Uinta Mts., Smith and Morehouse Cyn., *Goodrich 21436* (BRY, NY).

aff. var. *fulcrata* (approaching or introgressed with *H. viscida*)

U.S.A. TEXAS. Jeff Davis Co.: Mt. Livermore, *Jenkins 59* (SRSC).

aff. var. *fulcrata* (approaching *H. mucronata* var. *harmsiana*)

MEXICO. COAHUILA. Ca. 140 km NW of Muzquiz, Cuesta del Plomo area, *Nesom & Mayfield 743* (MEXU, TEX).

9.2 *Heterotheca fulcrata* (E.L. Greene) Shinnars var. *amplifolia* (Rydb.) Semple, comb. et stat.

nov. *Chrysopsis amplifolia* Rydb., Bull. Torr. Bot. Club 31: 648. 1904. *Chrysopsis foliosa amplifolia* (Rydb.) A. Nels. in Coult. & Nels., Man. Bot. Rocky Mts., 493. 1909. TYPE: U.S.A. COLORADO. Longmont, *Tweedy 4898* (Holotype: NY!; isotype: RM!)

Chrysopsis caudata Rydb., Bull. Torr. Bot. Club 31: 648. 1904. TYPE: U.S.A. COLORADO. [Pike's Peak] Ruxton Dell, 2950 m, 2 Aug 1901, *Clements 143* (Holotype: NY!; isotypes: DH!, GH!, MIN!, RM!, US!)

Chrysopsis nitidula Wooten & Standley, Contrib. U.S. Nat. Herb. 16: 179. 1913. TYPE: U.S.A. NEW MEXICO. Mogollon Mts. on the West Fork of the Gila R., ca. 2250 m, 20 Aug 1903, *Metcalfe 552* (Holotype: US-495550!; isotypes: GH!, NMC!)

STEMS several to many, ascending-erect, (20)-26-36-40-(48) cm tall, moderately to densely hispid-strigose and non-glandular; (10)-14-23-32-(42) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (22)-27-36-45-(50) cm long, (6)-6.4-8.2-10.1-(12.3) mm wide, subpetiolate to merely cuneate, moderately strigose-canescens on both surfaces, eglandular. UPPER STEM LEAVES ovate to lanceolate, (17)-18.5-25.6-32.7-(40) mm long, (5)-5.6-8.4-11.2-(15) mm wide, sessile, eglandular to very sparsely glandular and densely to very densely strigose, 0-1-3-(7) glands/mm², (28)-34-75-115-(150) hairs/mm². CAPITULESCENCE cymose-corymbiform, heads 2-5-7-(8); peduncles densely strigose-canescens, non-glandular; bracts few, sometimes nearly equal to upper leaves in size, sometimes much reduced, ovate-broadly lanceolate and subpetiolate, indument like upper leaves. INVOLUCRES (6)-6.4-7.8-9.2-(10) mm high; phyllaries in 4-5 imbricate series, outer ones 1/4 the length of the inner, narrowly triangular, non-glandular, moderately strigose, margins hyaline, wide, fimbriate-ciliate apically; inner ones similar to more lanceolate. RAY FLORETS (5)-10-15-19-(21), strap (8.5)-9.1-11.6-14.1-(15.8) mm long, (0.8)-1.1-1.7-2.2-(2.5) mm wide.

DISC FLORETS (16)-27-40-53-(60), corolla (5.3)-5.5-6.0-6.5-(7.5) mm long, lobes (0.5)-0.6-0.7-0.8-(0.9) mm long. ACHENES (1.5)-2-2.5-3.1-(3.9) mm long, moderately strigose; inner whorl of 35-45 barbellate bristles (5)-5.2-5.9-6.7-(7.8) mm long. Chromosome number: $2n = 18$.

Flowering Period: (June)-JULY-AUGUST-SEPTEMBER-(October)

Distribution and habitat: Scattered in mid to higher montane zone in Wyoming, Colorado, New Mexico, Utah and Arizona (Fig. 28B); open ponderosa forests, spruce-fir-aspen zone, disintegrated granite slopes, high rocky summits, dry grasslands with sagebrush, roadsides, transition zone, ponderosa pine-oak assoc., pinyon-juniper zone at edge of Upper Sonoran Desert; dry gravelly soils, coarse granitic soils; (1350)-1800-3050-(3500) m ((4400)-6000-10000-(11600) ft.) elevation. The range is similar to that of var. *fulcrata*, but it is more common in southern Utah and diagonally across Arizona on the Mogollon Plateau than the typical variety and not present in México and Texas.

Discussion: Variety *amplifolia* is similar in most ways to var. *fulcrata* but the leaf indument is densely short-strigose (50-200 hairs/mm²) with very few or no glands rather than sparsely to moderately hispid-strigose and glandular (Fig. 30B). It shows the same range in leaf shape that occurs in var. *fulcrata* (Fig. 29). As the varietal epithet denotes, the upper stem leaves can be large and ovate, although the type specimen represents the extreme; an epithet indicative of the dense pubescence would be more informative of the shared characteristic of members of this taxon. More commonly, the upper leaves are narrowly ovate to lanceolate. Some plants maintain the lower leaf shape well up the stem with only the upper few leaves being narrowly ovate-lanceolate. Such plants are easily misidentified as members of other densely pubescent taxa, particularly *H. villosa* var. *pedunculata*. In these cases, careful examination of the uppermost leaves and the peduncular bracts just below the head will reveal the identity. Variety *pedunculata* (Fig. 45) never produces the narrowly ovate (often nearly petiolate) peduncular bracts that are diagnostic for *H. fulcrata*. In southern Utah and eastern Arizona, small-leaved plants of var. *amplifolia* can look similar to plants of *H. zionensis*, which typically have densely glandular phyllaries in that area of the state (Fig. 38) or *H. villosa* var. *pedunculata*, which typically has narrow oblanceolate leaves and lacks ovate peduncular bracts.

Narrow-leaved plants of var. *amplifolia* from eastern Arizona and adjacent New Mexico were treated as *H. pumila* in Semple (1987; Semple & Heard 8021 and 8027 WAT). The results of an unpublished multivariate analysis indicated that these had the diagnostic bracts, high hair number, and other traits within the range of variation of var. *amplifolia* to which the specimens were assigned with high probability.

Specimens examined: U.S.A. ARIZONA. *Greene s.n.* (UC), *Kuntze 23228* (NY). "Northern Arizona", *Lemmon 3316* (GH). Apache Co.: Alpine, *Goodding 1259* (CAS, NY, WTU), *Semple & Heard 8021* (WAT), *Turner 5700* (TEX). Greer, *Peebles 12555* (LL). N of Greer, *Earle s.n.* (ASU), *Sexton s.n.* (ASU). Lee Valley Lake area, *Lambson s.n.* (ASU). E of Nutrioso, Escudilla Mt., *Parker & McClintock 7545* (CAS). Sheep Crossing Campground, *Pinkava, Brown & McLeod 503* (ASU). Coconino Co.: Flagstaff, *Jones s.n.* (RSA), *Schallert s.n.* (CAS (2)), *Thornber s.n.* (CAS). Near Flagstaff, *Shallet s.n.* (MIN), *Schallert s.n.* (PH); N of Museum of N. Arizona, *Hogue 316* (RSA). N of Flagstaff, *Breedlove 1202* (CAS), *Howell & True 45068* (CAS), *Semple & Chmielewski 9005* (WAT), *Semple & Chmielewski 9005a* (WAT). Grand Cyn. N.P., *Allen s.n.* (NY), *Harshberger s.n.* (PH); SE of Grand View Pt., *Harms 1886* (KANU, WAT); North Rim, *Howell & Eastwood 7008* (CAS), N of Ranger Station, *Halvorson 123* (ASU), N of Bright Angel Pt., *Halvorson 215* (ASU), between Cape Royal and Point Imperial, *Keil K11715* (ASU). N of Grand Cyn., *Nash & Nash N264* (ASU). S of Grand Cyn., *Jaeger 25* (RSA). E of Jacob Lake, *Semple & Heard 7890* (WAT). SE of Jacob Lake, *Moore, Pinkava & Lehto 7011* (ASU). W of Jacob L. Lodge, *Anderson 2148* (DS, GH, SASK). Kaibab N.F., *Milner 8974a* (UC), *Moir 360* (RM, USFS); near Sowats, *Mann M-53* (USFS). San Francisco Pks., *Heiser & Heiser 1567* (UC), *Pinkava, Keil, Reeves & Hevly P13756* (ASU, JCS). Walnut Cyn, *MacDougal 358* (NY, PH, RM, UC). Gila Co.: N of Pibe, *Collom s.n.* (ASU). Graham Co.: White Mts, Black R., *Goodding 602* (NY, RSA). Yavapai Co.: SE of Sedona, *Pinkava & Pinkava 14083* (ASU). COLORADO. Pingree Hill, *Hapeman s.n.* (RM). Sulphide, *Ramaley 10303* (RM). Boulder Co.: Allens Park, *Johnston 276* (RM), *Zobel s.n.* (CAS, MIN, RM). Boulder, *Ramaley 9722* (RM), *Robbins 2140* (RM), *Vestal 466* (DS). Near Boulder, *Robbins 2562* (RM), *Tweedy 4897* (NY), *Tweedy 5847* (NY, RM). W of Boulder, *Atwood & Higgins 5618* (BRY). Crescent, *Ramaley 9964* (RM). S of Raymond, *Wagenknecht 2987* (KANU, SASK). Valmont, *Ramaley 10565* (RM). Ward, *anon. s.n.* (MIN), *Clokey 2673* (NY, RM, UC). Clear Creek Co.: Idaho Springs, *Degener & Peiler 16876* (NY). Near Lawson, *Lee L-2* (USFS). El Paso Co.: Colorado Springs, *Warren 1955* (RM). Pike's Peak, *Harms 2009* (KANU, SASK), *Hunnewell 3252* (GH), *Hunnewell 3253* (GH), *Macbride 2663* (RM), *Ownby 946* (WS), *Schneider 1* (RM). Gilpin Co.: N Central City, *Ewan 11470* (LL). Jefferson Co.: Bergen Park, *Waterfall 3457* (GH). S of Evergreen, *Burden & Keil 13* (ASU). Evergreen to Conifer, *Clokey 3885* (CAN, CAS, DS, GH, LL, MIN, NY, RM, RSA, UC, WS, WTU). Golden,

Greene s.n. (GH). Near Golden, *Ehlers 8265* (TEX). South Table Mt., *Yeatts 753* (BRY). Larimer Co.: Big Thompson Cyn., *anon. 4590* (WTU). Chambers L., *Osterhout 6320A* (RM). Estes Park, *anon. G-15* (WTU). Estes Park, *Cooper s.n.* (MIN, NMC), *Smith s.n.* (PH); Skyland, *Nelson & Nelson 5231* (RM, RSA, TEX). S of Estes Park, *Barclay & Thompson 1117* (LL). Kenosha Pass, *Craven s.n.* (WIS). Lake Ridge, *Johnston & Hedgcock 276* (RM). Livermore, *Osterhout 1329* (RM). W of Livermore, *Osterhout 36513* (WIS). Long's Pk., *Cooper s.n.* (NMC), *Hunnell 3254* (GH), *Osterhout 5452* (RM, RSA). Teller Co.: SW of Colorado Springs, E of Helen Hunt Falls, *Harms 2026* (KANU, SASK). Pikes Pk., *Semple & Heard 7723* (WAT); North Cheyenne Canyon, *Bessey s.n.* (NY). **NEW MEXICO.** Catron Co.: E of Beaverhead, *Dunn 7716* (RSA). Datil N.F., *Ewing 6* (RM). W of Luna, *Semple & Heard 8027* (ASU, JCS, MT, RM, WAT). **NEW MEXICO.** Catron Co.: W of Luna, *Semple & Heard 8027* (ASU, JCS, MT, RM, WAT). Mogollan Mts., *Rusby 168* (MIN, NY(3), PH). Bear Wallow Mt., *Hess 2394* (NMC). Sierra Co.: E of Beaverhead, Taylor Creek, *Spellenberg, Soreng & Wahl 6598* (NMC). Socorro Co.: Mogollan Mts., Middle Fork, Gila R., *Wooton s.n.* (NMC). **UTAH.** Washington Co.: Pine Valley, *Gierisch 570* (WTU), *Maguire & Richards 13371* (GH). E of Pine Valley, *Gould 2066* (DS, GH, NY, UC). **WYOMING.** "Rocky Mts.", *Thomas s.n.* (MIN). Albany Co.: Medicine Bow Mts., Nash's Fork, *Nelson 7736* (RM); summit of pass on Hwy-30, *Yunker & Yunker 12313* (NY, TEX). Johnson Co.: ESE of Buffalo, *Dueholm 8452* (RM). W of Buffalo, *Wood s.n.* (WIS).

aff. var. *amplifolia*

U.S.A. ARIZONA. Apache Co.: W of Eager, *Lehto, Pinkava, Keil, & Pase L19221* (ASU, WAT). White Mts., *Moldenke & Moldenke 27846* (LL). Coconino Co.: Coconino N.F., Black Springs, *Talbot, Hill C-12* (USFS). Grand Canyon, North Rim, *Jones 21059* (WTU). Near Sunset Crater, *Howell & Eastwood 6964* (CAS). Sycamore Canyon Wilderness Area, *Pinkava, Stewart & Keil 5838* (ASU). **COLORADO.** Boulder Co.: Lower Boulder Cyn., *Osterhout 2413* (RM). Larimer Co.: Estes Park, Big Thompson Canyon, *Engleman & Nelson 3401* (MIN). W of Estes Park, *Mickelson s.n.* (WIS). **NEW MEXICO.** Catron Co.: Mogollan Mts., *Rusby 167* (UC). Socorro Co.: Socorro, *Demaree 59017* (RSA).

aff. var. *amplifolia* (indument near that of var. *fulcrata*)

U.S.A. ARIZONA. Coconino Co.: SE of Lake Mary, *Williams HW-x* (USFS). Kaibab N.F., Pine Flat Hunting Camp, *Darrow 2962* (CAS). **COLORADO.** Co.: Pike N.F., Bald Mt., *Guthrie 71-G* (RM). Boulder Co.: Allens Park, *Johnston 276* (RM). Estes Park, *Osterhout 5859* (RM). Ward, *Osterhout 2444* (NY). **UTAH.** Washington Co.: Pine Valley Rec. Area, *Warrick 2601* (BRY, NY, RM).

aff. var. *amplifolia* (approaching *H. villosa* var. *foliosa*)

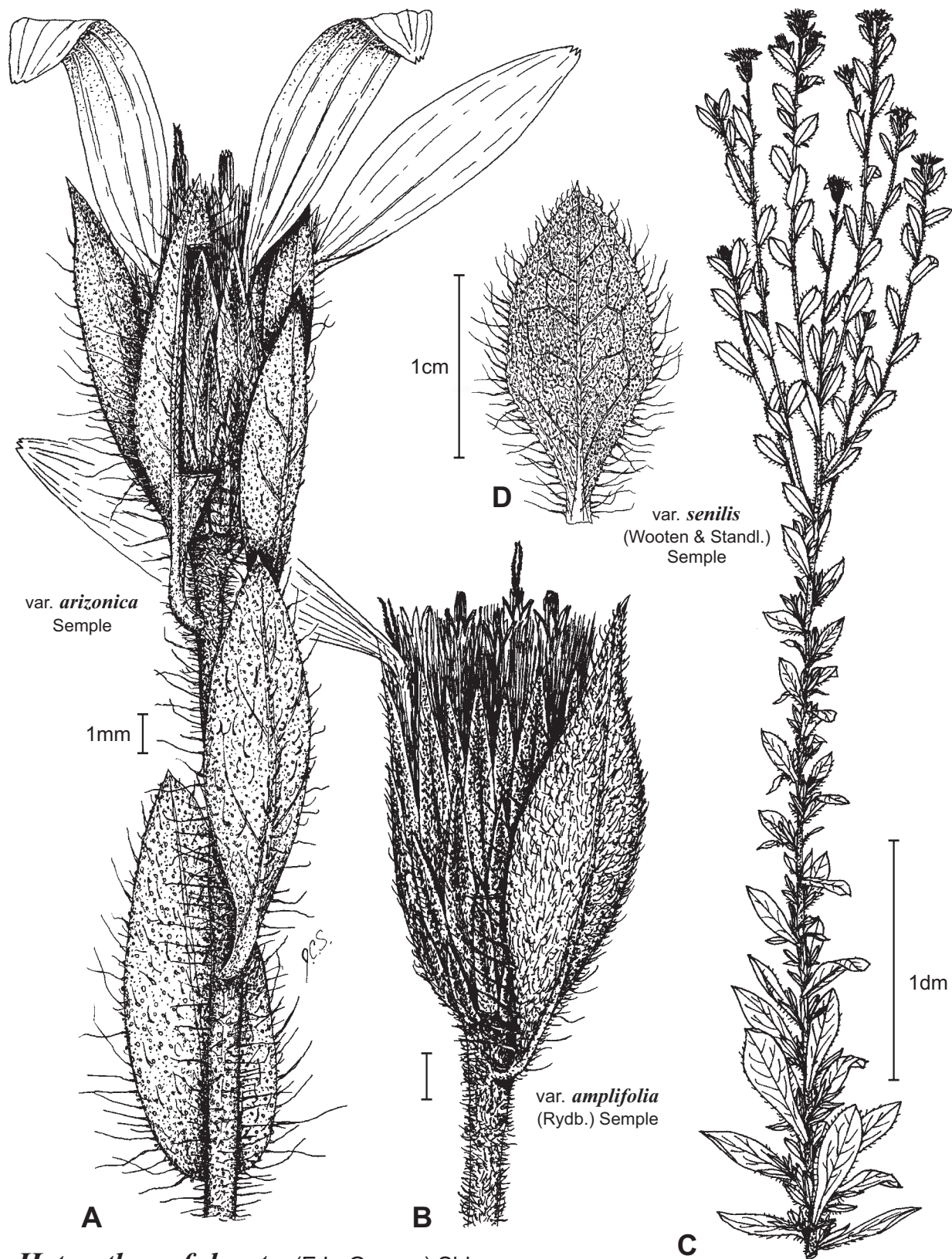
U.S.A. COLORADO. Teller Co.: Green Mountain Falls, *Young s.n.* (TEX). **WYOMING.** WY. Albany Co.: Tie City, *Nelson 8224* (BRY, KANU, MIN, NY).

9.3 *Heterotheca fulcrata* (E.L. Greene) Shinnars var. *arizonica* Semple, Brittonia 39: 380. 1987.

TYPE: U.S.A. ARIZONA. Gila Co.: AZ-87, 0.3 km NW of East Verde R., NW of Payson, 13 Sept 1985, *Semple & Heard 7923* (Holotype: NY!; isotypes: ASU!, MO!, US!, WAT!).

STEMS several to many, ascending-erect, (17)-21-35-49-(75) cm tall, sparsely hispid-strigose and moderately stipitate-glandular; (14)-20-34-49-(63) leaves per stem. LOWER STEM LEAVES oblanceolate, (13)-14-20-26-(34) mm long, 3.5-5.2-7.5-(11) mm wide, subpetiolate to merely cuneate, sparsely glandular and strigose-canescens on both surfaces. UPPER STEM LEAVES linear-ovate to linear-lanceolate, (12)-14-16.5-19.4-(22) mm long, 3.8-5.1-6.4-(8) mm wide, sessile, moderately glandular and sparsely to moderately strigose, (7)-13-9-18-(39) glands/mm², 3-21-39-(56) hairs/mm². CAPITULESCENCE cymose-corymbiform, heads (1)-9-18-(39); peduncles moderately strigose-canescens, moderately stipitate-glandular; bracts few, sometimes nearly equal to upper leaves in size and subtending heads, indument like upper leaves. INVOLUCRES (5.7)-6.1-7.2-8.4-(10) mm high; phyllaries in 4-5 imbricate series, outer ones 1/4-1/3 the length of the inner ones, narrowly triangular, densely stipitate-glandular, sparsely strigose, margins hyaline, wide, fimbriate-ciliate apically; inner ones lanceolate, indument similar. RAY FLORETS (9)-12-15-19-(22), strap (7.3)-8-9.6-11.1-(12) mm long, (0.9)-1.1-1.5-1.9-(2.5) mm wide. DISC FLORETS 32-48-65-(81), corolla (4.9)-5-5.6-6.2-(6.9) mm long, lobes 0.5-0.6-0.7-(7.5) mm long. ACHENES (1.9)-2-2.5-2.9-(3.3) mm long, sparsely strigose; inner whorl of 35-45 barbellate bristles (4.3)-4.7-5.5-6.3-(6.9) mm long. Chromosome number: *2n* = 18, more than a half dozen reports.

Figure 30. Morphology of *Heterotheca fulcrata* var. *amplifolia*, var. *arizonica* and var. *senilis*. A. Var. *arizonica*; upper stem and head (only some florets drawn); a portion of a leaf obscuring the view of the head has been removed. B. Var. *amplifolia*; head with only some florets drawn. C-D. Var. *senilis*. C. Robust shoot. D. Branch leaf; adaxial surface on left, abaxial surface on right. ➡



Heterotheca fulcrata (E.L. Greene) Shinnars

Flowering Period: JULY-OCTOBER-(November)

Distribution and habitat: A narrow zone running from southeastern Nevada to southern New Mexico and scattered in the mountains of Trans-Pecos Texas and Coahuila, México (Fig.28A). Exposed rocky embankments and cracks in rock outcrops at mid elevations to lower elevations of oak-pine woodlands.

Discussion: Variety *arizonica* is a lower elevation race of the species distinguished by its small, usually ovate, leaves with a more glandular indument (Fig. 30A). The foliar bracts subtending the heads tend to be small and few in number. It is similar to xeric, more glandular forms of *H. villosa* var. *scabra* and can be confused with less pedunculate individuals of *H. viscida*, especially in Texas where plants of var. *arizonica* have indument features approaching var. *senilis* on the one hand and var. *fulcrata* on the other. In Texas, some plants of var. *arizonica* have long, linear-oblong bracts subtending the heads and very narrow leaves, which taken together give the plants an appearance rather like *H. stenophylla* var. *stenophylla*.

Representative Specimens: MÉXICO. CHIHUAHUA. Chihuahua, *Stearns 55* (F). U.S.A. ARIZONA. Cochise Co.: Bowie, *Jones 4296* (RSA). Coconino Co.: S of Flagstaff, *Dearing & Dearing 5489* (ASU). Miami, *Gentry 3168* (CAS). Gila Co.: Devils Cyn., E of Queen Creek Tunnel, *Lehto & McGill L20750* (ASU). Near Globe, *McCleary s.n.* (ASU). McFadden Pk., *Nash N282* (ASU). Pinal Mts., *Forbes 1165* (ASU), *Forbes 1404* (ASU); S of Globe, *Forbes 1659* (ASU); N of Pioneer Pass Rec. Area, *Keil 3609* (ASU); Signal Pk., *Forbes 1353* (ASU), *Keil 3844* (ASU(2)). Salt R. Canyon crossing, *McGill & Lehto L20640* (ASU), *Semple & Semple 10497* (ASU, WAT); N of river, *Lehto & McGill L20647* (ASU). NE of Salt R. Cyn. Bridge, *Romans s.n.* (ASU). SW of Seneca, *Semple & Chmielewski 9028* (WAT). Sierra Ancha Mts., Parker Cr., *Gould 3729* (LL, UC). Sierra Ancha N.F., *Pase 1042* (USFS). E of Superior, *Semple & Semple 10498* (ASU, WAT). Winkelman, *McGill & Pinkava P13817* (ASU). Graham Co.: Galiuro Mts., eastern foothills, *Keil & Keil 21263* (ASU). Pinaleno Mts., Jacobson Cyn., *Bingham 1861* (ASU); Van Gausig Mt., *Bingham 2256* (ASU). Greenlee Co.: Clifton, *Davidson s.n.* (UC), *Gooding, Jacks & Johnson G5-40* (ASU). N of Clifton, *Maguire 11821* (NY), *Semple & Heard 8003* (WAT). Morenci, *Semple & Heard 8004* (WAT). San Francisco Mts., *Greene s.n.* (NDG, NY, RSA). Maricopa Co.: W of Queen Creek Tunnel, *Pinkava, Keil, & Lehto L18905* (ASU). Mohave Co.: Upper Francis Cr., *Butterwick & Parfitt 5098A* (ASU). E of Kingman, *Braem 562* (LL). Pima Co.: Santa Catalina Mts., Redington Pass, *Benson 9753* (POM), *Glendenning 85* (ASU). Santa Rita Mts., *Pringle 326-2* (GH). Pinal Co.: Apache Trail, Apache Gap, *Gillespie 8540* (GH, UC). Mescal Mts., *Jones s.n.* (RSA). Queen Creek, Superior-Miami Hwy, *Gillespie 8635.5* (DS, UC). Near Superior, *Harrison 2093* (LL); Devils Cyn., *Harrison & Kearney 6309* (NY, WIS), *Peebles & Harrison 4904* (LL), *Peebles, Harrison & Kearney 2999* (LL). Yavapai Co.: *O'Neil B-61* (ASU). N of Prescott, *Semple & Chmielewski 8999* (WAT), Granite Dells, *Harms 1865* (KANU(3), SASK), *Harms 19138* (KANU, WAT). NEW MEXICO. Dona Ana Co.: NNW of top of Bishop Cap, *Worthington 17556* (TEX). Doña Ana Mts., *Campbell 670* (USFS). Pyramid Pk., *Fosberg S3736* (LL, POM, RSA). Hidalgo Co.: Little Hatchet Pass, *Turner & Powell 6092* (TEX, UC). NEVADA. White Pine Co.: Jeff Davis Mt., *Tidestrom 11133* (LL). TEXAS. "W Texas to El Paso," *Wright 299* (GH(2), NY). Brewster Co.: S of Alpine, *Warnock 6616* (LL, SRSC). W of Alpine, *Sundberg 1226* (TEX). Cathedral Mt., *Jackson 125* (SRSC). Elephant Mesa, *Johnston 6424* (LL). Glass Mts., *Berkman s.n.* (SRSC). Goat Mt., *Campsey 319* (SRSC), *Campsey 1062* (SRSC). Goat Mt., *Warnock 20985* (RSA). Iron Mt., *Cory 44980* (TEX). Marathon, *Tharp s.n.* (TEX). SW of Marathon, *Johnston 3315* (SRSC). Packsaddle Mt., *McKenzie 302* (SRSC). Pena Blanca Mts., *Correll & Correll 26104* (LL). Terlingus Cr., *Fletcher 1081* (SRSC). Culberson Co.: Apache Mts., *Powell 3366* (SRSC, TEX). El Paso Co.: El Paso, *Stearns 154* (NY), *Wooton s.n.* (NMC). Franklin Mts., *Shiner 40920* (TEX). Hueco Mts., Hueco Tanks St. Pk., *Hinckley 4588* (NY, SRSC), *Peterson 1147* (TEX), *Powell & Powell 2996* (LL, SRSC), *Riskind 1615* (LL), *Van Devender s.n.* (TEX), *Waterfall 6640a* (GH, NY). Hudspeth Co.: Quitman Mts., Sierra Blanca, *Ferris & Duncan 2507* (CAS, DS, MIN). Presidio Co.: Capote Falls, *Warnock 20134* (SRSC). Capote Peak, *Hinckley 3245* (NY). Chinati Mts., *Hinckley 3971* (NY, SRSC), *Muller 8333* (LL). Chinati Pk., *Butterwick & Lott 3786* (TEX). Marfa, San Esteban L., *Hinckley s.n.* (SRSC), *Hinckley s.n.* (TEX), *Hinckley 2538* (GH, NY(2)). Van Horn Mts., S of Mica Mill, *Hinckley 2154* (NY(2)). Near Vieja, Tierra Vieja Mts., *Hinckley 2085* (NY). Watts Ranch, *Hinckley 2846* (NY). Terrell Co.: *Albers 46172* (TEX). Val Verde Co.: Pecos R., *Read 245* (SRSC), *Tharp 8868* (TEX), *Turner 2* (TEX), *Warnock 22717* (SRSC).

aff. var. arizonica

MÉXICO. COAHUILA. Sierra de Hechiceros Canyon del Filipe, near Chihuahuan boundary NE from Rancho El Tule, *Johnston & Muller 1357* (TEX). U.S.A. ARIZONA. Gila Co.: Salt R. Cyn. Bridge, *Pinkava, Keil & Lehto 14243* (ASU). Graham Co.: Turkey Cr., *Bingham 2551* (ASU). NEW MEXICO. Hidalgo Co.: Big Hatchet Mts., 2 air mi NE from to of Big Hatchet Peak *Worthington 22426.5* (TEX). TEXAS. Brewster Co.: Cathedral Mt., *Jobes & Doyle 104* (SRSC). Del Norte Mts., *Churchill 4106* (NY). UTAH. Washington Co.: Leeds, *Cottam 5400* (LL). UTAH. Juab Co.: Mt. Nebo, *Semple & Chmielewski 8889* (BRY, RM, WAT; probably adventive).

aff. var. arizonica (approaching var. *fulcrata*)

U.S.A. ARIZONA. Coconino Co.: Oak Creek, *Fulton 7343* (LL).

aff. var. arizonica (approaching var. *senilis*)

MÉXICO. CHIHUAHUA. Sierra de Moscos, *Chiang, Wendt & Johnston 8711A* (TEX). COAHUILA. Cañon de Indio Felipe, Sierra Hechiceros, *Stewart 522* (F, TEX). U.S.A. ARIZONA. Pinal Co.: Oak Flat, *Baker & Trushell 4817* (ASU). TEXAS. Brewster Co.: Chisos

Mts, Mt. Emory, *Warnock 9706* (SRSC). Elephant Mt., *Vaughn 524* (SRSC). Jeff Davis Co.: Lower Madera Cyn., *Weedin & Crabtree 785* (SRSC). Presidio Co.: Chinati Mts., *Correll & Johnston 24401* (LL, NY).

9.4 *Heterotheca fulcrata* (E.L. Greene) Shinnars var. *senilis* (Wooten & Standley) Semple, Brittonia 39: 380. 1987. *Chrysopsis senilis* Woot. & Standl., Contrib. U.S. Nat. Herb. 16: 179. 1913. TYPE: U.S.A. NEW MEXICO. Dona Ana Co.: Organ Mts., 4800', 1 Sep 1897, *Wooton 509* (Holotype: US!; isotypes: MIN!, NDG!, NY!)

STEMS several to many, ascending-erect, (24)-32-~~44~~-56-(63) cm tall, moderately hispid-strigose and sparsely to moderately stipitate-glandular; (15)-23-~~35~~-47-(69) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (17)-20-~~27~~-34-(40) mm long, (5)-5.7-~~7.6~~-9.5-(11) mm wide, subpetiolate to merely cuneate, sparsely glandular and strigose-canescenscent on both surfaces. UPPER STEM LEAVES ovate to lanceolate, (12)-15-~~21~~-27-(30) mm long, (4)-4.9-~~7.3~~-9.7-(13) mm wide sessile, very sparsely to moderately glandular and sparsely to moderately densely strigose, 0-1-~~9~~-18-(25) glands/mm², (7)-9-~~32~~-55-(90) hairs/mm²; margins sometimes somewhat undulate, long hairs many. CAPITULESCENCE cymose-corymbiform, heads 1-~~4~~-8-(13); peduncles sparsely to moderately strigose-canescenscent, sparsely to moderately stipitate-glandular; bracts few, sometimes nearly equal to upper leaves in size and subtending heads, sometimes much reduced and remote from heads, indument like upper leaves, INVOLUCRES (7.5)-7.8-~~8.5~~-9.2-(10) mm high; phyllaries in 4-5 imbricate series, outer ones 1/4-1/3 the length of the inner ones, narrowly triangular, densely stipitate-glandular, sparsely to moderately strigose, margins hyaline, wide, fimbriate-ciliate apically; inner ones lanceolate, indument similar. RAY FLORETS (10)-15-~~22~~-27-(34), strap (9.5)-10.2-~~11.6~~-13.1-(14) mm long, (1.0)-1.1-~~1.6~~-2.1-(2.7) mm wide. DISC FLORETS (21)-44-~~71~~-98-(110), corolla (4.8)-5.2-~~5.8~~-6.3-(6.8) mm long, lobes (0.5)-0.6-~~0.7~~-0.75 mm long. ACHENES (1.5)-1.7-~~2.0~~-2.4-(2.7) mm long, sparsely to moderately strigose; inner whorl of 35-45 barbellate bristles (4.9)-5.2-~~5.7~~-6.3-(6.9) mm long. Chromosome number: $2n = 18$, about a dozen reports.

Flowering Period: (May)-JUNE-SEPTEMBER-(November)

Distribution and habitat: Southern New Mexico and Trans Pecos Texas; rare in southern Arizona and across northern México (Fig. 28B); margins of often seasonally dry creeks in pinyon-juniper-oak woodlands, oak-pine-fir and mixed mountain shrubs; limestone slopes, crevices of rocks, rocky igneous and limestone soils, silty soils; 700-2450 m (2300-8000 ft.) elevation.

Discussion: Variety *senilis* is the most hispid pubescent form of the species and generally has many large spreading hairs along much or all of the leaf margins (Figs. 30C,D). The leaf margins are sometimes undulate like *H. sessiliflora* ssp. *sessiliflora* (Fig. 15), and the two could be confused, but the ranges do not overlap (Fig. 14). The variety varies considerably in height and leaf size, and a number of collections are so reduced in size that identification is difficult; e.g. some collections from the Chisos Mts, Brewster Co., Texas. These are easily mistaken for some odd form of *H. villosa* var. *minor* (Fig. 46) or *H. viscida* (Fig. 27). Scattered throughout the range are specimens that have a leaf indument approaching var. *fulcrata* and may represent a primitive undifferentiated form of the species. Specimens from southern Arizona are often similar to var. *fulcrata*. When hair density is high, leaf surfaces are obscured and the plants appear light grayish-green in color the same way that plants of *H. marginata* usually appear.

Specimens examined: MÉXICO. CHIHUAHUA. Sierra de los Hechiceros, Canyon Encampanado, below Rancho Encampanado W of jct. with Canyon de Indio Felipe, *Wendt & Adamcewicz 425* (TEX). Sierra en Media, *Nelson 6472* (GH). COAHUILA. SE of Big Bend N.P., S end of Sierra del Carmen, Canyon de Centinella, S side of Pico de Centinella, *Henrickson 11659* (TEX). Cyn de la Fronteriza, 2 mi NE of Rancho San Isido, end of Cyn del Alamo, *Henrickson & Prigge 15033* (TEX(2)). Mun. Villa Acuña, Sierra del Carmen, Cañon de Sentenela, Hacienda Piedra Blanc, *Wynd & Mueller 593* (GH, TEX). Mun. Ocampo, Maderas del Carmen Mts., *Riskind, Bursleson and Baker 1705* (TEX). SONORA. Sonora, base of San Luis Mts., *Mearns 2080* (DS). U.S.A. ARIZONA. Cochise Co.: Dos Cabezas Mts., Cooper Pk., *Bingham 2534* (ASU); Government Pk., *Bingham 2654* (ASU). Graham Co.: below Arcadia campground, *Keil, Pinkava & Lehto 10092* (ASU). Pima Co.: Coyote Mts., Mendoza Cyn., *Mittleman 461* (ASU). Rincon Mts., Happy Valley Rd., *Pultz & Phillips 1923* (CAS). Pinal Co.: Pinal Mts., near Craig Ranch, *Shreve 7464* (WTU). Superstition Mts., Le Barge Cyn., *Lehto 1819* (ASU). Santa Cruz Co.: Santa Rita Mts., Madera Cyn., *McLaughlin 4297* (ASU, WAT). WAT, Madera Cyn. Trail,

Reeves R1806 (ASU); Mt. Hopkins Rd., E of Amado, *McLaughlin 4300* (ASU, *Keil & Pinkava 19025* (ASU, WAT). **NEW MEXICO.** Dona Ana Co.: between Boyd Ranch and Lapoor Ranch, *Dunn 8503* (RSA). Dona Ana Mts., N of Las Cruces, *Spellenberg 1941* (NY). Organ Mts., *Cockerell s.n.* (NMC); Aguirre Springs, *Semple 8831* (WAT), *Ward & Arsuffi 81-156* (NMC), *Semple & Semple 10510* (ASU, WAT), *Turner 93-18* (TEX(2)); Peña Blanca, *Wooton & Standley s.n.* (NY); VanPatten's, *Wooton s.n.* (NMC). San Augustin Pass between San Andres and Organ Mt. Ranges, *Harms 1839* (KANU, SASK(2), WAT), *Harms 1839-B* (SASK, WAT). Luna Co.: Florita Mts., *Jones s.n.* (RSA). **OKLAHOMA.** "On the False Washita, between Ft. Cobb and Ft. Arbuckle," *Palmer s.n.* (NY; The location data on the label are undoubtedly in error.). **TEXAS.** *Wright s.n.* (GH). "from W Texas to El Paso," *Wright 299* (NY). Brewster Co.: S of Alpine, Mt. Ord, *Jobes 314* (SRSC). Big Bend N.P., Chisos Mts., *Mueller s.n.* (NY), *Mueller 8199* (NY), *Warnock s.n.* (ASU); Boot Spring, *Muller s.n.* (TEX); Casa Grande, *Warnock 1139* (TEX); Cattail Falls, *Powell & Powell 4205* (SRSC, WAT); Emory Peak, *Correll 29749* (LL), *Moore & Steyermark 3212* (CAS, DS, GH, MIN, NY, RM), *Mueller s.n.* (GH); Green Gulch, *Lundell & Lundell 13266* (LL); crest of Juniper Cyn., *Ferris & Duncan 2790* (CAS, DS, NY); Nail Place, *Young s.n.* (TEX); North Wall, *Cory 44872* (LL, NY); Pulliam Cyn., *Sperry 417* (SRSC), *Warnock 6955* (SRSC); Pulliam Bluff, *Warnock 767* (TEX); Window Trail, *Cory 44772* (TEX). Glass Mts., Altuda Pt., *Warnock 11380* (SRSC), *Warnock 15644* (SRSC); Old Blue Mt., *Rose, Innis & Moon 1222* (TEX), *Warnock 15696* (SRSC, TEX); Jail Cyn, *Warnock 23231* (SRSC). SE of Marathon, *Powell 1254* (SRSC). Culberson Co.: Guadalupe Mts, *Semple & Heard 8177* (WAT); Bear Cyn., *Oatman & Rowlett s.n.* (TEX), *Semple & Heard 8170* (WAT), *Semple & Heard 8171* (WAT), *Semple & Heard 8173* (WAT), *Semple & Heard 8174* (WAT), *Turner & Warnock 121* (GH, SRSC); Bowl Trail, *Semple & Heard 8184* (WAT); above Frijole, *Lundell & Lundell 14390* (LL); McKittrick Cyn., *Moore & Steyermark 3529* (DS, GH, NY, UC, MIN); S. McKittrick Cyn., *Warnock 11925* (SRSC, CAS, TEX), *Warnock 23365* (SRSC); McKittrick Ridge, *Higgins 17964* (NY). Hurd's Draw, *Janszen 40* (TEX). Pipe Line Cyn., *Warnock & Johnston 16583* (SRSC). Pine Springs Cyn., *Correll & Johnston 24249* (LL, TEX). Sierra Diablo Mts., Victorio Cyn., *Sikes & Smith 552* (LL). El Paso Co.: *Warnock 8241* (LL, SRSC). El Paso, *Whitehouse s.n.* (TEX). Franklin Mts., *Correll 15054* (LL), *Sauleda 6532* (WAT), *Warnock 14230* (LL, SRSC); McKelligon Cyn., *Patterson & Riskind 37* (WAT). Jeff Davis Co.: Davis Mts., Fern Cyn., *Cory 9644* (LL); Madera Cyn., *Corell 13997* (NY). Presidio Co.: *Hinckley 2718* (NY). Chinati Mts., Indian Cace Cr., *Scudday 590* (UC). Cottonwood Cyn., *Hinckley 1966* (NY). Panther Cyn., vicinity of Colorado Cyn., *Butterwick & Strong B-1009* (TEX). Sierra Vieja Mts., Capote Cyn., *Sikes & Smith 658* (LL); Holland Cyn., *Hinckley 1764* (NY), Vieja Pass, *Warnock & Turner 8938* (SRSC). Val Verde Co.: ESE of Langtry, ruins of Vinagaroon, *Poole & Watson 1574* (TEX). Winkler Co.: NE of Kermit, *Warnock 23586* (SRSC).

aff. var. *senilis*

MÉXICO. CHIHUAHUA. near Rio Grande, NE of Sierra Mulato, upper part of Colorado Canyon, *Johnston 12876* (TEX). Sierra de los Hechiceros, Cañon Encampanado, *Wendt & Adamcewicz 526* (MEXU). **COAHUILA.** Monclava, Gloria Mts, *Marsh 1892* (F, TEX). **SONORA.** Sonora, San Luis Mts., *Mearns 2080* (DS; possibly Pima Co., AZ). **U.S.A. ARIZONA.** Pima Co.: Santa Catalina Mts., *Lemmon 206* (GH), *Lemmon 208* (GH), *Lemmon Herb. s.n.* (UC); Helens Dome, *UC 206* (UC). Santa Rita Mts., Upper Josephine Cyn, *Clark 12416* (RM). White House Cyn., *Clausen 580* (DS ex Carn. Wash). **TEXAS.** Brewster Co.: S of Alpine, Elephant Mt., *Vaughn 525* (SRSC). Big Bend N.P., Chisos Mts., Boot Spring Cyn., *Warnock 12660* (SRSC); Casa Grand, *Warnock 1139* (GH, NY, SRSC, TEX); Nail Place, *Young s.n.* (SRSC). Culberson Co.: Lobo, *Pinkava & Reeves P13170* (ASU, JCS). El Paso Co.: Franklin Mts., N of McKelligan Cyn., *Warnock & Johnston 17007* (SRSC). Jeff Davis Co.: Lower Madera Cyn., *Weedin & Crabtree 833* (SRSC). Presidio Co.: Vieja Mts., Vieja Pass, *Warnock 19649* (SRSC). Hudspeth Co.: W of Allamoore, *Warnock 13660* (ASU, LL).

aff. var. *senilis* (indument approaching var. *arizonica*)

MÉXICO. COAHUILA. Canyon de Indio Felipe, Sierra Hechiceros, close to the Chihuahuan boundary, *Stewart 522* (F, TEX). **U.S.A. TEXAS.** Brewster Co.: Glass Mts., Maple Cyn., *Warnock W275* (DS, GH, SRSC, TEX, UC). El Paso Co.: upper Fusselman Cyn., Franklin Mt., *Carr & McNeal 10225* (TEX). Jeff Davis Co.: canyon of San Carlos Tunnel, *Powell 1533* (SRSC, TEX).

aff. var. *senilis* (indument approaching var. *fulcrata*)

U.S.A. ARIZONA. Santa Cruz Co.: Santa Rita Mts., Madera Cyn., *Reeves R1037* (ASU, NY). **NEW MEXICO.** Dona Ana Co.: W of the Organ Mts, Filmore Cyn., *Wooton s.n.* (NMC). **TEXAS.** Brewster Co.: Chisos Mts., Mt. Emery, *Warnock 12348* (SRSC).

- 10. *Heterotheca rutteri* (Rothr. in G.M. Wheeler) Shinnery, Field & Lab. 19: 71. 1951. *Chrysopsis villosa* (Pursh) Nutt. var. *rutteri* Rothr. in G.M. Wheeler, Rep.U.S. Geogr. Surv. 6: 142. 1878. *Chrysopsis rutteri* (Rothr. in G.M. Wheeler) Greene, Erythea 2: 96. 1894. TYPE: U.S.A. ARIZONA. 1851, anon. 662 (Holotype: US?, not seen). Rothrock may have been the collector (Gray 1884); not stated in the protologue. *Chrysopsis foliosa* Nutt. var. *sericeo-villosissima* A. Gray, Syn. Fl. N. Amer. 1(2):123. 1884, pro syn. sub var. *rutteri*, illegit. This trinomial was not validly published earlier by Gray (Pl. Wright. 2: 81. 1852) because the variety epithet was presented by Gray only as part of a latin diagnosis of an unnamed variety. New names in Pl. Wright. were presented in capital letters, which was not done in this case. Gray listed the source of the uncited voucher in Pl. Wright. as "Valley between the San Pedro and the Sonoita, Sonora; Sept."**

Perennial from stout woody taproots; STEMS solitary to several, ascending-erect, (30)-33-42-51-(54) cm tall, moderately to densely strigose, long spreading hairs few to many; (25)-29-38-47-(54) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, 2-5 times as long as wide, (12.5)-14-18.8-24-(25) cm long, (4)-4.7-5.9-7 mm wide, subpetiolate to attenuate, strigose-canescens on both surfaces; margins entire, strigose, a few longer hispid hairs near base. UPPER STEM LEAVES ovate to lanceolate, (17)-18-20.9-23.7-

(25) mm long, 4.8-**6.2**-7.5-(8.3) mm wide, sessile, narrowly to broadly cuneate, acute, reduced upward, densely silky strigose, 85-160 hairs/mm², hairs 0.3-1 mm long, very sparsely glandular; margins entire, mucronate-spinulose. CAPITULESCENCE corymbiform, heads 4-10, subtended by one or more lanceolate foliar bracts 10-15 mm long, 1.8-4.5 mm wide; peduncles strigose-canescens, stipitate-glandular; bracts few, lower ones lanceolate, strigose like leaves, becoming linear and less pubescent and more glandular near heads. INVOLUCRES cylindrical to turbinate when fresh, campanulate-hemispheric upon drying, 8.5-**9.3**-10.2-(-10.5) mm high; phyllaries in 4-5 imbricate series, moderately to densely strigose, sparsely glandular, margins hyaline, fimbriate-ciliate apically, not anthocyanotic. RAY FLORETS (15)-17-**23**-30-(35), strap yellow, (12)-13.6-**14.5**-15.5-(16) mm long, (1.2)-1.4-**1.6**-1.9-(2.1) mm wide. DISC FLORETS (23)-29-**43**-57-(65), yellow, corolla barely ampliate, (6.5)-6.6-**7.2**-7.9-(8.3) mm long, lobes 0.6-0.8 mm long, hairs few, 0.1-**0.27**-0.4-(0.5) mm long. ACHENES (1.5)-1.7-**2.4**-3.1-(3.6) mm long, sparsely moderately densely strigose, ribbed; pappus off-white, double, outer whorl of linear scales 0.5-1 mm long, inner whorl of 35-45 barbellate bristles (7)-7.4-**8.1**-8.7-(9) mm long at anthesis, exceeding the corolla lobes. Chromosome number: $2n = 18$, several reports.

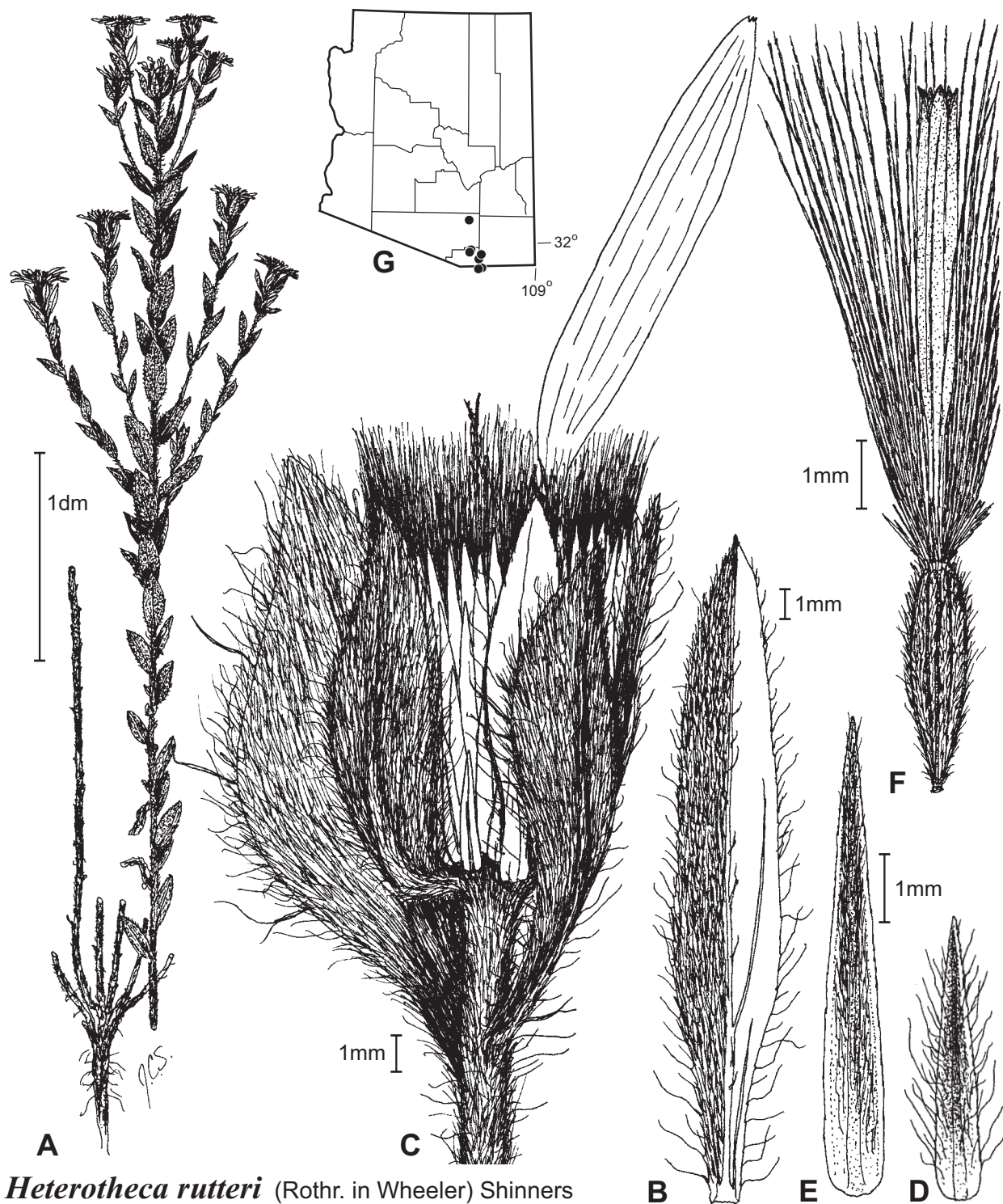
Flowering Period: (August)- SEPTEMBER-(October)

Distribution and habitat: Plains and grassy slopes of extreme southern Arizona in the vicinity of the lower Huachuca Mts. and Santa Rita Mts. and into adjacent Sonora, México (Fig. 31G); grasslands with occasional mesquite, grassy understory in oak woodlands, grassy flood plains; sandy, loamy soils; 1000-1500 m (3500-5000 ft.) elevation.

Discussion: *Heterotheca rutteri* is distinguished by its typically very light green to silvery-white very densely pubescent leaves which are narrowly ovate to lanceolate, sharply acute upper stem leaves and by its large foliar bracts with similar indument (or more glandular) subtending the showy heads (Fig. 31). A few herbarium collections examined had merely densely pubescent leaves, which would therefore be some darker shade of green in the field and brown on older herbarium specimens. The capitulescence branches can be nearly bractless below the heads, which are closely subtended by large lanceolate bracts. The pappus bristles are generally 10-15% longer than the long disc corollas. It is one of those species that once seen is never confused with another taxon.

The species is an obvious member of the *fulcrata* complex. It is sufficiently similar to *H. fulcrata* that it could be included in that species as a very distinct subspecies. It is not difficult to conceive of *H. rutteri* as the end product of isolation and divergence from some proto-*amplifolia* lineage during the fluctuations in distribution that occurred as a consequence of glacial-period induced climatic changes in the late Pleistocene-Holocene. No obvious hybrids between *H. fulcrata* and *H. rutteri* were seen in this study, and species status is supported on morphological grounds. Gray (1884) cited *Greene s.n.* (GH!: COLORADO. [Jefferson Co.:] Golden City, 1870) as a link to more typical "*C. foliosa*". The specimen is a member of *H. fulcrata* var. *amplifolia*, which is the taxon most similar to *H. rutteri*, but var. *amplifolia* has much shorter hairs; only smaller leaved plants have a silvery white color and these always have much smaller heads than *H. rutteri*. No evidence indicates that *H. rutteri* is closely related to the *H. villosa* complex that includes var. *foliosa*. The *foliosa* epithet has been erroneously applied to individuals of *H. fulcrata*.

Specimens examined: MÉXICO. SONORA. N of Cananea, Los Fresnos cienega, *Warren, Anderson, Saucedo, & Rudman s.n.* (ARIZ). 6 mi S of Nogales, along RR tracks, *Matthews & Matthews 481* (TEX(2)). U.S.A. ARIZONA. Cochise Co.: Ft. Huachuca, *Keil, Luckow & Luckow 13514* (ASU, OBI), *Goodding 668-58* (ARIZ), *Harrison & Kearney 5737* (ARIZ, LL), *Wilcox s.n.* (NY), *Malusa s.n.* (ARIZ). Huachuca Game Preserve, *Goodding 654-49* (ARIZ); near Ft. Huachuca, *Peebles, Harrison & Kearney 3487* (ARIZ, LL). Huachuca Mts, *Jones s.n.* (POM). N of Huachuca Mts., *Lemmon 2739* (GH, NY). Pima Co.: Buenos Aires N.W.R., *McLaughlin & Bowers 5023* (ARIZ). Santa Cruz Co.: N of Patagonia, *Darrow 3513* (ARIZ). SE of Patagonia, *Pinkava, Keil, & Lehto 14770* (ASU). Patagonia Mts., W of Sycamore Canyon and Italian Canyon intersection, *Morris, Ramsden and Hodgson 4636* (NY); base, *Kearney & Peebles 10025* (LL); near Patagonia Mts. close to Mexican Border, *Peebles & Harrison 4732* (LL). Sonoita, *Harrison & Fulton 8189* (ARIZ). N of Sonoita, *Parker 8116* (ARIZ, CAS, LL, MIN, NY, RSA, UC, WS). SW of Sonoita, *Niles 135* (ARIZ), *Semple & Chmielewski 9030* (ASU, JCS, MO, MT, NY, RM, WAT, UC), *Semple 10386* (ASU, WAT), *Semple & Semple 10505* (ASU, WAT).



Heterotheca rutteri (Rothr. in Wheeler) Shinnars

Figure 31. Morphology and distribution of *Heterotheca rutteri*. A. Habit, robust shoot. B. Mid-upper stem leaf of a small plant, adaxial surface, pubescence only shown on left. C. Head with only some florets drawn, indument of phyllaries not shown. D-E. Outer and mid series phyllary with chlorophyllous zone dark. F. Mature achene with disc corolla attached. G. Distribution in Arizona and adjacent Sonora.

11. *Heterotheca marginata* Semple, sp. nov. TYPE: U.S.A. ARIZONA. Maricopa Co., Superstition Mts., Apache Trail (AZ-88), 1.8 mi E of Tortilla Flat, sonora desert scrub, disturbed margins of road right-of-way, near pavement, locally abundant, all material from one plant, 16 Oct 1993, *Semple 10384* (Holotype: WAT!; isotypes: ARIZ!, ASU!, DAO!, MO!, MT!, NY!, RM!, TEX!, UC!, US!)

Heterothecae fulcratae var. *senili accedens sed foliis lanceolatis rigidis marginibus hispidis trichomatibus grandibus numerosis, capitulescentiis paniculiformibus, bracteis subter capitulis paucis parvis oblanceolatis.*

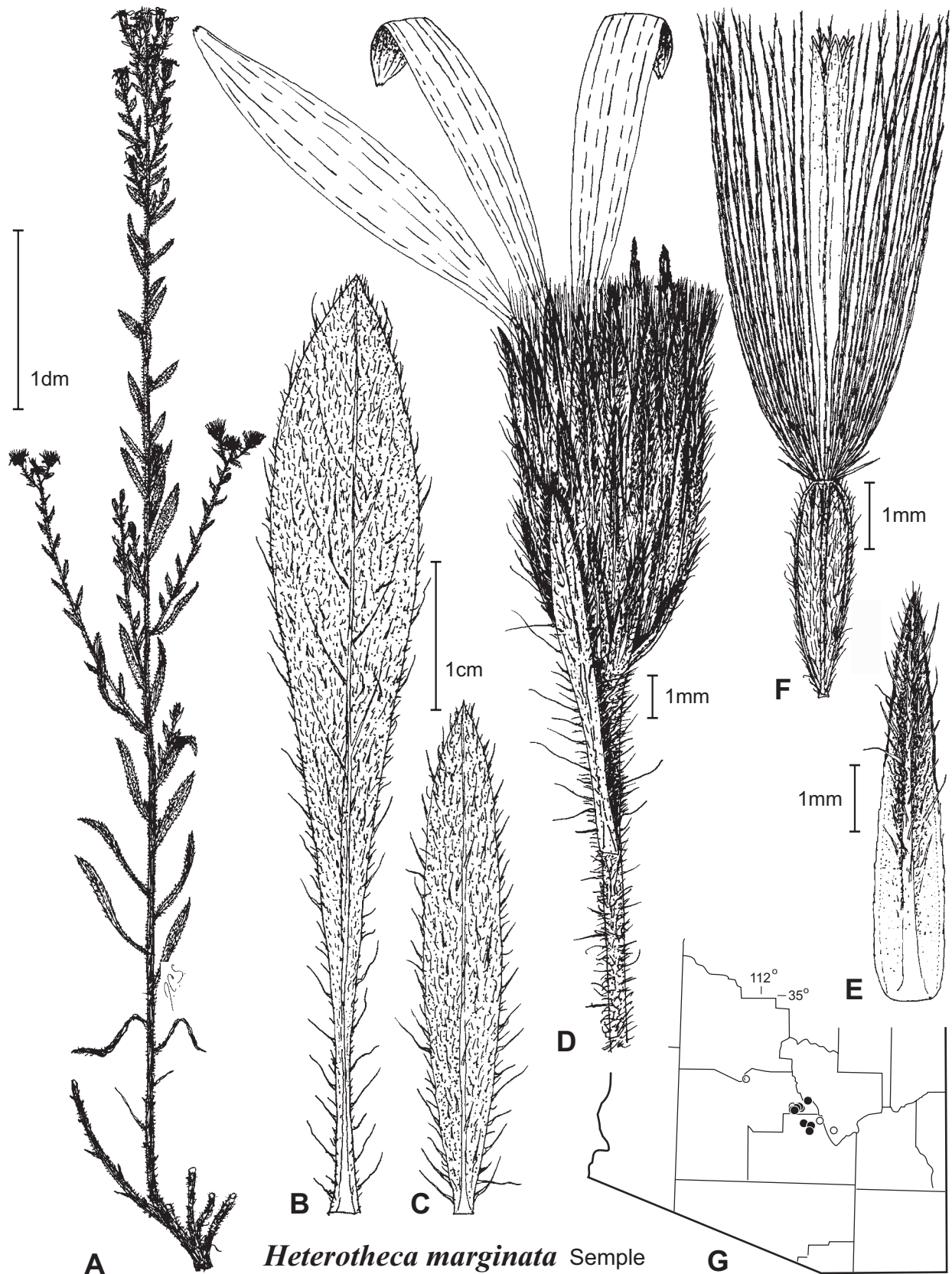
Perennial from stout woody taproots, STEMS several to many, ascending-erect, (38)-40-54-64-(80) cm tall, hispid-scabrous, long spreading hairs numerous; 22-37-50 nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (18)-24.4-37-49.2-(55) cm long, (4)-4.3-5.8-7.3-(9) mm wide, petiolate, cuneate, mucronate, sparsely to moderately hispid-scabrous and sparsely glandular on both surfaces, stiff; margins entire, strigose, many longer spreading hairs along margins. UPPER STEM LEAVES oblanceolate, 14-18.6-23-(31) mm long, 3.3-3.9-4.5-(5.2) mm wide, sessile, reduced upward, acute, stiff, indument similar to lower, (0)-1-2-4-(6) glands/mm², (12)-28-42-54-(56) hairs/mm², margins flat, many longer hispid hairs along margins. CAPITULESCENCE open cymose-paniculiform, heads 8-31-52-(78); peduncles moderately to densely hispid-strigose and sparsely glandular, (12)-14-20-26-(29) mm long; bracts none or few, linear-oblanceolate, usually greatly reduced, rarely foliar and linear-oblanceolate, indument like leaves. INVOLUCRES narrowly campanulate when fresh, campanulate-hemispheric upon drying, (6.5)-7.1-8.2-9.3-(10) mm high; phyllaries in 4-5 imbricate series, outer ones 1/5-1/4 the length of the inner ones, narrowly triangular-lanceolate, moderately strigose, some larger hairs to 1 mm long, eglandular to very sparsely glandular, margins hyaline narrow, fimbriate-ciliate and anthocyanotic apically; inner lanceolate, indument similar. RAY FLORETS (10)-11-12-13-(15), strap yellow, (8.9)-9.5-11.3-13-(14.5) mm long, 1-1.5-2-(2.5) mm wide, glabrate. DISC FLORETS (25)-31-39-46-(50), yellow, glabrate, corolla barely ampliate, (4.5)-4.9-6.0-7-(7.5) mm long, lobes 0.4-0.6-0.7-(0.9) mm long, hairs few or absent, 0.1-0.2-0.3 mm long. ACHENES 1.5-2.2-2.9-(3.2) mm long, moderately strigose; pappus off-white, double, outer whorl of linear scales 0.5-1 mm long, inner whorl of 35-45 barbellate bristle (4.6)-5.1-6.2-7.3-(7.4) mm long. Chromosome numbers: $2n = 18$, several reports; 36, one report.

Flowering Period: (February-September)-OCTOBER-(November)

Distribution and habitat: Upper Sonoran desert in Superstition Mts. and Pinal Mts., Arizona (Fig. 32G); sonoran desert scrub-Arizona upland with *Carnegiea gigantea*, *Cercidium* spp., *Simmondsia*, *Opuntia* spp., *Fouquieria*; desert-grassland hillsides around streams, chaparral transition areas; roadside margins and banks, dry hillsides; gravelly soils and crevices in sandstone outcrops; 600-900 m (2000-3000 ft.) elevation.

Discussion: *Heterotheca marginata* is characterized by its numerous, long, hispid-strigose hairs along the entire margins of its upper leaves and peduncular bracts and by its large heads not subtended by larger bracts (Fig. 32). The hairs give the plants a light gray-green appearance from a distance due to light reflected from the numerous marginal hairs. The leaves are stiff, unlike any other taxon in the section. It is similar to *H. fulcrata* var. *arizonica*, which is more glandular and typically has narrowly ovate to lanceolate bracts subtending smaller heads (Fig. 30), and *H. fulcrata* var. *senilis*, which can be similar in indument but typically has more ovate leaves and heads subtended by narrowly ovate to lanceolate bracts (Fig. 30). It also is similar to *H. villosa* var. *scabra* and *H. shevockii* which have few large hispid-strigose hairs on the leaf margins and are more glandular (Figs. 47 and 50, respectively). Head size variation is in part like due to the occurrence of both diploids and tetraploids within *H. marginata*.

The species is the only member of sect. *Phyllotheca* endemic to the Superstition and Pinal Mts. of south central Arizona; these are characterized by Upper Sonoran Desert vegetation of numerous species of cacti, creosote bush, ocotillo, and desert herbs. *Heterotheca fulcrata* var. *arizonica* occurs in the general area, but



Heterotheca marginata Semples

was not found to be locally sympatric with *H. marginata*. Unlike other taxa in Arizona, *H. marginata* grows exclusively in habitats too dry for pines.

Specimens examined: U.S.A. ARIZONA. Maricopa Co.: Superstition Mts., Apache Trail, Fish Cr., *Eastwood 15924* (LL, NY), E of Mesa, *Hill 60* (ASU); near Roosevelt, *Foster, Arnold 28* (GH); SW of Roosevelt, *Johnson, s.n.* (KANU). E of Tortilla Flats, *Landrum & Landrum 5299* (ASU), *Semple 10385* (CAN, UC, WAT), *Semple & Semple 10499* (ASU, WAT); Horse Mesa area, *Eastwood 17379* (CAS), *Harms 1863* (KANU, SASK(2), WAT), *Peebles 11670* (ARIZ, GH, LL). W of Tortilla Flats, *Semple 10383* (ASU, DAO, KANU, RM, WAT); S of Canyon L., *Keil, Pinkava & Lehto K11336A* (ASU, JCS); SW of Canyon L. Lookout, *Keil 1216* (ASU); Fish Cr. Cyn., *Darrow s.n.* (ARIZ); S of Fish Cr. Bridge, *Keil 1333* (ASU); Fish Cr. Hill, *Johnson 1578* (KANU); S of Fish Cr. Hill Lookout, *Keil 1321* (ASU). Pinal Co.: Devils Cyn., *Harrison & Fulton 3102* (ARIZ), *Harrison & Kearney 6315* (ARIZ, LL), *Peebles, Harrison & Kearney 3192* (ARIZ). ENE of Florence, *Pinkava, Sundell & Zavada 11708* (ASU), *Pinkava, Sundell, & Zavada 11714* (ASU). Florence Junction, W of Boyce Thompson Arboretum, *Keil 6042* (ASU). NE of North Butte, *Mittleman 14* (ARIZ, ASU). Superior, *Whitehead S325* (ARIZ). W of Superior, *Harrison & Kearney 6321* (ARIZ), *Kearney & Peebles 9250* (ARIZ, DS, RSA).

aff. *marginalis* (approaching *H. fulcrata* var. *arizonica*)

Gila Co.: S of Globe, *Semple & Chmielewski 9029* (ASU, WAT). Maricopa Co.: Lake Pleasant Regional Park, NE of upper dam, *Lehto 16499* (BRY; introduced?). Pinal Co.: Devils Cyn., *Peebles & Harrison 4904* (ARIZ, LL).

12. *Heterotheca pumila* (E.L. Greene) Semple, Brittonia 39: 383. 1987. *Chrysopsis pumila* E.L. Greene,

Erythea 2: 95. 1894. "High mountains toward the headquarters [headwaters] of Bear Creek, in Middle Colorado." TYPE: U.S.A. COLORADO. Upper Bear Creek, Jul 1889, *Greene s.n.* (Holotype: NDG-053930!)

Chrysopsis alpicola Rydb., Bull. Torr. Bot. Club. 31: 648. 1904. TYPE: U.S.A. COLORADO. Larimer Co.: Clark's Peak, 11,700', 1 Aug 1896, *Baker s.n.* (Lectotype designated by Semple (1987): NY!; isolectotype: NY!)

Chrysopsis cooperi A. Nels., Bot. Gaz. 40: 63-64. 1905. TYPE: U.S.A. COLORADO. Boulder Co.: Long's Peak, near timber line, 11 Aug 1904, *Cooper 50* (Holotype: RM!; isotype: MIN!)

Chrysopsis alpicola glomerata A. Nels., Bot. Gaz. 40: 64. 1905. TYPE: U.S.A. COLORADO. Larimer Co.: Estes Park, Aug 1904, *Cooper 174* (Holotype: RM!). The combination was published as a trinomial.

Perennial from stout woody taproots; STEMS several to many, decumbent to ascending-erect, (7)-12.5-21-29-(37.5) cm tall, moderately appressed strigose, hispid hairs few; 8-14-21-(38) nodes below capitulescence. LOWER STEM LEAVES narrowly oblanceolate, 25-34-42-(56) mm long, 4-5.8-7-(9) mm wide, petiolate, strigose on both surfaces; margins entire, strigose, a few long hispid hairs near base. UPPER STEM LEAVES similar, acute, little reduced to slightly larger upward, (24)-27-34-41-(49) mm long, (4.5)-5.1-6.8-8.5-(11) mm wide, moderately strigose, sparsely to moderately glandular, 18-31-42-(60) hairs/mm², (0)-2-7-13-(18) glands/mm², margins entire, rarely slightly undulate. CAPITULESCENCE corymbiform, heads 1-4-9-(20), usually subtended by one to several large narrowly oblanceolate foliar bracts, 6.6-11-15 mm long, 0.9-1.6-2.2-(2.5) mm wide; peduncles strigose-canescens, very sparsely stipitate-glandular; bracts few, similar to leaves, reduced below head. INVOLUCRES cylindrical to turbinate when fresh, campanulate-hemispheric upon drying, (6.3)-7.6-9.1-10.6-(12) mm high; phyllaries in 4-5 imbricate series, moderately strigose, eglandular to sparsely stipitate-glandular, margins hyaline, fimbriate-ciliate apically, slightly anthocyanotic apically. RAY FLORETS (10)-12-16-20-(23), strap yellow, (8)-9.7-11.8-13.8-(15) mm long, 1-1.5-2-(2.5) mm wide. DISC FLORETS (16)-24-43-60-(73), yellow, corolla barely ampliate, (4.6)-5.3-5.9-6.6-(7.1) mm long, lobes (0.5)-0.6-0.7-0.8-(1.0) mm long, rarely with a few hairs 0.1-0.25 mm long. ACHENES 1.7-2.3-3 mm long, sparsely to moderately strigose; pappus off-white, double, outer whorl of linear scales 0.25-1 mm long, inner whorl of 35-45 barbellate bristles (4.7)-5-5.9-6.7-(7.1) mm long at anthesis, 80-110% length of corolla. Chromosome numbers: 2n = 18, a few reports; 36, about a dozen reports.

↪ **Figure 32. Morphology and distribution of *Heterotheca marginata*.** A. Habit. B-C. Lower stem leaf and upper stem leaf, respectively, adaxial surface. D. Head with only some florets drawn. E. Mid series phyllary with chlorophyllous zone dark; upper margins usually anthocyanotic. F. Mature achene with disc corolla attached. G. Distribution in southern Arizona based on all collections seen.

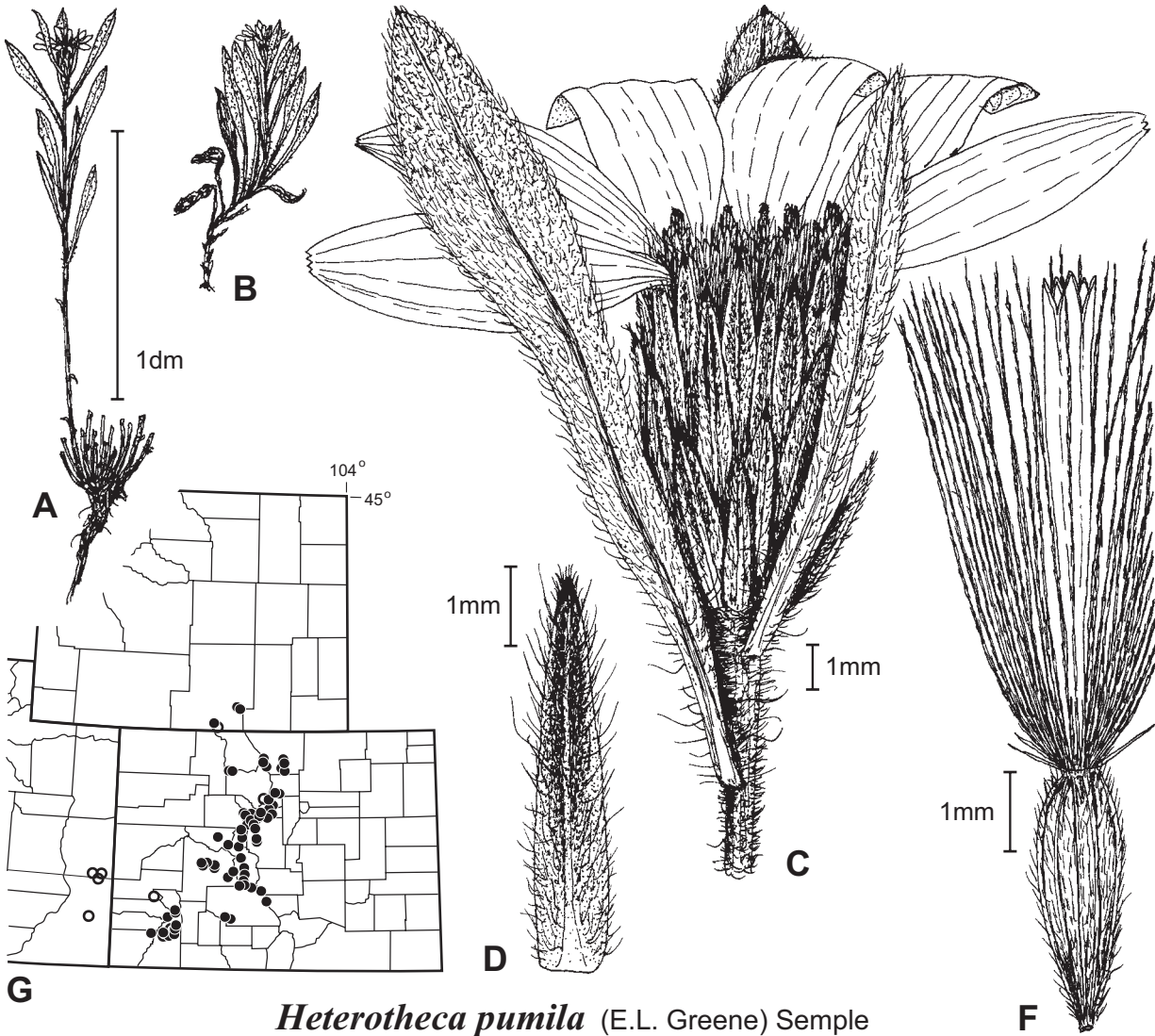
Flowering Period: JULY-AUGUST-(September)

Distribution and habitat: Subalpine and alpine sites in the Rocky Mts. of Colorado and very rare in adjacent Wyoming and southeastern Utah (Fig. 33F); granitic outcrops, roadsides, rocky soils, clay or shale soils; (2900)-3000-3800m [(9,500)-10,000-12,500 ft.] elevation.

Discussion: *Heterotheca pumila* is distinguished by its narrow oblanceolate, moderately strigose and sparsely glandular upper stem leaves which often are longer than the lower ones and frequently extend beyond the involucre, by heads usually subtended by long oblanceolate foliar bracts, by its rather long and wide ray straps, and by its phyllaries that are often anthocyanotic near the tips and sometimes along the upper margins (Fig. 33). The combination of many stems and large heads with long rays can make individuals of this species very showy. Collections from high elevations in southeastern Utah treated here as “aff. *H. pumila*” are similar to higher elevation forms of var. *minor*, which have large heads but smaller upper stem leaves than typically found in *H. pumila*. Wyoming plants include typical and more *minor*-like specimens.

This species appears to be a higher elevation race of the *fulcrata* complex close to the narrow-leaved *resinolens* morph of *H. fulcrata* var. *fulcrata* (Fig. 29). Alternatively, *H. pumila* may be more closely allied to *H. villosa* var. *minor* (Fig. 46). Most plants are tetraploid; the few diploids known are atypical with smaller heads and a more *minor*-like reduction in upper leaf size. Diploid plants from Arizona and New Mexico reported earlier as members of this species (Semple 1987) are now recognized to be narrow-leaved, *H. fulcrata* var. *amplifolia* with small ovate-lanceolate bracts subtending the heads.

Specimens examined: U.S.A. COLORADO. “Colorado Territory”, *Coulter s.n.* (PH(3)), *Meehan s.n.* (NY), *Penard* (UBC). Arkansas Valley, *McCosh & Greene s.n.* (NY(2)). South Park, *Wolf 552* (NY). Hall Valley, *Smith s.n.* (PH). Limecreek Rd, *Heil 218* (BRY). San Isabel N.F., *Taylor 359* (USFS), *Taylor 372* (USFS). Silver Lake, *Eastwood & Phelps s.n.* (CAS). Boulder Co.: W of Nederland, near Caribou, *Jones 34613* (UC), *Jones 36313* (UBC). Chaffee Co.: W of Buena Vista, *Beetle 2154* (GH, RM). Hoosier Pass, near town of Blue River, *Lepper 119a* (WIS). Manassas Crk, *Clokey 3498* (CAN, CAS, DS, GH, MIN, NY, POM, TEX, UC, WS, WTU). E of Monarch Summit, *Neese 15928* (BRY, RSA). Clear Creek Co.: Near Empire, *Patterson s.n.* (GH(2)). N of Empire, *Patterson 305* (GH, NY, MIN, PH, UC). Georgetown, near Clear Lake, *Shear 4532* (NY, RM). Loveland Pass, *Semple & Zhang 10467* (RM, WAT). E of Loveland, *Harms 2094* (KANU, SASK). Mt. Evans, *Semple et al. 6595* (JCS, WAT). Above Echo Lake along rd to Mt. Evans, *Heckard 1442* (UC). Pike N.F., Smelter Gulch, *Gierisch 2655* (USFS). Custer Co.: W of Westcliffe, Sangre de Cristo Mts, *Mosquin & Gillett 5392* (DAO, DS). Eagle Co.: Red Cliff, *Osterhout 2705* (NY, RM). Tennessee Pass, *Clokey s.n.* (POM), *Clokey 3485* (CAN, CAS, DS, GH, MIN, NY, POM, RM, TEX, UC, WS), *Clokey 3629* (CAN, CAS, GH, NY, RM, TEX, UC), *Jepson 14684* (CAN, JEPS), *Jepson 14685* (CAN). W of Vail Pass, *Semple & Chmielewski 8362* (WAT). Fremont Co.: Sangre de Cristo, *Brandege 730* (NY, UC). Gilpin Co.: Tolland, *Cox 1969* (UT), Grand Co.: Berthoud Pass, *Degener & Peiler 16726* (NY). N of Berthoud Pass, *Peirson 12539* (RSA). W slope Berthoud Pass, *Nelson 10938* (DS, PH, RM). Gunnison Co.: NW Cottonwood Pass, *Iltis & Iltis 19058* (UC, WIS). N of Crested Butte, *Wherry C3702* (PH). NW of Crested Butte, *Higgins 2173* (BRY). W of Crested Butte, Kebler Pass, *Semple & Heard 7770* (WAT). Gothic, *Langenheim 218* (MIN). N of Gothic, *Spongberg 64-206* (GH). S of Gothic, *Langenheim 3946* (UC). N of L. Brennan, near Ruby Peak, *Rollins 1452* (DS, UC, USFS). Monarch Pass, *Harms 2081* (KANU, SASK), *Semple & Heard 7745* (JCS, WAT). Mt. Ouray, *Baker 861* (GH, NY, POM). N of Pitkin, *Headlee 432* (BRY). La Platta Co.: La Plata N.F., Big Elk Cr, *Abbott 224* (USFS). LaPlata Mts, rd from LaPlata to Eagle Pass, *Mosquin & Gillett 5429* (DS). Lake Co.: W slope of Fremont Pass, *Greene 301* (PH). Independence Pass, *Pinkava 6261* (ASU). E slope of Independence Pass, *Ewan 18266* (GH), *Semple & Zhang 10461* (RM, WAT). Tennessee Pass, *Osterhout 2172* (NY, RM), *Osterhout 2711* (NY, RM, WIS), *Osterhout 3350* (RM), *Osterhout 3350* (RM), *Maguire 12740* (GH, WS). Near Leadville, *Ehlers 8216* (TEX, WTU), *Tidestrom 654* (WIS). N of Leadville, *Harms 2088* (KANU, SASK(2), WAT). Weston Pass, *Gierisch 1277* (NY, USFS). Larimer Co.: *Baker s.n.* (POM). Cameron Pass, *Baker 329* (POM). Chambers L., *Osterhout 4386* (MIN, WIS), *Osterhout 6320* (RM), *Osterhout 6339* (RM). Clark’s Peak, *Baker 19* (POM). Estes Park, *Cooper 221* (RM). Longs Peak, Mills Park, *Clements s.n.* (NY). Rocky Mt. N.P., Specimen Mt, *McNeal 291* (RM). Twin Lakes, *Coulter s.n.* (NY), *Clements 425* (NY). Yankee Doodle L., *Ramaley 10721* (RM, WTU). Montezuma Co.: Montezuma N.F., Deadwood Gulch, *Cayton C-2* (USFS). Montrose Co.: Marshall Pass, *Baker 884* (GH, MIN, NY, POM, RM, UC(2)). Ouray Co.: S of Ouray, N of Red Mt. Pass, *Harms 2071* (KANU, SASK(2), WAT). NE of Red Mt Pass, *Hendrickson 1855* (RSA). Red Mt. Rd., *Underwood & Selby 338* (NY). Park Co.: Boreas Pass Rd 4 mi E of State Hwy 9, *Nelson 725* (BRY). S of Fairplay, *Neely 2861* (RM). W of Fairplay, Pennsylvania Mt., *Dorr 1809* (TEX). Hoosier Pass, *Thorne 34120* (RSA). Pitkin Co.: E of Aspen, *Semple & Zhang 10453* (RM, WAT), *Weber 18788* (TEX). SE of Aspen, *Semple & Zhang 10454* (RM, WAT). Aspen Mt., *Wood s.n.* (WIS). Routt Co.: Rabbit Ear Pass, *Luckow 958* (OBI). W of Rabbit Ears Pass, *Semple et al. 5776* (WAT), *Semple et al. 5781* (WAT). Sagauche Co.: Cochetopa N.F., *Sandson 47* (USFS), *Whillen 189* (USFS). Cochetopa Pass, *Ramaley & Gambill 16912* (RSA, TEX). Perry Creek drainage, *Mooers 397* (NY), *Mooers & Dufford 581* (NY). Sangre de Cristo, *Clements 352* (NY). San Juan Co.: San Juan N.F., Andrews L., *Kass & Meyer 1418* (BRY). S of Silverton, *Peirson 12506* (RSA, UC), *Rollins 1544* (GH, LL, NY), *Harms 2063* (KANU, SASK), *Harms 2064* (KANU), *Waterfall 11706* (UC). San Miguel Co.: Trout Lake, *Payson & Payson 4121* (GH,



Heterotheca pumila (E.L. Greene) Semple

Figure 33. Morphology and distribution of *Heterotheca pumila*. A-B. Habit and shoots. C. Upper stem leaf, adaxial surface and head with only some florets drawn. D. Mid series phyllary with chlorophyllous zone dark, pubescent morph. E. Mature achene with disc corolla attached. F. Distribution in Colorado and adjacent southeastern Utah and southern Wyoming (o aff. *H. pumila*).

RM, UC(2), WTU). Summit Co.: Breckenridge, *Oakley 12* (USFS), *Mackenzie 260* (NY, PH, RM, WIS). S of Breckenridge, *Ferris 11465* (DS, WTU). N of Fremont Pass, *Semple & K. Shea 2246* (WAT). NE of Fremont Pass, *Harms 2089* (KANU, SASK). Gray's Peak, *Brown 194* (NY), *Corringdown s.n.* (GH), *Meehan s.n.* (NY), *Osterhout 2773* (NY, RM), *Smith s.n.* (PH); Gray's Pk., *Smith s.n.* (PH). Leadville N.F., *Smith 360* (USFS). Loveland Pass, *Watson 505* (TEX), S of pass, *Harms 2093* (KANU, SASK). Mt. Harvard, *Clements s.n.* (NY). NE of Racen, *Harms 2090* (KANU, SASK). W of Frisco, *Mosquin & Gillett 5358* (DS). WYOMING. Carbon Co.: Battle Mt., *Semple & Zhang 10412* (RM, WAT). Kennaday Pk., E of Saratoga, *Harman 19822* (RM).

aff. *pumila* (lower elevation forms close to *H. villosa* var. *minor* or higher elevation forms of var. *minor*)

U.S.A. COLORADO. Chaffee Co.: W of Garfield, *Harms 2082* (KANU, SASK). Gunnison Co.: Gothic, *Ugent 140* (WIS). La Plata Co.: San Juan N. F., Purgatory Campsite, *Harms 2058* (KANU, SASK). Larimer Co.: summit of North Park Range, *Goodding 1826* (DS, NY, PH, RM). Montezuma Co.: San Juan N.F., Cascade Cr, *Kass 2543* (BRY). Montrose Co.: SW of Montrose, *Rollins 1599* (LL, NY, RM, USFS). Ouray Co.: N of Red Mt. Pass, *Harms 2072* (SASK). San Juan Co.: NE of South Mineral Falls, *Harms 2065* (KANU, SASK, WAT).

UTAH. Grand Co.: *Franklin & Franklin 4103* (BRY). Abajo Mts., *Cottam 14389* (RSA). LaSal Mts, *Payson & Payson 4013* (DS, GH, RM, UC). NW corner Beaver Basin, *Franklin 2279* (BRY, CAN, NY). Dark Cyn, *Franklin 906* (BRY, NY). NNW of Mt. Peale, *Franklin 4289* (BRY, NY, RM). WYOMING. Albany Co.: near Centennial, *Yunker & Yunker 11964* (NY, TEX). Carbon Co.: Sierra Madre, SW of Encampment, *Nelson & Blunt 4097* (NY, RM).

13. *Heterotheca stenophylla* (A. Gray) Shinnery, Field & Lab. 29: 68. 1951. *Chrysopsis hispida* (Hook.) DC. var. *stenophylla* A. Gray, J. Boston Nat. Hist. Soc. 6: 223. 1850. *Chrysopsis villosa* (Pursh) Nutt. var. *stenophylla* (A. Gray) A. Gray, Synopt. Fl. N. Amer. 1, 2: 123. 1884. *Chrysopsis stenophylla* (A. Gray) E.L. Greene, Erythea 2: 96. 1894. TYPE: U.S.A. TEXAS. Llana, growing in the crevices of smooth granite rocks, Nov 1847, *Lindheimer 631* (Holotype: GH!; isotypes: CAN!, DS!, K!, ND-G!, NY(2)!, US!)

Perennial from stout woody taproots, STEMS several to many, ascending-erect, (18)-24-35-46-(65) cm tall, sparsely to densely hispid and strigose (hairs often broken off, especially near base), sometimes becoming densely glandular and moderately pubescent above, often brown and brittle; (18)-23-35-46-(61) nodes below capitulescence; very short lateral branches often present along upper half of stem. LOWER STEM LEAVES linear oblanceolate, (15)-24-31-38-(42) mm long, (2)-3.3-4.8-6.2-(8.4) mm wide, petiolate, cuneate, acute, sparsely to moderately hispid-strigose and sparsely to moderately glandular on both surfaces or moderately to densely hispid-strigose and non-glandular, margins entire, strigose, longer hispid hairs near base. UPPER STEM LEAVES narrowly to broadly oblanceolate, sessile, usually little reduced upward, (9)-16.5-21.5-26.4-(30) mm long, (1.5)-2.2-3.2-4.3-(6) mm wide, non-glandular to densely glandular 0-10-24-(50) glands/mm², sparsely to moderately densely hispid-strigose, (5)-20-80-145-(245) hairs/mm², the hairs often scabrous and somewhat pustulate, margins flat, often with numerous large hairs. CAPITULESCENCE corymbiform, branches ascending, heads (1)-2-9-16-(30); peduncles sparsely to densely hispid-strigose and non-glandular to densely glandular; bracts few, lower ones oblanceolate, leaf-like, sometimes little reduced upward, (2)-4-6.1-8.2-(13.5) mm long, (0.2)-0.5-0.9-1.3-(1.8) mm wide. INVOLUCRES cylindrical to turbinate when fresh, narrowly campanulate upon drying, (4.5)-5.5-6.7-7.9-(11) mm high; phyllaries in 5-6 imbricate series, outer 1/5-1/4 length of inner, mid series narrowly triangular, very sparsely to densely glandular, very sparsely to moderately strigose, margins hyaline, fimbriate-ciliate apically. RAY FLORETS (10)-12-18-24-(36), strap yellow, (5.1)-6.7-9.1-11.5-(16.5) mm long, (0.7)-0.9-1.2-1.5-(2.1) mm wide. DISC FLORETS (12)-23-39-55-(70), yellow, corolla slightly ampliate, (4.3)-4.9-5.7-6.4-(7.0) mm long, lobes (0.4)-0.5-0.6-0.8-(0.9) mm long, very sparsely pilose, hairs on lobes 0.1-0.25 mm long. ACHENES (1)-1.5-2.0-2.5-(3.1) mm long, sparsely to moderately strigose; pappus off-white, double, outer whorl of a few linear scales 0.25-0.5 mm long, inner whorl of 25-40 barbellate bristles (4)-5.2-6.0-6.8-(7.5) mm long. Chromosome numbers: $2n = 18, 36$; many reports.

Flowering Period: MAY-JUNE-JULY to October.

Distribution and habitat: Rocky soils and outcrops of prairies and hills from central Texas to southeastern South Dakota (Figs. 34E and 35E); 180-1700 m (600-6000 ft.) elevation.

Discussion: *Heterotheca stenophylla* is divided into two seemingly quite distinct varieties that differ in gland and hair density. The ranges of the two overlap to a great extent and plants with intermediate indument traits occur scattered throughout the range. The typical variety usually has linear-oblanceolate scabrous-strigose leaves with large globose glands and usually large broad-based hairs along the leaf margins (Figs. 34). The heads are often closely subtended by foliar peduncular bracts as seen in *H. fulcrata* (Figs. 29-30) and *H. sessiliflora* ssp. *sessiliflora* (Fig. 15), but in *H. stenophylla* such bracts are usually narrowly oblanceolate. Variety *angustifolia* is superficially like *H. villosa*, but the type and many other specimens indicate it is the hairy sister-group to var. *stenophylla*. The species is thought to be related to the *Fulcrata* Group or the *Mexicana* Group neither of which are present in the range of *H. stenophylla*. *Heterotheca canescens* may also share a common ancestry with *H. stenophylla*. Both *H. stenophylla* and *H. canescens* often have numerous leaves along the stem that overlap and often bear fascicles of leaves in their axes.

13.1 *Heterotheca stenophylla* (A. Gray) Shinners var. *stenophylla*

Chrysopsis scabrifolia A. Nels., Bot. Gaz. 37: 264. 1904. TYPE: U.S.A. OKLAHOMA. Woods Co., 29 June 1900, White s.n. (Holotype: RM!)

STEMS several to many, ascending-erect, (18)-20-**34**-47-(64) cm tall, sparsely to moderately hispid and strigose (hairs often broken off, especially near base), becoming densely glandular and moderately pubescent above, usually brown and brittle; (23)-27-**39**-51-(61) nodes below capitulescence. LOWER STEM LEAVES linear oblanceolate, 22-**28**-35-(40) mm long, (2)-2.9-**3.9**-4.9-(5) mm wide, petiolate, acute, very sparsely to moderately hispid-strigose and moderately glandular on both surfaces. UPPER STEM LEAVES linear oblanceolate (rarely broadly so), little reduced upward, (9)-13.5-**19.1**-24-(27) mm long, (1.5)-1.7-**2.7**-3.7-(5) mm wide, sparsely to densely glandular, (4)-3.5-**21**-38-(50) glands/mm², sparsely to moderately hispid-strigose, (2)-9-**23**-37-(50) hairs/mm², the hairs usually scabrous and somewhat pustulate, margins often with numerous large hairs. CAPITULESCENCE corymbiform; heads 1-**9**-17-(30); peduncles sparsely to moderately hispid-strigose and moderately to densely glandular; bracts few, lower ones oblanceolate, leaf-like, sometimes little reduced upward and foliar, (2)-3.5-**5.5**-7.5-(10) mm long, (0.2)-0.3-**0.7**-1.2-(1.8) mm wide. INVOLUCRES (5.5)-5.8-**6.3**-6.8-(7.4) mm high; phyllaries sparsely to densely glandular, very sparsely to sparsely strigose. RAY FLORETS (11)-12-**18**-24-(36), strap (6.7)-8.6-**10.3**-12-(13.7) mm long, (0.7)-0.9-**1.2**-1.5-(1.8) mm wide. DISC FLORETS (12)-16-**32**-47-(65), corolla (4.3)-4.5-**5.2**-5.9-(7.0) mm long, lobes 0.5-**0.6**-0.65-(0.7) mm long. ACHENES (1)-1.2-**1.7**-2.1-(2.3) mm long, inner whorl of barbellate bristles (4)-4.7-**5.5**-6.2-(7.0) mm long. Chromosome numbers: $2n = 18$, numerous reports; 36, a few reports.

Flowering Period: May-JUNE-JULY-October.

Distribution and habitat: Prairies and rocky hills from central Texas to southeastern South Dakota in a half dozen disjunct areas, most common in western Oklahoma and adjacent Texas and Kansas (Fig. 34E); rocky soils and outcrops; 180-1500 m (600-5000 ft.) elevation.

Discussion: Variety *stenophylla* is easily recognized by its distinctive narrowly oblanceolate leaves that are usually sparsely to moderately hispid-strigose and moderately glandular (Fig. 34). The hairs often are very broad based and have been described as pustulate by Harms (1963, 1968); these add to the distinctness of the foliage, although this trait is not always well developed. The presence of large, broad-based hairs along the margins of the upper leaf and peduncular bracts also contribute to the general appearance of the plant. The numbers of hairs and glands varies greatly and only the hairiest leaves take on a somewhat grayish-green color; usually the leaves are bright green. Although the heads are usually at least short pedunculate, the long ascending leaves and bracts give the impression that the heads are sessile and subtended by several bracts such as found in *H. sessiliflora* ssp. *sessiliflora* from the strand of southern California and northern Baja (Fig. 15). The lower stems are often brown and naked, the leaves having dropped off before anthesis, and the stems are usually rather brittle.

It is postulated that var. *stenophylla* is a very divergent member of the *Fulcrata-Viscida* complex and had its origins in the mountains of Trans-Pecos Texas or adjacent México. Plants similar to var. *stenophylla* occur in *H. fulcrata* var. *arizonica* (see discussion of that taxon; Fig. 30) in the Chisos Mountains of the Big Bend region in Texas. The present distribution of *H. stenophylla* probably developed during the Holocene following climatic changes accompanying deglaciation of North America (Bryant and Holloway 1985). The very-linear oblanceolate leaves typical of var. *stenophylla* may be a relatively recent adaptation permitting expansion of the range of the species onto the southern Great Plains. At the same time this was occurring, sister taxa in the complex were evolving and adapting in different ways in habitats that allowed expansion northward into the central Rocky Mts. The same scenario could have begun in México with an ancestral form of the *mucronata* complex similar in indument and leaf shape to Coahuilan collections of *H. mucronata* var. *harmsiana*. Migration northeastward into Texas and a series of founder effect events could have resulted in the evolution of proto-*H. stenophylla*.

Specimens examined: U.S.A. COLORADO. Yuma Co.: Wray, *Osterhout 4033* (RM, NY), *Shantz s.n.* (NY). IOWA. Lyon Co.: NW part of county, *Thomas s.n.* (MIN). Gitchie Manitou S.P., *Fults 2940* (WTU), *Thorne 14210* (MIN), *Shimek s.n.* (WS), *Lassetter 1548* (BRY), *Lassetter 1560* (BRY), *Thorne 16092* (RSA). NW corner of county, *Schimek s.n.* (NY). KANSAS. Barber Co.: N of Aetna, *McGregor 15105* (KANU). W of Hardtner, *Rydberg & Imler 630* (KANU, NY). S of Lake City, *Harms 649* (KANU, SASK), *Harms 651* (KANU, SASK), *Harms 654* (KANU), *Harms 865* (KANU, SASK). SW of Medicine Lodge, *Harms 1346* (KANU(2), SASK(2)), *Harms 19097* (KANU, SASK), *Rydberg & Imler 690* (KANU, NY). W of Medicine Lodge, *Harms 864* (KANU, SASK), *McGregor 13765* (KANU), *Stephens 90280* (KANU). S of Sawyer, *Horr & Franklin s.n.* (KANU), *Horr & Franklin E335* (KANU(2), LL, WIS). Comanche Co.: E of Coldwater, *Harms 1352* (KANU, SASK). SE of Kings, *McGregor 10947* (KANU). Ellsworth Co.: W of Canerio, *Harms 688* (KANU(2), SASK), *Harms 690* (KANU, SASK, WAT), *Jackson 90* (KANU, NY, UNCC), *Johnson 1767* (KANU). S of Ellsworth, *Harms 713* (KANU, SASK). Kanopolis Reservoir, Horsethief Canyon, *McGregor 30367* (KANU, NY). N of Langley, *Johnson 1334* (KANU). Finney Co.: S of Garden City, *Rydberg & Imler 994* (KANU, NY). Kiowa Co.: *Ward s.n.* (NY). Meade Co.: W of Englewood, *Rydberg & Imler 823* (KANU, NY). SE of Mead, *Horr & McGregor 3881* (GH, KANU, LL, NY). W of Meade, *Rydberg & Imler 796* (KANU, NY). Meade County State Park, *Bare 72* (KANU). Pratt Co.: S of Sawyer, *Horr & Franklin E335* (ASU, CAS, GH, IN, MIN, NY, RM, UC, WS). Saline Co.: S of Brookville, *McGregor 35628* (KANU). W of Brookville, *Hancin 1890* (KANU). Seward Co.: NE of Liberal, *Harms 812* (KANU). Stevens Co.: NE of Hugoton, *Harms 754* (KANU, SASK, WAT), *Harms 755* (KANU, SASK), *Harms 19108* (KANU, SASK), *Semple & K.Shea 2220* (WAT). NEBRASKA. Adams Co.: NE of Heartwell, *Birkholz 2351* (GH, KANU). Antelope Co.: US-275 E of county line, *Semple & Brouillet 4499* (WAT). W of Oakdale, *Rohrbaugh 33* (TEX). Brown Co.: Long Pine, *Bates s.n.* (GH, NY, RM). Jefferson Co.: S of Helvey, *Rohrbaugh 15* (GH). Keya Paha Co.: SW of Norden, *Freeman 1488* (WIS). Saunders Co.: Meadville, *Clements 2954* (NY, UC). NEW MEXICO. Roosevelt Co.: SW of Clovis, *Harrison s.n.* (GH). Union Co.: SW of Clayton, *Harms 1862* (KANU). OKLAHOMA. Canadian R., *Bigelow s.n.* (GH, NY). Cimarron Valley, *Carlton s.n.* (DS, UC). Ft. Smith to Rio Grande-Whipple Exp. near 35th Parallel, *Bigelow s.n.* (GH). Kashie Hills, *Van Vleet s.n.* (RM). Beaver Co.: E of Forgan, *Waterfall 7408* (GH, TEX). E of Slapout, *Semple & K.Shea 2215* (WAT). Blaine Co.: near Longdale, *Stevens 820* (DS, GH, MIN(2)). Caddo Co.: SE of Hinton, *Crowder s.n.* (TEX). Comanche Co.: near Cache, *Stevens 1327* (DS, GH, MIN). N of Cache, *Stephens 37496* (KANU). W of Lawton, *Massey & Harrison 2130* (UNCC). Lost Lake, *Gordon 54* (TEX). Medicine Park, *Demaree 13024* (DS, NY(2)). Wichita Mts. N.W.R., *Davis 33* (WIS), *Marcy s.n.* (GH). Wichita N.F., *Schultz s.n.* (UNCC). Custer Co.: E of Butler, *Stephens 27231* (KANU). SW of Weatherford, *Waterfall 5510* (RSA). W of Weatherford, *Seigler 1436* (TEX). Dewey Co.: near Canton, *Stevens 867* (DS, GH, MIN(2)). S of Carmaigo, *Semple & K.Shea 2213* (WAT). SW of Seiling, *Stephens 27179* (KANU). E of Vici, *Harms 1705* (KANU). N of Vici, *Harms 1700* (KANU, SASK(2)). S of Vici, *Harms 1710-B* (KANU). Greer Co.: S of Mangum, *Waterfall 7689* (GH, TEX). Quartz Mt. S.P., *Semple & K.Shea 1498* (WAT). NE of Willow, *Harms 1728* (KANU). Harmon Co.: near Hollis, *Stevens 1092* (GH, MIN). W of Vinson, *Waterfall 7701* (GH, TEX). Harper Co.: E of Buffalo, *Harms 1988* (KANU, SASK), *Smith 10* (TEX), *Stephens 71415* (KANU). S of Buffalo, *Stephens & Brooks 216298* (KANU). Kiowa Co.: Snyder, *Richards 3750* (SASK). W of Snyder, *Waterfall 8745* (GH, TEX). Major Co.: N of Chester, *Harms 1695* (KANU, SASK), *Stephens 27151* (KANU). Cleo, *Stevens 1735* (DS, GH, MIN, NY). W of Orienta, *Stephens & Brooks 27142* (KANU). OK-58 N of county line, *Semple & Brammall 2731* (WAT). Roger Mills Co.: Antelope Hills, *Goodman & Lawson 8416* (KANU), *Nelson, Nelson and Goodman 5343* (RM). Near Antelope Hills, *Bigelow s.n.* (NY), *Bigelow s.n.* (NY(2)). W of Cheyenne, *Sooter s.n.* (TEX). Texas Co.: OK-3 E of Chiquita Creek, *Semple & K.Shea 2217* (NY, WAT), *Semple & K.Shea 2218* (CAN, WAT). E of Hardesty, *Harms 1973* (KANU(2), SASK(3), WAT(2)). Washita Co.: E of Cordell, *Smith & Van Valkenburg 308* (UC). Woods Co.: *White s.n.* (MIN). NE of Alva, *Nighswonger 1170* (UNCC). NW of Alva, *Nighswonger & Shorter 538* (KANU), *Nighswonger 851* (BRY). W of Alva, *Stephens 71364* (KANU). Near Freedom, *Stevens 756* (DS, GH, MIN, WTU). NE of Freedom, *Harms 1992* (KANU, SASK(2), WAT). N of Waynoka, *Harms 1691* (KANU, SASK(2)), *Harms 1692* (KANU, SASK). S of Waynoka, *Harms 1694* (KANU, SASK(3)). Hwy-64 W Hwy-34 & 50, *Harms 1989* (SASK!, and progeny, SASK!). Woodward Co.: N Moreland, *Stephens & Brooks 21655* (KANU). S of Woodward, *Harms 1698* (KANU(2)). SW of Woodward, *Springer 169* (KANU). SOUTH DAKOTA. Moody Co.: Dell Rapids, *Thornber s.n.* (UC). TEXAS. Near Paloduro Canyon, *Young s.n.* (TEX). Between the San Pedro and Pecos, *Bigelow 511* (NY). Archer Co.: *Reverchon 461* (NY). Blue Spring, *Reverchon 462* (NDG). Elm Spring, *Reverchon 23* (GH, NY). Burnet Co.: Inks Lake St. Pk., *Johnson 1907-a* (KANU), *Semple & K.Shea 2198* (WAT, TEX). Childress Co.: *Biology Class s.n.* (TEX). E of Memphis, *Higgins 7248* (NY). Clay Co.: NE of Henrietta, *Cory 40773* (TEX). Collingsworth Co.: W of Quail, *Higgins 4511* (ASU, BRY). NW of Wellington, *Stephens 80945* (KANU). Custer Co.: E of Thomas, *Seigler, May & Hilu DS-8587* (LL). Donley Co.: SE of Hedley, *Shinners 8004* (NY, RM, UC). Eastland Co.: E of Cisco, *Warnock 46387* (TEX). Gray Co.: L. McClellan, *Higgins 9498* (BRY). W of McClean, *Semple & K.Shea 1490* (JCS). S of Pampa Valley, *Stephens 71905* (KANU). Hall Co.: *Smith 305* (UC). Estelline, *Reverchon 3995* (NY). Hardeman Co.: Medicine Mound, *Correll 15149* (LL), *Correll 15150* (LL). Hays Co.: ENE of Fischer (Comal Co.), *Nesom et al 7230* (TEX). San Marcos, *Stanfield s.n.* (NY(2)). NNW of Wimberly, *Walker 8* (TEX). Wimberly, *Correll 13398* (NY). Hemphill Co.: 5 mi E of Canadian, *Rowell 4071* (TEX). W of Canadian R. on Hwy-2266, *Higgins 12674* (ASU, BRY). Hutchinson Co.: Canadian R., *Drake 132* (TEX). Llano Co.: *Bray 331* (TEX), *Tharp 7356* (LL). E of Enchanted Rock, *Butterwick & Lamb 2996* (TEX). Between Llano and San Saba, *Lundell & Lundell 14576* (LL). Potter Co.: NE of Amarillo, *Shinners 8071* (RM). N of Canadian R., *Higgins 4433* (ASU, BRY, NY), *York & Rogers 45* (TEX). Taylor Co.: S of Abilene, *Johnston 6515* (LL). Travis Co.: Hamilton Pool Rd. at Pedernales R, *Ertter & Larke 5146* (NY, RSA, TEX), below Hamilton Pool, *Johnston s.n.* (TEX). Wheeler Co.: W of Kellerville, *Stephens 76516* (KANU). S of Shamrock, *Cory 50226* (DS, NY, RM, UC, WS). SW Wheeler, *Stephens 81721* (KANU).

aff. var. stenophylla (close to var. *angustifolia* or mixed population)

U.S.A. NEBRASKA. Wheeler Co.: NE of Bartlett, *Stephens & Brooks 24225* (DS, KANU). OKLAHOMA. Comanche Co.: N of Meers,

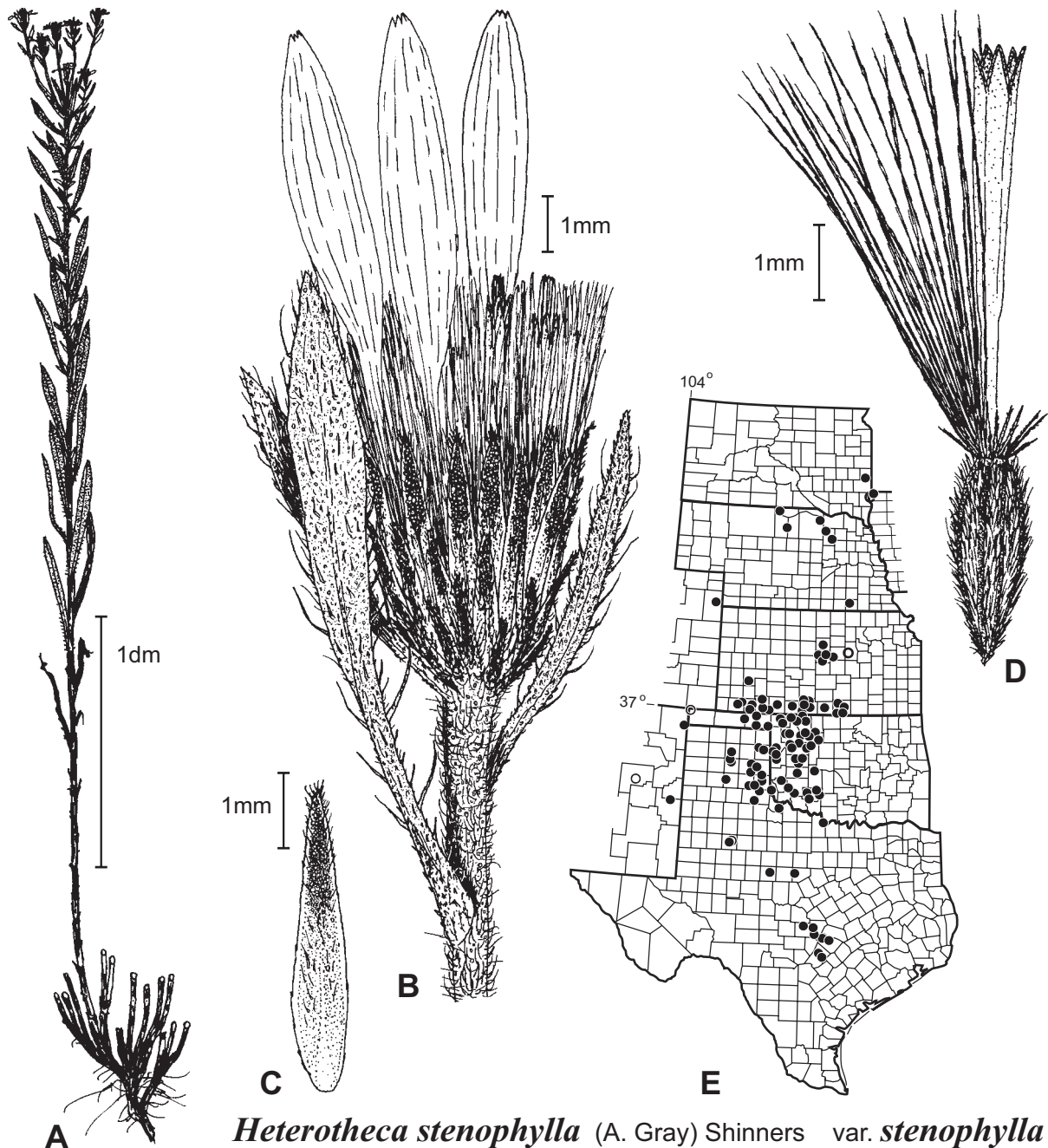


Figure 34. Morphology of *Heterotheca stenophylla* var. *stenophylla*. A. Habit, tall shoot. B. Upper stem leaf and head; only some florets drawn. C. Mid series phyllary with chlorophyllous zone dark. D. Mature achene with disc corolla attached. E. Distribution; South Dakota to New Mexico and Texas (° aff. var. *stenophylla*).

Hopkins, Nelson & Nelson 812 (GH, NY, WIS, WTU). **SOUTH DAKOTA.** Minnehaha Co.: Dell Rapids near Big Stone Lake, *Johnson 71* (NY, TEX, WTU). **NEW MEXICO.** Guadalupe Co.: SE of Santa Rosa, *Turner 15830* (TEX). **MISSOURI.** E.L. Greene Co.: Springfield, *Standley s.n.* (NY; probably introduced and not established). **TEXAS.** Garza Co.: W of Post, *Harms 1767* (KANU, SASK(2)).

13.2 *Heterotheca stenophylla* (A. Gray) Shinners var. *angustifolia* (Rydb.) Semple, Novon 4: 53. 1994. *Chrysopsis angustifolia* Rydb., Bull. Torr. Bot. Club 37: 128. 1910. *Chrysopsis villosa* (Pursh) Nutt. var. *angustifolia* (Rydb.) Cronquist., Bull. Torrey Bot. Club 74: 150. 1947. *Heterotheca villosa* (Pursh) Shinners var. *angustifolia* (Rydb.) Harms, Wrightia 4: 16. 1968. TYPE: U.S.A. NEBRASKA. Hooker Co., near Mullen, Middle Loup River, 14 Sept 1893, *Rydberg 1766* (Lectotype NY!; isolectotypes: GH!, NY!, US!).

STEMS several to many, ascending-erect, (21)-26-**36**-45-(57) cm tall, moderately to densely hispid and strigose (hairs rarely broken off), non-glandular to very sparsely glandular, sometimes brown and brittle; (18)-21-**32**-43-(50) nodes below capitulescence; sometimes spreading by rhizomes and forming new tufts of shoots. LOWER STEM LEAVES linear to broadly oblanceolate, (15)-25-**32**-39-(42) mm long, (3)-3.6-**5.1**-6.6-(8.4) mm wide, petiolate, acute, moderately hispid-strigose and non-glandular on both surfaces. UPPER STEM LEAVES linear to narrowly oblanceolate (rarely broadly so), little reduced upward, (14)-18.7-**23**-27-(30) mm long, (2)-2.6-**3.6**-4.5-(6) mm wide, non-glandular to very sparsely glandular, 0-2-5-(7) glands/mm², moderately hispid-strigose, (21)-30-**42**-53-(65) hairs/mm², the hairs sometimes scabrous and somewhat pustulate, margins sometimes with numerous large hairs. CAPITULESCENCE corymbiform; heads (2)-3-**9**-15-(24); peduncles moderately hispid-strigose and non-glandular; bracts few, lower ones oblanceolate, leaf-like, sometimes little reduced upward and foliar, (3)-4.4-**6.5**-8.6-(12) mm long, (0.5)-0.6-**1.0**-1.3-(1.8) mm wide. INVOLUCRES (4.5)-5.6-**7.0**-8.5-(11) mm high; phyllaries non-glandular, sparsely to moderately strigose. RAY FLORETS (10)-13-**18**-24-(30), strap (5.1)-5.8-**8.3**-10.8-(16.3) mm long, (0.8)-0.9-**1.2**-1.5-(2.1) mm wide. DISC FLORETS (21)-28-**32**-47-(65), corolla (4.9)-5.4-**6.0**-6.6-(6.9) mm long, lobes (0.4)-0.5-**0.7**-0.8-(0.9) mm long. ACHENES (1.5)-1.8-**2.3**-2.7-(3.1) mm long, inner whorl of barbellate bristles (5)-5.7-**6.4**-7.1-(7.5) mm long. Chromosome numbers: $2n = 36$ many reports; several triploid counts from putative intervarietal hybrids.

Flowering Period: May-JUNE-AUGUST-October.

Distribution and habitat: Prairies and hills from central Texas to southern South Dakota to eastern Colorado and New Mexico (Fig. 35E); sandy prairies, sandy, gypsiferous and rocky soils and outcrops; 300-1700 m (1000-5500 ft.) elevation.

Discussion: Variety *angustifolia* is distinguished from var. *stenophylla* by its usually densely hispid stems with many long spreading hairs and its densely hispid-strigose non-glandular leaves and phyllaries (Fig. 35). The most densely pubescent individuals are not always easily distinguished from sympatric forms of *H. canescens* in the southern part of the range. Both diploid or tetraploid individuals of *H. canescens* (Fig. 36) usually have more than 100 hairs/mm² of leaf surface versus less than 60 hairs/mm² of leaf surface in both varieties of *H. stenophylla*. This difference manifests itself in whitish or silvery versus light green leaves respectively. Both often have fascicles of short leaves (very short lateral branches) arising in the axes of the many mid and upper stem leaves. Stems of *H. villosa* usually have relatively longer nodes and a less densely leafy appearance. The leaves are about equally densely pubescent.

The leaves are usually narrowly oblanceolate, but plants with broader oblong leaves have been collected in western Kansas and Nebraska. These approach *H. villosa* var. *foliosa* in general appearance. Some collections from southeastern Wyoming treated here as var. *foliosa* might in fact be aberrant marginal population forms of var. *angustifolia*. A search for more typical var. *angustifolia* in southeastern Wyoming may demonstrate that the taxon does occur in that state. As noted in the discussions under *H. villosa*, eastern Wyoming is occupied by a mixture of typical and atypical forms of *H. villosa*. It would be easy to overlook atypical forms of var. *angustifolia* among this melange of hairy forms of *H. villosa*. Hybrids between broadly oblong-leaved var. *foliosa* and narrowly oblanceolate-leaved var. *villosa* might have leaves similar in character to var. *angustifolia*. No specimens from Wyoming assignable without hesitation to var. *angustifolia* were encountered in this study.

Previously, var. *angustifolia* has been included in *H. villosa* or *Chrysopsis villosa* (e.g., Harms 1963, 1968; Great Plains Flora Association 1986). Placement of the variety in *H. stenophylla* is based on field

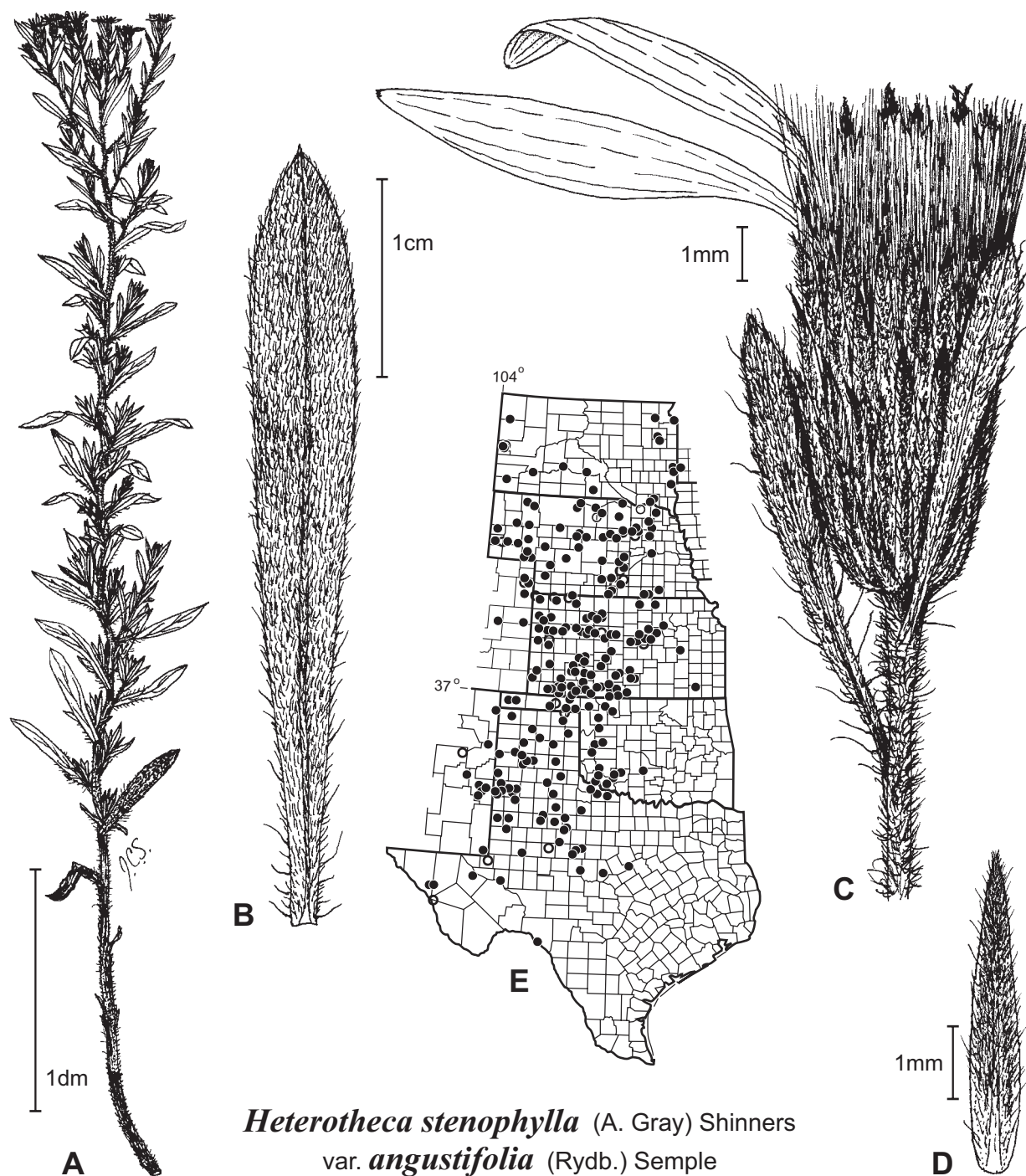


Figure 35. Morphology and distribution of *Heterotheca stenophylla* var. *angustifolia*. **A.** Habit, robust shoot. **B.** Mid stem leaf, can be narrower or broader. **C.** Head and peduncular bracts; only some florets drawn. **D.** Mid series phyllary with chlorophyllous zone dark (obscured by overlying hairs). **E.** Distribution; South Dakota and adjacent Minnesota to New Mexico and Texas.

studies and the results of multivariate analyses comparing var. *angustifolia* with typical *H. stenophylla*, *H. villosa* from the northern Great Plains and typical *H. canescens* from the central and southern Great Plains. The type of var. *angustifolia* is morphologically closer to many individuals of var. *stenophylla* than it is to either *H. canescens* or typical *H. villosa*. In particular, the leaf shape and margin hairs of the type specimen are like those of var. *stenophylla*. 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. The investigation suggests that tetraploid var. *angustifolia* originated from diploid var. *stenophylla* and subsequently converged toward tetraploid *H. canescens* due to putative occasional hybridization with the latter. Of note is the fact that the range of var. *angustifolia* is generally the same as that of var. *stenophylla* from Oklahoma northward, except that var. *angustifolia* occurs over a slightly greater area and in the gaps between the disjunct populations of var. *stenophylla*. Alternatively, var. *angustifolia* might have originated via allopolyploid from more hairy and less glandular diploid *H. stenophylla* var. *stenophylla* and *H. canescens*. Because most other species include both more glandular and more hairy races hybridization does not need to be invoked to account for this same duality in *H. stenophylla*.

Specimens examined: U.S.A. Neutral Strip, *Carleton* 385 (NMC). COLORADO. Kit Carson Co.: S of Burlingame, *Menhusen* 523 (SASK(2)). Lincoln Co.: SW edge of Hugo, *Stephens* 62673 (KANU). Phillips Co.: 12 mi S of Holyoke, sand dunes, *Weber* 50181 (WTU). Yuma Co.: US-34 S of US-385, *Semple & Heard* 7709 (WAT), *Semple & Heard* 7710 (WAT). KANSAS. Barber Co.: N of Aetna, *McGregor* 14786 (KANU), *McGregor* 15113 (KANU, NY). NW of Hardtner, *Harms* 659 (KANU), *Harms* 660 (KANU), *Harms* 1341 (KANU, SASK, WAT), *Harms* 1343 (KANU). Between Kiowa and Hardtner, *Rydberg & Imler* 633 (KANU, NY). S of Lake City, *Harms* 653 (KANU), *Harms* 654 (KANU, SASK). Medicine Lodge, *McGregor* 14896 (KANU). S of Medicine Lodge, *Harms* 1349 (KANU(2)). SW of Medicine Lodge, *Harms* 655 (KANU(3), SASK(2), WAT), *Harms* 655-B (SASK), *Harms* 19096 (KANU(2)). NW of Medicine Lodge, *Harms* 19099 (KANU). W of Medicine Lodge, *Harms* 867 (KANU), *McGregor* 37432 (KANU). S of Sun City, *McGregor* 10690 (KANU), *McGregor* 10969 (KANU). US-160 8.4 km E of county line, *Semple & Brammall* 2729 (WAT). Barton Co.: Pawnee Rock, *Semple & Brouillet* 7318 (JCS), *McGregor* 4623 (KANU), *Harms* 1997-A (KANU). Cheyenne Co.: N of St. Francis, *Stephens* 9762 (KANU), NE of St. Francis, *Harms* 1238 (KANU, SASK), SW of St. Francis, *McGregor* 15204 (KANU), *McGregor* 40025 (KANU), *McGregor* 40033 (KANU). Clark Co.: *Jackson* 49 (KANU(2)), *McGregor* 39207 (KANU), *McGregor* 40025 (NY). Ashland, *Harms* 19102 (KANU). E of Ashland, *Harms* 1359 (KANU). N of Ashland, *Bare* 2457 (KANU(2)). W of Ashland, *Harms* 846 (KANU) S of Minneola, *Harms* 843 (KANU). NE of Sitka, *Harms* 849 (KANU). Comanche Co.: E of Coldwater, *Harms* 1353-B (KANU), *Harms* 1357 (KANU), *McGregor* 14638 (KANU). N of Coldwater, *McGregor* 10640 (KANU). S of Coldwater, *Harms* 854 (KANU), *Harms* 19100 (KANU(2)), *Harms* 19101 (KANU(2)). SW of Coldwater, *Rydberg & Imler* 222 (KANU), *Stephens* 79170 (KANU). E of Protection, *Harms* 850 (KANU), *Harms* 850-B (KANU(2)). Decatur Co.: NE of Cedar Bluff, *Stephens* 19068 (KANU). S of Oberlin, *Harms* 18496-B (KANU). Edwards Co.: S of Kinsley, *McGregor* 10576 (KANU(2)). Ellis Co.: NE of Ellis, *Stephens* 86995 (KANU). SW of Hays, *Rydberg & Imler* 1257 (KANU, NY). E of Pfeifer, *Harms* 959 (KANU). N of Pfeifer, *Harms* 948 (KANU(2)), *Harms* 954 (KANU(2)). NE of Pfeifer, *Harms* 949 (KANU). E of Schoenchen, *Harms* 722 (KANU, SASK), *Harms* 722-B (SASK), *Harms* 723 (WAT). Ellsworth Co.: W of Brookville, *Jackson* 85 (KANU). E of Carneiro, *Wagenknecht* 1944 (KANU). W of Dodge City. *Semple & Brammall* 2723 (WAT), *Semple & Brammall* 2724 (WAT). Kanopolis, *Fearing & Latham s.n.* (KANU(2)). NW of Kanopolis, *Fearing & Latham s.n.* (KANU, TEX). SE of Kanopolis, *Stephens* 17935 (KANU). E of Terra Cotta, *Magrath & Johnson* 3398 (KANU), *McGregor* 9220 (KANU), *McGregor* 12385 (KANU), *McGregor* 12399 (GH, KANU, MIN), *McGregor* 12640 (GH, KANU, MIN). E of Vernango, *Harms* 679 (KANU(2), SASK(3), WAT), *Harms* 683 (KANU, SASK, WAT), *Harms* 1376 (KANU, WAT). E of Wilson, *Harms* 716 (KANU, SASK), *Harms* 718 (KANU). Ford Co.: E of Dodge City, *Harms* 629 (SASK). NE Dodge City, *McGregor* 3964 (KANU). SW of Dodge City, *Harms* 726 (KANU, SASK, WAT), *Harms* 735 (KANU, SASK), *Harms* 735-B (KANU, SASK, WAT), *Harms* 1960 (KANU). W of Dodge City, *Harms* 736 (KANU, SASK), *Harms* 737 (KANU, SASK, WAT), *Stephens* 50451 (KANU). NE of Ford, *McGregor* 11006 (KANU). E of Howell, *Stephens* 9796 (KANU). Gove Co.: Monument Rocks, *Stephens* 9004 (KANU). E of Quinter, *Harms* 1020 (KANU). Graham Co.: W of Bogue, *Imler s.n.* (KANU). E of Hill City, *Harms* 18495 (KANU(2)). N of Morland, *Stephens* 59416 (KANU). Gray Co.: W of Dodge City, *Semple & Brammall* 2725 (WAT). N of Montezuma, *Gates* 16008 (WIS). Greeley Co.: NE of Tribune, *McGregor* 24715 (KANU). Harper Co.: W of Attica, *Harms* 869 (KANU, WAT), *Harms* 870 (KANU, WAT). Haskell Co.: SW of Satanta, *Stephens* 87564 (KANU). Hodgeman Co.: S of Jetmore, *Harms* 1374 (KANU), *McGregor* 3990 (KANU). SE of Jetmore, *Stephens* 50489 (KANU). SW of Jetmore, *Harms* 1374 (WAT). Kingman Co.: W of Kingman, *Bare* 2492 (KANU(2)), *Bare* 2502 (KANU), *McGregor* 10718 (KANU). Kiowa Co.: *Semple & Brammall* 2726 (WAT). W of Belvedere, *McGregor* 10992 (KANU). E of Coldwater, *Semple & Brammall* 2727 (WAT). SW of Coldwater, *Rydberg & Imler* 722 (NY). Lincoln Co.: *Hitchcock* 221 (GH, NMC, NY, RM). W of Beverly, *Magrath et al.* 4135 (KANU). Logan Co.: Elkador, *Harms* 1041 (KANU, SASK). Logan Co.: N of Elkador, *Harms* 1043 (KANU). Logan County State Lake, *McGregor* 13632 (KANU). Russell Springs, *Stephens* 57183 (KANU), *Stephens* 86521 (KANU). W of Russell Springs, *Harms* 1157 (KANU). Lyon Co.: Emporia, 8.0 mi SW, *Torres* 1652 (KANU). Meade Co.: W of county line, *Barker* 1924 (GH, KANU(2)). Advance Flag Station, *Horr* 3449 (GH, KANU). E of Meade, *Harms* 641-A (KANU), *Harms* 641-B (KANU, SASK), *Harms* 825 (KANU, SASK), *Harms* 836 (KANU, SASK), *Harms* 19103

(KANU). SW of Meade, *Bare* 2461 (KANU), *Harms* 814 (KANU), *Harms* 1360 (KANU). W of Meade, *Harms* 815 (KANU(2), SASK), *Harms* 818 (KANU). State Park, *McGregor* 4013 (KANU(2)). XI Ranch, *Horr s.n.* (GH), *Horr* 44-106 (KANU(2)). Montgomery Co.: S of Sycamore, *Barker* 2203 (KANU). Norton Co.: ENE of Clayton, *Keil & Keil* 14106 (OBI). Ottawa Co.: Minneapolis. *Benke* 5171 (GH). Pawnee Co.: S of Larned, *Stephens* 50603 (KANU). Pratt Co.: Pratt, *Barker* 1605 (KANU). NE of Prat, *Bare* 2410 (KANU). S of Pratt, *Harms* 1338 (KANU). NE of Preston, *Harms* 1336 (KANU). S of Sawyer, *Horr s.n.* (KANU). Ranton Co.: N of Pawnee Rock, *McGregor* 4623 (KANU). Rawlins Co.: E of Atwood, *Harms* 1251 (KANU, SASK), *Harms* 1255 (KANU, SASK), *Harms* 1260 (WAT). SE of McDonald, *Freeman & Brooks* 3225 (KANU). Reno Co.: NE of Arlington, *Harms* 883 (KANU), *Harms* 1333 (KANU, WAT). Republic Co.: Pawnee Monument, *Morley* 937-3 (KANU). SW of Republic, *Morley* 548 (NY, UC). Rooks Co.: N of Falco, *Stephens* 86916 (KANU). NE of Palco, *Stephens* 90493 (KANU(2)). Rockport, *Bartholomew s.n.* (NY). Rooks, *Imler s.n.* (KANU). Stockton, *Kellogg s.n.* (WIS). Russell Co.: S of Gorham, *Harms* 930 (KANU(2)). N of Russell, *Harms* 909 (KANU). Saline Co.: NW of Brookville, *Hancin* 1929 (KANU), *Hancin* 1930 (KANU). N of Coronado Heights, *Hancin* 1944 (KANU). Salina, *Carleton s.n.* (NY). Scott Co.: N of Scott City, *Harms* 1053 (KANU), *Harms* 1073 (KANU, SASK), *Harms* 1080 (KANU). State Park, *Harms* 1118 (KANU, SASK), *McGregor* 38424 (KANU). Seward Co.: NE of Hayne, *Harms* 19105 (KANU), *Harms* 19107 (KANU). SW of Hayne, *Harms* 808 (KANU), *Harms* 808-B (KANU). Liberal, *Rose & Fitch* 17128 (NY). E of Liberal, *Harms* 1361 (KANU), *Rydberg & Imler* 879 (KANU). NE of Liberal, *Harms* 805 (KANU, SASK), *Harms* 1363 (KANU, SASK), *Stephens* 57522 (KANU). Sherman Co.: N of Goodland, *McGregor* 5207 (KANU). S of Goodland, *Harms* 1200 (SASK, WAT), *McGregor* 13603 (KANU), *Stephens* 86463 (KANU). SW of Goodland, *McGregor* 36542 (KANU). State Park, *McGregor* 24654 (KANU). Stanton Co.: N of Saunders, *McGregor* 4525 (KANU). S of Syracuse, *McGregor* 4579 (KANU). Stevens Co.: NE of Hugoton, *Harms* 757 (KANU). W of Woods, *Harms* 786 (KANU, SASK, WAT), *Harms* 794 (KANU, SASK, WAT), *Harms* 797 (KANU, SASK, WAT), *Harms* 782 (KANU, SASK, WAT), *Harms* 788 (KANU, SASK), *Semple & Semple* 2219 (CAN, WAT). Thomas Co.: S of Brewster, *McGregor* 24643 (KANU). Trego Co.: S of Collyer, *Harms* 982 (KANU), *Harms* 1007 (KANU, SASK). SE of Collyer, *Harms* 997-B (KANU, SASK). NE of Ogallah, *McGregor* 9335 (KANU). S of Ogallah, *McGregor* 32016 (KANU). S of Wakeeney, *Harms* 977 (KANU), *Harms* 990 (KANU). KS. Wallace Co.: *Snow s.n.* (KANU). S of Kanorado, *Gates* 16772 (MIN). E of Sharon Springs, *Lowry & Miller* 3537 (RM), *McGregor* 13622 (KANU). S of Wallace, *McGregor* 17288 (KANU). MINNESOTA. Pipestone Co.: Altona Twp., *Moore* 26559 (CAS, MIN). NEBRASKA. Green River, *Edwards s.n.* (NY). Pushelville, *Clements* 2953 (NY). Antelope Co.: W of Elgin, *Stephens & Brooks* 24201 (KANU). S of Neligh, *Stephens & Brooks* 11840 (KANU). Arthur Co.: Arapaho prairie., *Vescio & Kruse* 165 (NY). S of Arthur, *Jones s.n.* (WIS). Banner Co.: *Rydberg* 85 (NY), *Rydberg* 146 (NY(2)). Blaine Co.: W of Dunning, *Stephens* 28211 (KANU). Box Butte Co.: Alliance, *Webber s.n.* (NY). Boyd Co.: S of Butte, *Stephens & Brooks* 15475 (KANU). Brown Co.: NW of Long Pine, *Stephens & Brooks* 34357 (KANU). Buffalo Co.: Ft. Kearney, *Dunn & Cox* 16285 (ASU), *Engelmann s.n.* (GH), *Fendler s.n.* (GH(2)). Cedar Co.: S of Hartington, *Stephens & Brooks* 14134 (KANU). W of Randolph, *Hamerstrom & Hamerstrom s.n.* (WIS). Chase Co.: N of Imperial, *Stephens* 45603 (KANU). Cherry Co.: Valentine, *Bates s.n.* (MIN). S of Valentine, *Tolstead* 721 (GH). Custer Co.: N of Miller, *Bergseng & Christensen* 301 (WIS). Dawes Co.: S of Chadron, *Keil* 17732 (OBI). Deuel Co.: *Rydberg* 149 (NY). E of Chappell, *Stephens & Brooks* 16024 (KANU), *Stephens* 50174 (KANU). McColligan Cyn, *Rydberg* 148 (GH). Franklin Co.: NW of Franklin, *Brooks* 16024 (KANU). N of Macon, *Ewan* 14787 (CAS). Garden Co.: NE of Lewellen, *McGregor* 20181 (KANU). SSE of Lewellen, *Harms* 18499 (KANU, SASK). N of Oshkosh, *Stephens & Brooks* 24852 (KANU), *Sutherland & Bartlett* 6824 (NY). Garfield Co.: *Barker* 2938 (KANU). N of Burwell, *Iltis* 18571 (WIS). NE. Hall Co.: near Grand Is., *Heller* 14286 (DS, WTU). Holt Co.: N of Atkinson, *Barker* 3038 (KANU). S of Atkinson, *Stephens & Brooks* 15523 (KANU). W of Atkinson, *Barker* 2982 (KANU). Holt Co.: WSW of Ewing, *Iltis* 18498 (MIN, WIS). Hooker Co.: N of Mullen, *Semple, Sripto & Ahmed* 9196 (WAT). Howard Co.: SE of Boelus, *Stephens* 48616 (KANU). S of St. Paul, *Stephens* 51247 (KANU). Jefferson Co.: S of Helvey, *Rohrbaugh* 162 (TEX). Kearney Co.: Kearney, *Stephens* 6745 (KANU). Minden, *Hapeman s.n.* (DS), *Hapeman s.n.* (KANU), *Hapeman s.n.* (NY), *Hapeman s.n.* (MIN(2)), *Hapeman s.n.* (PH), *Hapeman s.n.* (RM), *Hapeman s.n.* (WIS). N of Minden, *Bare & McGregor* 1701 (KANU, NY). Keith Co.: W of Brule, *Menhusen* 533 (KANU(2), SASK). N of Kingsley Dam, *Jones s.n.* (WIS). S of Kingsley Dam, *Jones s.n.* (WIS). E of Ogallala, *Mason* 4009 (ASU), *Solbrig* 3226 (GH). N of Ogallala, *Kiener* 17545 (GH), *McGregor* 18864 (KANU). Keya Paha Co.: N of Springview, *Stephens* 29304 (KANU). Lincoln Co.: North Platte, *Weakley* 13 (LL). Logan Co.: W of Arnold, *Iltis* 18633 (WIS). Loup Co.: NW of Taylor, *Stephens* 6880 (KANU). Madison Co.: W of Meadow Grove, *Harms* 589 (KANU, SASK). Morrill Co.: SW of Bridgeport, *Stephens & Brooks* 16093 (KANU). Morrill Co.: SE of Broadwater, *Keil* 12843 (ASU, OBI). Perkins Co.: SE of Roscoe, *Iltis & Kowal* 26873 (WIS). Phelps Co.: N of Funk, *Bare & McGregor* 1684 (KANU). Pierce Co.: NE of Hadar, *Stephens & Brooks* 38641 (KANU). Rock Co.: N of Bassett, *Sutherland & Churchill* 4283 (NY). S of Bassett, *Stephens* 6902 (KANU). Sheridan Co.: S of Gordon, *Turner* 15665 (TEX). E of Hay Springs, *Churchill* 1601 (NY). E of Lakeside, *Stephens & Brooks* 41362 (KANU). Thayer Co.: *Semple & Brouillet* 7345 (WAT). SW of Hebron, *Harms* 2182 (KANU, SASK(2), WAT). Thomas Co.: Halsey, *Krautter s.n.* (PH). Nebraska N.F., Bessey Div., *Gierisch* 1750 (USFS). Webster Co.: Red Cloud, *Bates* 5656 (MIN). SW of Red Cloud, *McGregor* 24451 (KANU). Wheeler Co.: S of O'Neill, *Barker* 22941 (KANU). NEW MEXICO. *Fendler s.n.* (GH). DeBaca Co.: E of Taiban, *Stephens & Brooks* 25694 (KANU). Lea Co.: S of Jal Shinnery, *McGregor* 40732 (KANU). Otero Co.: S of La Junta, *Weber & Wittmann* 18705 (COLO, TEX). Quay Co.: N of Logan, *Stephens* 79820 (KANU). Roosevelt Co.: N of Elida, *Stephens* 80122 (KANU). ENMU Natural History Preserve, *Secor* 67 (TEX). N of Portales, *Stephens & Brooks* 25661 (KANU). Union Co.: SE of Clayton, *Dallas* 426 (KANU). OKLAHOMA. Beaver Co.: S of Beaver, *Stephens* 71523 (KANU). W of Elmwood, *Harms* 1976 (SASK), *Harms* 1977 (KANU, SASK), *Harms* 1978 (KANU, SASK), *Harms* 1979 (KANU, SASK). NE of Forgan, *Stephens* 79258 (KANU). E of Slapout, *Semple & Semple* 2216 (CAN, WAT). W of Slapout, *Harms* 1982 (KANU, SASK). Beckham Co.: *Semple & Semple* 2211 (TEX, WAT). SW of Elk City, *Harms* 1722 (KANU, SASK). Cimarron

Co.: W of Boise City, *Brooks & McGregor 16454* (KANU), *Harms 1969* (SASK), *Harms 1970* (KANU, SASK). Comanche Co.: Cache, *Hopkins 827* (NY). Near Cache, *Stevens 1305* (GH, MIN, NY). NW of Cache, *Kaeiser 8* (PH). N of Meers, *Hopkins, Nelson & Nelson 814* (DS, RM, TEX, UC, WTU). Wichita Wildlife Reservation, *Atkins 37* (TEX), *Hopkins & Nelson & Nelson 820* (TEX), *McMurray 567* (TEX). Custer Co.: *Harms 1713* (SASK). Dewey Co.: E of Vici, *Harms 1703-B* (KANU). S of Vici, *Harms 1706* (KANU, SASK), *Harms 1710-A* (KANU, SASK(2)). Garvin Co.: Erin Springs, *Sheldon 174* (MIN). Harper Co.: S of Buffalo, *Harms 1985* (SASK). Jackson Co.: N of Alva, *Harms 1687* (KANU, SASK). NE of Altus, *Stephens 27317* (KANU). Jackson Co.: S of Altus, *Harms 1729* (KANU(2), SASK). Kiowa Co.: *Semple & K.Shea 2208* (WAT), *Semple & S 2209* (NY, WAT). Roger Mills Co.: N of Carpenter, *Harms 1718* (KANU, SASK, WAT). Texas Co.: E of Hardesty *Harms 1974* (KANU, SASK(2)), *Harms 1974-B* (KANU, SASK, WAT). Tillman Co.: Frederick, *Duncan 1917* (RM). Woods Co.: NE of Freedom, *Harms 1992-B* (KANU, SASK). N of Waynoka, *Harms 1690* (KANU, SASK). Woodward Co.: Woodward, *Bailey 2644* (RM). NW of Woodward, *Harms 1697* (KANU). SOUTH DAKOTA. Codington Co.: NW of Watertown, *Stephens & Brooks 42395* (KANU). Day Co.: NE of Enemy Swim Lake, *Croat 2250* (KANU). Fall River Co.: 10 mi SW of Hot Sprs, *McIntosh 812* (RM). Hemlin Co.: NW of Watertown, *Stephens & Brooks 14304* (KANU). Harding Co.: Bad Lands, Sheep Mt., *Hayward 556* (NY). Lawrence Co.: Black Hills Teachers College, Northern Black Hills, *Bennett 369* (WIS). Minnehaha Co.: S of Dell Rapids, *Stephens & Brooks 31899* (KANU), *Stephens & Brooks 36494* (KANU). E of Sioux Falls, *Harms 2160* (KANU, SASK(2), WAT), *Harms 18482* (KANU, SASK). Roberts Co.: SW shore of Big Stone Lake, *Johnson 70* (NY). Tripp Co.: SW of Winner, *Stephens 49261* (KANU). Yankton Co.: bluff of Lewis and Clark L., *Walz 102* (BRY). W of Yankton, *Harms 2158* (KANU, SASK, WAT), *Harms 2495* (KANU, SASK), *Harms 18486* (KANU, SASK). TEXAS. Sulphur Draw, *C. F. s.n.* (TEX). Bailey Co.: Near Coyote L., *Ferris, Duncan 3449* (CAS, DS, NY). S of Muleshoe, *Ferris & Duncan 3408* (CAS, DS, NY, POM), *Shinners 8348* (DS), *Stephens 73167* (KANU). SE of Muleshoe, *Johnston 6547* (LL). Bexar Co.: south San Antonio, *School s.n.* (TEX). Briscoe Co.: W of Quitaque, *Stephens 72185* (KANU). Brown Co.: W of Brownwood, *Chamberlain 16* (LL). Crane Co.: N of Buena Vista, *Warnock 15590* (LL, SRSC). Crosby Co.: Crosbyton, *Tharp 4536* (TEX). E of Crosbyton, *Correll 15137* (LL), *Hamby 1197* (RSA). W of Crosbyton, *Rowell 5843* (TEX). Culberson Co.: N end of Van Horn Mts., *Waterfall 4556* (CAS, NY). TX. Dallam Co.: N of Dalhart, *Stephens 73631* (KANU). Deaf Smith Co.: S of Glenrio, *Waller 1251* (ASU). Dickens Co.: E of Dickens, *S 10335* (WAT). Donley Co.: N of Clarendon, *Stephens 71956* (KANU). Gaines Co.: 3 mi S of Seagraves, *Tharp s.n.* (TEX). Garza Co.: E of Post, *Huchins 572* (LL). Spur, *Ruth 1404* (LL). Gray Co.: S of Pampa, *Stephens 71821* (KANU). Hall Co.: near Memphis, *Fairview School 6467* (TEX). Hamilton Co.: E of Hico, *Massey 345* (LL). Hardeman Co.: Chilicothe, *Ball 976* (LL). Hemphill Co.: SW of Canadian R., *Stephens 81825* (KANU). Hockley Co.: NW of Witharral, *Stephens 72986* (KANU). Hudspeth Co.: E of Van Horn, *Powell 2782* (SRSC, TEX). Hutchinson Co.: near Fritch, *Higgins 5675* (BRY), *Higgins 9677* (ASU). Kent Co.: Kent Co. county line N of Snyder, *Semple & Heard 8225* (WAT). Kleberg Co.: Santa Gertrude is Division of King Ranch, *Johnston 53.280.160* (TEX), *Johnston 541143* (TEX). Knox Co.: N of Benjamin, *Higgins 6051* (BRY). Lamb Co.: E of county line, *Johnston 6539* (LL). N of Fieldton, *Stephens 80368* (KANU), *Stephens 80381* (KANU). N of Littlefield, *Turner & Melchert 4828* (TEX). Martin Co.: Stanton, *Eggert s.n.* (NY). NE of Stanton, *Cory 13899* (TEX). Motley Co.: S of Matador, *Stephens 72405* (KANU). Ochiltree Co.: S of Perryton, *Stephens 71652* (KANU). SE of Perryton, *Wallis 7882* (TEX). Oldham Co.: N of Vega, *Stephens 81422* (KANU). Parmer Co.: SE of Farwell, sandy prairie, *Whitehouse 17202* (NY). Potter Co.: *Semple & Chmielewski 6476* (LL, WAT). Randall Co.: N of Canyon, *Higgins 9541* (ASU, BRY), *Higgins 16994* (NY, UT). NE of Canyon, *Higgins 5675* (BRY). SE of Canyon, *Higgins 12122* (BRY). S of Umbarger, *Higgins 11317* (ASU, BRY, NY). Runnels Co.: E of Ballinger, *Gould 7072* (TEX). Scurry Co.: NE of Snyder, *Cole 226* (SRSC). Stonewall Co.: W of Swenson, *Harms 1750* (KANU, WAT). Taylor Co.: near Abilene, *Tolstead 7465* (TEX). S of Abilene, *Henderson 63-1759* (TEX). SW of Abilene, *Henderson 63-1007* (TEX). S of Happy Valley, *Mahler 3452* (TEX). Terry Co.: *Tharp 42-83* (GH, LL, TEX). Wellman, *Reed 37 87* (LL). Travis Co.: Austin, campus of U. of T., *Gough s.n.* (GH). Val Verde Co.: NW side of Pecos R., *Correll 34054* (LL). Wichita Co.: S of Electra on TX-25, *Seigler 1463* (TEX). Yoakum Co.: E of Plains, *Harms 1777* (KANU, SASK, WAT), *Harms 1777-B* (KANU, SASK).

aff. var. *angustifolia* (close to or introgressed with var. *stenophylla*)

U.S.A. NEBRASKA. Brown Co.: Long Pine, *Bates s.n.* (MIN). Dodge Co.: Fremont, *Kiener 19691* (GH). Knox Co.: Pishelville, *Clements 2741* (MIN). KANSAS. Barber Co.: SW of Medicine Lodge, *Harms 19096* (KANU(2)). Cheyenne Co.: NW of St. Francis, *Harms 1221* (KANU, SASK, WAT). Dewey Co.: S of Vici, *Harms 1706* (WAT). Ellis Co.: 12 mi N of Hays, *Bondy 222* (PH, RM). Ford Co.: SW of Dodge City, *Harms 727* (KANU(2), SASK). Kearny Co.: *Harms 1371* (KANU(2), SASK(2), WAT(2)), *Harms 1371-B* (SASK, WAT). Seward Co.: NE of Liberal, *Harms 806* (KANU(2), SASK, WAT).

aff. var. *angustifolia* (close to or introgressed with *H. canescens*)

U.S.A. TEXAS. Kent Co.: W of Claremont, *Harms 1762-B* (KANU, SASK, WAT). Knox Co.: E of Goree, *Harms 1738* (KANU, SASK). Mitchell Co.: E of Colorado City, *Cory 49343* (SRSC).

aff. var. *angustifolia* (close to *H. villosa* var. *villosa*)

U.S.A. IOWA. Lyon Co.: Gitchie Manitou S.P., *Shimek s.n.* (UC). NEBRASKA. Antelope Co.: Neligh, *Harper s.n.* (WIS). Kearney Co.: Minden *Hapeman s.n.* (CAN, DS). Thomas Co.: E of Thedford, *Semple & K.Shea 2268* (CAN, WAT). SOUTH DAKOTA. Jackson Co.: W of Bellidere, *Harms 2149* (KANU, SASK(2), WAT).

aff. var. *angustifolia* (close to *H. villosa* vars. *ballardii*, *foliosa* or *minor*)

U.S.A. NEBRASKA. Butler Co.: S of Columbus, *Harms 2179* (KANU, SASK(2)). Sioux Co.: N Scottsbluff, *Richardson & Robertson 1531* (KANU, NY). KANSAS. Geary Co.: SE of Milford, *Gates 18511* (MIN, TEX, UC). Wallace Co.: NW of Sharon Springs, cultivated, *Harms 1177* (KANU(2), SASK(2), WAT).

14. *Heterotheca canescens* (DC.) Shinnery, Field & Lab. 19: 68. 1951. *Aplopappus canescens* DC., Prod. 5: 317. 1836. *Chrysopsis cansescens* (DC.) Torr. & Gray, Fl. N. Amer. 2: 256. 1841. *Chrysopsis villosa* (Pursh) Nutt. var. *canescens* (DC.) A. Gray, Synopt. Fl. N. Amer. 1, 2: 123. 1884. SYNTYPES: TEXAS. "Comancherie orient.", 1828, *Berlandier 1830* (Holotype: G-DC!). *Berlandier 1877* (G-DC!, NY!, WIS!). *Berlandier 2043* (G-DC!).

Chrysopsis berlandieri Greene, Erythea 2: 96. 1894. Based on *Aplopappus canescens* DC.

Perennial from stout woody taproots, frequently rhizomatous; STEMS several to many, ascending-erect, (15)-20-31-41-(65) cm tall, densely strigose, hispid hairs usually few, sometimes brown and brittle; (16)-19-28-38-(48) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (19)-21-24-28-(32) mm long, (2)-2.8-3.9-5.0-(6) mm wide, petiolate or sessile-cuneate, acute, to densely to extremely densely strigose on both surfaces, hispid hairs few; margins entire, strigose, longer hispid hairs near base, flat. UPPER STEM LEAVES linear-oblanceolate, sessile, little reduced upward, (11)-15-20-24-(29) mm long, (2)-2.4-3-3.7-(5) mm wide, acute, non-glandular, very to extremely densely strigose, hispid hairs usually few, (90)-108-131-154-(180) hairs/mm², margins flat. CAPITULESCENCE solitary to corymbiform, branches ascending, heads 1-4-9-(15); peduncles densely strigose and usually only very sparsely hispid, bracts few, lower ones oblanceolate, leaf-like, sometimes little reduced upward and foliar, (4)-4.6-5.9-7.2-(8) mm long, (0.5)-0.6-0.9-1.3-(1.7) mm wide. INVOLUCRES cylindrical to turbinate when fresh, narrowly campanulate upon drying, (5)-5.6-6.3-6.9-(7.4) mm high; phyllaries in 4-6 imbricate series, outer 1/5-1/4 length of inner, mid series narrowly triangular, non-glandular, moderately strigose, margins hyaline, fimbriate-ciliate apically. RAY FLORETS (10)-13-16-19-(22), strap yellow, (5.1)-5.6-7.2-8.8-(10.5) mm long, (0.8)-0.9-1.0-1.2-(1.4) mm wide. DISC FLORETS (14)-22-31-40-(49), yellow, corolla somewhat ampliate, (4.7)-5.1-5.6-6.1-(6.5) mm long, lobes (0.5)-0.54-0.6-0.7-(0.75) mm long, sparsely pilose, hairs on lobes 0.1-0.25 mm long. ACHENES (1.2)-1.4-1.9-2.5-(3.1) mm long, moderately strigose; pappus off-white, double, outer whorl of a few linear scales 0.25-0.5 mm long, inner whorl of 25-40 barbellate bristles (5.1)-5.5-6.2-6.8-(7.5) mm long. Chromosome numbers: $2n = 18$, many reports; 36, few reports.

Flowering Period: MAY-JULY-(September)

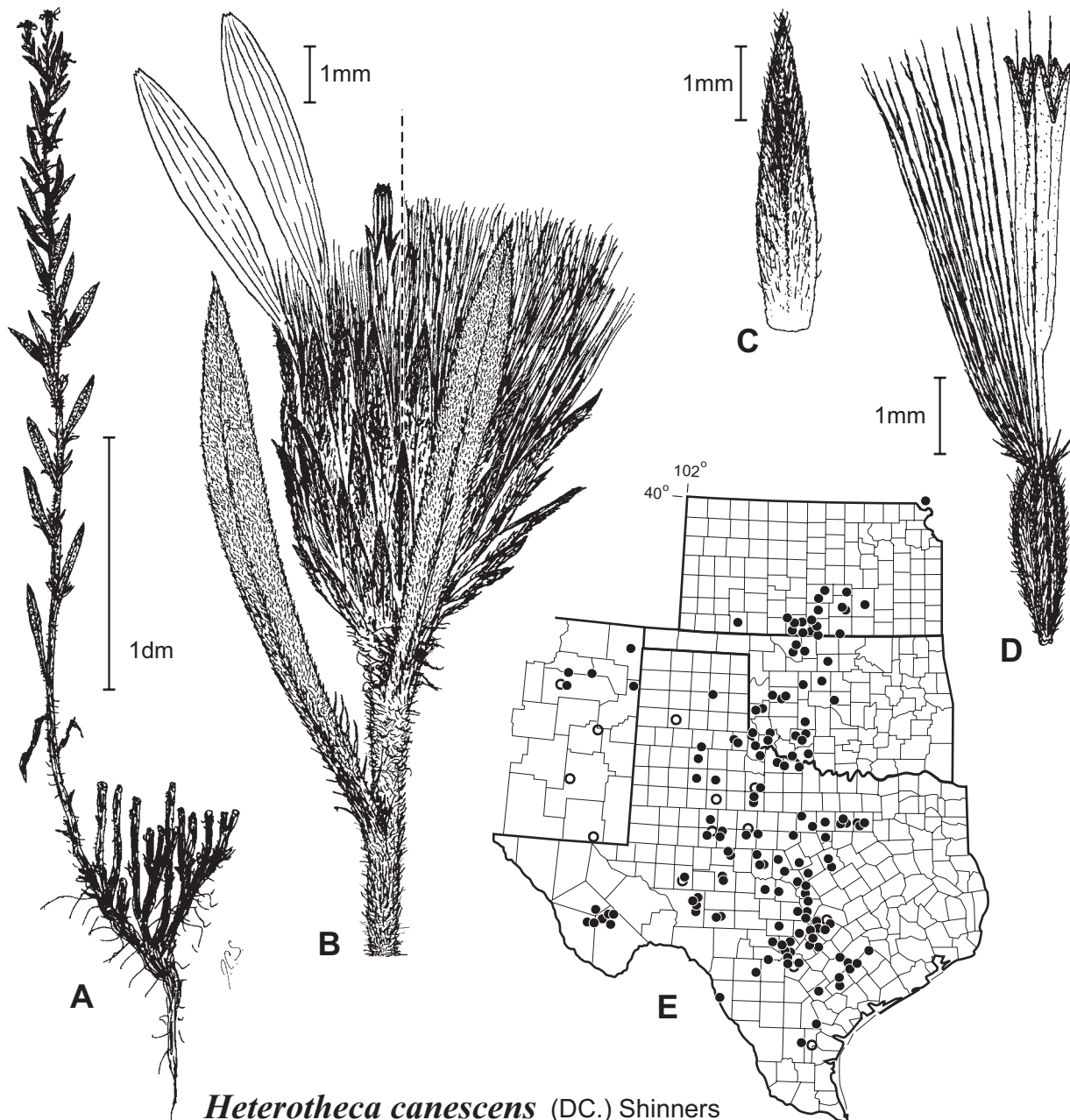
Distribution and habitat: Prairies, open hills, roadsides, and fencerows from southcentral Kansas to southern Texas and west to extreme eastern New Mexico; disjunct in the Davis and Glass Mts. of Trans-Pecos Texas (Fig. 36E); red, brown or black sandy calcareous clay soils, igneous soils, sandy gypsiferous loamy soils, gravelly soils; 100-1800 m (300-6000 ft.) elevation.

Discussion: *Heterotheca canescens* is distinguished by its narrow nonglandular leaves with very dense indument of appressed hairs (usually more than 100 per mm²). The phyllary apices are usually tinted red (Fig. 36). Field observations suggest that clones sometimes form via short rhizomes to a greater degree than other species, and solitary headed capitulescences are common as well. Tetraploids have more hispid stems and a more branched capitulescence than the diploids. These can be similar to forms of *H. stenophylla* var. *angustifolia* growing sympatrically in West Texas and Oklahoma (Fig. 35). The tetraploids apparently hybridize forming local swarms of parent-like and hybrid individuals. Diploids with traits more like those of var. *angustifolia* have been treated in the past as members of variety *angustifolia* or the poorly understood *H. villosa* var. *foliosa*. All pubescent plants on the southern prairies are assigned here to either *H. canescens* or *H. stenophylla* var. *angustifolia*. Usually these have narrow oblanceolate leaves.

Specimens examined: U.S.A. KANSAS. "plains of Kansas {sic}", *Canby s.n.* (NY). Barber Co.: N of Aetna, *McGregor 14785* (KANU). Kiowa, *Rydberg & Imler 656* (KANU, NY). W of Kiowa, *Harms 1686* (KANU, SASK). Medicine Lodge, *Agrelius & Stevens s.n.* (WIS). E of Medicine Lodge, *McGregor 15095* (KANU, SASK). N of Medicine Lodge, *Harms 866* (KANU). NE of Medicine Lodge, *McGregor 14604* (KANU). NW of Medicine Lodge, *Harms 658* (KANU, SASK), *Harms 660* (KANU, SASK). W of Medicine Lodge, *Harms 868* (KANU, SASK, WAT), *McGregor 40664* (KANU). US-160 8.4 km E of county line, *Semple & Brammall 2728* (WAT). S of Sun City, *McGregor 14013* (KANU). Butler Co.: S of Leon, *Stephens 6617* (KANU). Geary Co.: S of Junction City, *Stephens 56927* (KANU). Harper Co.: W of Anthony, *Harms 1685* (KANU, SASK). Attica, *Palmer 41833* (NY). SW of Attica, *Harms 1996* (KANU, SASK). S of Duquin, *Harms 871* (KANU, SASK(2), WAT). Harvey Co.: E of Adams, *Harms 1681* (KANU). E of Newton, *Harms 1324* (KANU(2),

SASK(4), WAT), *Harms 2525* (SASK, WAT), *Harms 18489* (KANU). Kingman Co.: N of Rago, *Harms 875* (KANU, SASK(2)). Meade Co.: Meade, *Smyth 133* (NY). Reno Co.: NE of Arlington, *Harms 19095* (KANU). 9.5 mi S of Arlington, *Harms 876* (KANU, SASK). Sedgewick Co.: NE of Partridge, *Harms 1332* (KANU, SASK). E of Wichita, *Bartley 1155* (NY), *Harms 1331* (KANU(2), SASK(3), WAT). Sumner Co.: S of South Haven, *Menhusen 506* (SASK(2)). MISSOURI. Holt Co.: Mound City, *Bush 12350* (NY), *Bush 12354* (NY(2)), *Bush 12358* (MIN, NY), *Bush 12361* (MIN), *Bush 12382*(MIN), *Bush 12382* (NY), *Bush 12382* (NY). NEW MEXICO. Eddy Co.: Washington Ranch, *McKechnie 238* (POM, WIS). Chaves Co.: W of Roswell, *Earle & Earle 510* (NY). Mora Co.: E of Watrous, *Arséne & Benedict 17400* (LL). Quay Co.: W of Mosquero, *Bradford* (NMC). Nara Visa, *Fisher s.n.* (MIN). San Miguel Co.: E of Las Vegas, *Hill 14513* (NY). ESE of Las Vegas, *Hill & Levandoski 11964* (NY). Union Co.: Clayton, *Evans s.n.* (NMC). WSW of Clayton, *Harms 19110* (KANU, SASK). OLAHOMA. Alfalfa Co.: E of Carmen, *Semple & Brammall 2730* (WAT). Beckham Co.: N of fork of Red R., *Semple & K.Shea 2210* (WAT). Blaine Co.: N of Eagle City, *Semple & Brammall 2732* (WAT). Caddo Co.: N of Apache, *Jackson s.n.* (KANU, progeny; SASK, WAT). Comanche Co.: Ft. Sill, *Anderson 2403* (WIS), *Clemens 11808* (CAS, GH, RM, WIS), *Palmer 11808* (NY(4)), *Small & Wherry 11808* (NY). Medicine Park, *Demaree 13002* (NY). Wichita Wild Life Reservation, *Hopkins, Nelson & Nelson 820*(UC). Cotton Co.: SE of Temple, *Waterfall 7224* (GH). Custer Co.: NE of Hammon, *Semple & K.Shea 2212* (TEX, WAT). NW of Weatherford, *Seigler 1566* (TEX). SW of Weatherford, *Waterfall 5516* (GH), *Waterfall 1589* (GH, NY(2)). Garfield Co.: Enid, *Ward 41* (NY). Harmon Co.: near Hollis, *Stevens 1163* (GH, MIN). Jackson Co.: S of Altus, *Harms 1730* (SASK). E of Blair, *Burden 32* (ASU). SE of Blair, *Burden 19-20* (ASU). Kingfisher Co.: Huntsville, *Blankenship s.n.* (GH). Oklahoma Co.: N of Bethany, *Waterfall 1705* (NY(2)). Tillman Co.: SE of Grandfield, *Williams, Houser, Castaner & Wiseman 411* (TEX). Washita Co.: Okla-152 E of county line, *Semple & Love 266* (WAT). Woods Co.: *White s.n.* (RM). E of Alva, *Harms 1995* (SASK). NE of Alva, *Nighswonger 1263* (UNCC). Near Alva, *Stevens 2861* (DS, GH, MIN, NY). TEXAS. *Linheimer s.n.* (TEX), *Nealley s.n.* (NDG), *Reverchon 460* (UC), *Riddell s.n.* (NY), *Thurber s.n.* (NY), *Wright s.n.* (NY(2)); "western Texas, Rio Concho," *Harvard 89* (NY). Comanche Spring, *Lindheimer 894* (TEX). Comanche and Upper Guadeloupe, *Lindheimer 419* (CAN, DS, GH, NY, UC). Bandera Co.: F.Rd.-470 S of TX-16, *Miller, Brant & Noyes 5825* (TEX). Baylor Co.: SW of Seymour, *Harms 1735* (KANU, SASK, WAT). Bexar Co.: *Jermy s.n.* (NY(2)). Bracken, *Groth 162* (CAS, GH, NY), *Groth 242* (GH). Leon Springs, *Clemens & Clemens 946* (RSA). San Antonio, *Jermy 41* (GH). NW of San Antonio, *Metz 14* (NY, WIS, WTU). Scenic Loop, *Metz 3036* (CAS, NY). Blanco Co.: E of Blanco, *Webster 13800* (TEX). Bosque Co.: NW of Clifton, *Orzell & Bridges 11390* (TEX). Meridian, *Whitehouse 6648* (LL). Brewster Co.: Alpine, *Warnock T439* (GH, TEX). W of Alpine, *Warnock 6656* (LL, SRSC(2)). Althida, *Fletcher 487* (SRSC). Glass Mts, Altuda Pass, *Warnock 279* (GH, SRSC, TEX). S of Marfa, *Brown B-95* (LL, SRSC). Brown Co.: N of Brownwood, *Barbee 7* (TEX), *Palmer 11107* (DS). N of Zephyr, *Semple & K.Shea 1538* (WAT). Burnet Co.: E of Burnet, *Garcia 710* (NY, TEX). N of Burnett, *Semple & K.Shea 2196* (TEX, WAT). Marble Falls, *Plank s.n.* (NY). Caldwell Co.: *Tharp & Tyson 52-539* (TEX). Callahan Co.: NE of Abilene, *Johnston 88* (ASU). Childress Co.: NW of Childress, *Shinners 7993* (GH, UC). SE of Estilline, *Norris 2658* (RSA). Coke Co.: Ft. Chadburn, *Palmer 12466* (GH, NY, UC). Coleman Co.: NW of Coleman, *Johnston 6499* (LL). S of Novice, *Cate 23* (LL). Santa Anna, *Nealley s.n.* (PH). W of Santa Anna, *Horner 9* (ASU). Comal Co.: New Braunfels, *Lindheimer 356* (GH), *Lindheimer 894* (CAN, GH, NY, UC). NW of New Braunfels, *Pennell 5445* (NY). Crockett Co.: Ozona, *Cory 33347* (WTU). HWY-163 11 mi N of Ozona, *Read 398* (SRSC), *Cory 34622* (GH). Crosby Co.: Crosbyton, *Tharp 4536* (TEX). Dallas Co.: Dallas, *Reverchon s.n.* (NY), *Reverchon {1367}* (CAN, GH, KANU, MIN, NY, WIS(2)), *Reverchon 2040* (NY). DeWitt Co.: Cuero, *Blanch 15* (TEX). Above crk off Guadalupe R., *Semple & Brouillet 3346* (WAT). Dickens Co.: E of Dickens, *Correll & Johnston 24180* (LL). Duval Co.: San Diego, *Croft 42* (NY). Eastland Co.: S of Ranger, *Mahler 5015* (ASU, CAN). Erath Co.: *Gough 3592* (NY). Between Chalk Mt. and Stephenville, *Sanders s.n.* (LL). Floyd Co.: Floydada, *Reed 3746* (RM, TEX). Gillespie Co.: *Jermy s.n.* (NY). Gonzales Co.: Palwetto St. Park, *Albers 44115* (TEX). Gray Co.: Pampa, *Correll 38033* (LL). Hall Co.: *Fairview School 6467* (WIS). Hamilton Co.: *Stanford 600* (UNCC). S of Hamilton, *Semple & Chmielewski 6453* (TEX, WAT). Hardeman Co.: E of Chillicothe, *Gentry 1297* (TEX). N of Quanah, *Semple & K.Shea 2206* (WAT). Haskell Co.: S of Haskell, *Harms 1740* (SASK(2)), *Semple & K.Shea 2203* (WAT). Hays Co.: S of Dripping Springs, *Fryxell 1838* (ASU, LL). NW of Kyle, *Semple & Brouillet 3331* (TEX, WAT). San Marcos, *Stanfield s.n.* (NY). W of Wimberley, *Johnson 370* (TEX). Ranch Rd-3237 NE of Ranch Rd-12, *Semple & Brouillet 3334* (TEX, WAT). E of the junction of HWY-150 and Hwy-12, *Sundberg 1179* (TEX). Hood Co.: near Granbury, *Palmer 6549* (MIN). Jeff Davis Co.: Davis Mts., Mitre Peak, *Cory 45386* (LL). Karnes Co.: Karnes City, *Johnson 910* (TEX). NE of Karnes City, *Johnson 1016* (TEX). Kendall Co.: E of Comfort, *Ertter & Lavin 5173* (NY, TEX). E of Sisterdale, *Cory 45292* (LL, TEX). Sisterdale, *Palmer 9907* (DS). Spanish Pass, *Clemens & Clemens 945* (DS, NY, RM, RSA). Kerr Co.: *Whitehouse s.n.* (TEX). Kerrville, *Heller 1854* (GH, NY, UC). Knox Co.: E of Goree, *Semple & K.Shea 2204* (JCS). Lampasas Co.: S of Evant, *Mahler 1242* (ASU). NW of Lampasas, *Warnock W1095* (LL, NY, RM, RSA, WIS). Live Oak Co.: NW of Mathis, *Correll 20423* (LL). Mason Co.: Mason -Eden, *Whitehouse 7742* (TEX). McCulloch Co.: NW of Brady, *Semple & K.Shea 2200* (TEX, WAT). Maverick Co.: Eagle Pass on the Rio Grande R., *Palmer 482* (NY). Mills Co.: NE of Caradan, *Dryman 15* (LL, WAT). Mitchell Co.: SSE of Colorado City, *Shinners 8397* (LL, WS). Sandrocks in Colorado, *Eggert s.n.* (MIN). Nolan Co.: Roscoe, *Tharp s.n.* (TEX). Wastella, *Tharp s.n.* (GH, UC). Palo Pinto Co.: New Salem, *McCart 2140* (TEX). Possum Kingdom St. Pk., *Correll & Correll 24129* (LL). Parker Co.: W of Weatherford, *Gentry 684* (NY, TEX, WTU). Presidio Co.: NW of Paisano Campground, *Hinckley 3962* (SRSC). Reagan Co.: *Cory 4939* (GH). Reeves Co.: N of Arn, *Waterfall 4248* (GH). San Saba Co.: SW of Richland Springs, *McGregor* (LL). Scurry Co.: E of Snyder, *Johnston 6524* (LL). Sutton Co.: Pasture L., *Cory 39629* (TEX), *Cory 39630* (GH). Sonora, *Carr & Bergquist 11297* (TEX). Swisher Co.: W of Kress, *Reed 3768* (RM, TEX). Tarrant Co.: *Killian 6629* (LL), *Ruth s.n.* (RSA), *Ruth 116* (NY), *Ruth 236* (GH), *Ruth 410* (NY). Fort Worth, *Ruth 116* (NY). Taylor Co.: Abilene, *Tolstead 42468* (GH, TEX), *Semple & K.Shea 2202* (WAT). SW of Abilene, *Turner & Melchert 4836* (TEX). Camp Barkeley, *Tolstead 7671* (GH, NY). Hamby, *Pennell 19365* (GH). Tom Green Co.: San Angelo, *F.B. 303* (TEX), *Whitehouse 7741* (TEX). Travis Co.: Austin, *Hall 315* (NY(2), RSA), *Tharp 108* (GH, UC), *Young 139* (UC), *York s.n.* (TEX); U. of. Texas, *Ferguson 409* (TEX), *Watson 543*

(TEX). Daffan, *Bodin s.n.* (GH, MIN), *Bodin 7034* (NY). NW of Pedernales, *Barkley & Rowell 54* (GH, TEX, WIS). Hamilton Pool Rd., *F. Carr & McNeal 10910* (TEX), *Ertter & Larke 5150* (TEX). Onion Creek, *Tharp 1720* (TEX). Waller Creek, *Ferguson s.n.* (TEX). Uvalde Co.: N of Sabinal, *Correll & Johnston 18135* (LL, UC). Wichita Co.: N of Electra, *Whitehouse 10472* (NY, SMU), *Whitehouse 10485* (UC). W of Iowa Park, *Ferris & Duncan 3309* (CAS, DS, MIN). N of Wichita Falls, *Shinners 7971* (IND). Wilbarger Co.: E of Vernon, *Mahler 2431* (TEX). SE of Vernon, *Shinners 7977* (RM).



Heterotheca canescens (DC.) Shinners

Figure 36. Morphology of *Heterotheca canescens*. A. Habit, shoots can be shorter. B. Upper stem leaves and head; only some florets shown, anthocyanotic margins indicated dark. C. Mid series phyllary, chlorophyllous zone hidden by hairs. D. Mature achene with disc corolla attached. E. Distribution; Texas, Oklahoma, Kansas and eastern New Mexico (○ aff. *H. canescens*).

aff. *H. canescens* (close to *H. stenophylla* var. *angustifolia*)

U.S.A. NEW MEXICO. Chaves Co.: W of Roswell, *Earle & Earle 510* (NY). De Baca Co.: N of Taiban, *Secor 73* (TEX). San Miguel Co.: Las Vegas, *Arsène 21082* (UC). TEXAS. Kent Co.: W of Claremont, *Harms 1762* (KANU, SASK, WAT), *Harms 1762-B* (KANU, SASK, WAT). Randall Co.: Canyon, *Neeley 15* (TEX). Reagan Co.: *Cory 4938* (GH). Reeves Co.: N of Pecos, *Warnock 6230* (SRSC, TEX). Taylor Co.: Abilene, *Tolstead 42468* (GH, TEX). Wilbarger Co.: N of Vernon, *Harms 1731* (KANU, SASK).

15. ***Heterotheca jonesii* (S.F. Blake) Welsh & Atwood**, Great Basin Natur. 35: 336. 1975. *Chrysopsis jonesii* S.F. Blake in Tidestrom, Contrib. U.S. Nat. Herb. 25: 537. 1925. Based on *Chrysopsis caespitosa* M.E. Jones, Proc. Calif. Acad. ser.2. 5: 694. 1895. [non Nutt., J. Acad. Phila. 7: 33. 1834.] TYPE: U.S.A. UTAH. Springdale, in red sand, 4000 ft., 16 May 1894, *Jones 5249u* (Holotype: POM!; isotype: US!)

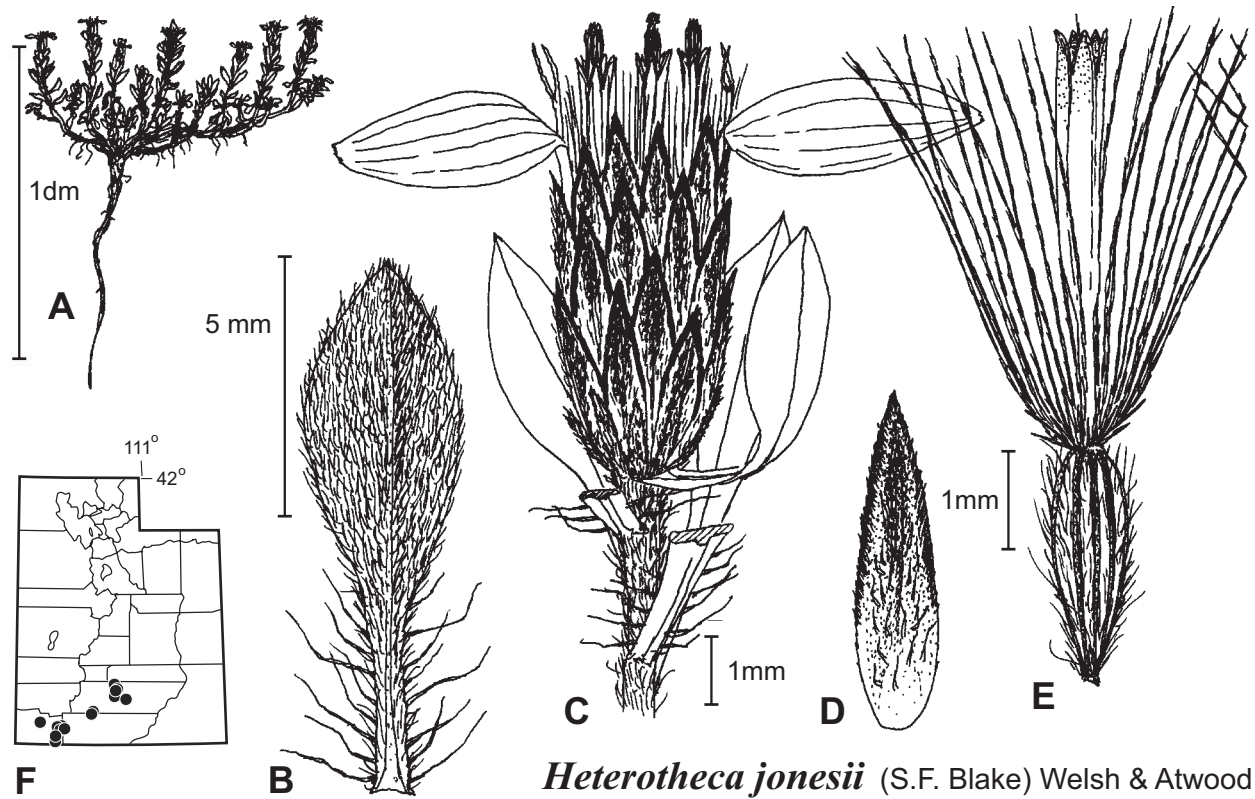
Perennial from stout woody taproots, STEMS several to many, decumbent to ascending, lower portions often buried in sand, (2.3)-3.6-**4.7**-5.7-(6) cm tall, to densely strigose, sparsely hispid, non-glandular; (9)-10-14-18-(22) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (4.8)-6.4-**9.5**-12.6-(15) mm long, (1.5)-1.6-**2.1**-2.7-(3) mm wide, subpetiolate, cuneate, acute, moderately to densely strigose on both surfaces, hispid hairs few; margins entire, strigose, longer hispid hairs near base, flat when fresh, often curling upon drying. UPPER STEM LEAVES narrowly to broadly oblanceolate, sessile, little reduced upward, (3.5)-5.0-**7.1**-9.2-(10) mm long, 1.1-**1.8**-2.4-(3.2) mm wide, non-glandular, moderately to densely hispid-strigose, (30)-53-**80**-107-(120) hairs/mm², margins flat, but sometimes curling upon drying. CAPITULESCENCE of solitary heads; peduncles short, densely strigose, hispid hairs few, bracts foliar, little reduced upward. INVOLUCRES cylindrical to turbinate when fresh, to narrowly campanulate upon drying, (5)-5.6-**6.2**-6.8-(7) mm high; phyllaries in 4-5 imbricate series, outer 1/5-1/4 length of inner, mid series lanceolate, non-glandular, moderately strigose, margins hyaline, fimbriate-ciliate apically. RAY FLORETS (7)-8-**9**-10-(11), strap yellow, (6.1)-6.5-**7.1**-7.8-(8.3) mm long, 0.6-**0.9**-1.3-(1.6) mm wide. DISC FLORETS (10)-13-**16**-19-(21), yellow, corolla somewhat ampliate, (3.6)-3.8-**4.2**-4.6-(4.8) mm long, lobes (0.3)-0.5-**0.6**-0.8-(1.0) mm long, sparsely pilose, hairs on lobes (0.1)-1.5-(0.3) mm long. ACHENES (1.1)-1.3-**1.8**-2.2-(2.5) mm long, moderately strigose; pappus off-white, double, outer whorl of a few linear scales 0.25-0.5 mm long, inner whorl of 25-35 barbellate bristles (3.9)-**4.1**-4.6-5 mm long. Chromosome number: $2n = 18$; several reports.

Flowering Period: JUNE-SEPTEMBER.

Distribution and habitat: Very rare in southwestern Utah (Fig. 37F); bare sandy or gravelly soils, sand pockets in rock crevasses, exposed Navajo and Kaiparowits sandstone formations; 1200-2750 m (4000-9000 ft.) elevation.

Discussion: *Heterotheca jonesii* is readily distinguished from other species by its very small stature, generally procumbent habit, sessile heads, and its short-strigose canescent, non-glandular indument (Fig. 37). Robust shoots are similar in general appearance to *H. villosa* var. *depressa*, which is endemic to the hot springs and geyser basin areas of Yellowstone National Park and Teton National Park, but such shoots lack the glands typical of the indument of var. *depressa* (Fig. 44). The species properly belongs on any state or national rare plants list. Being situated within several national parks, the species should be adequately protected. *Heterotheca jonesii* may be present at more sites within its range that have not been examined due to the difficulty of reaching such steep, exposed sandstone formations. Recent collections have begun to fill out the data base on its distribution. *Heterotheca jonesii* appears to be a dwarf, specialized member of the *Villosa* group. It frequently occurs sympatrically with *H. villosa* var. *scabra*, a glandular, green-leaved and more robust taxon that is highly unlikely to be confused with *H. jonesii*. The exposed sandstone habitats are subject to extremes in local climatic conditions, being very hot and dry in the summer and offering little or no protection from storms in the winter. A representative habitat, Hell's Backbone Ridge, is aptly named.

Specimens examined: U.S.A. UTAH. Garfield Co.: Box-Death Hollow Wilderness, *Franklin 6880* (UT). Dixie N.F., Sand Creek, *Franklin 6886* (WTU). N of Escalante, Hell's Backbone, *Cottam 9101* (BRY, LL), Aquarius Plateau, *Cottam 13485* (UT). *Harrison*



Heterotheca jonesii (S.F. Blake) Welsh & Atwood

Figure 37. Morphology and distribution of *Heterotheca jonesii*. A. Habit, often lower portions of shoots are buried in loose sand. B. Lower-mid stem leaf. C. Upper portion of shoot and head with only some florets drawn; for clarity some leaves are shown cut away. D. Mid series phyllary with chlorophyllous zone dark; anthocyanotic margins shown dark. E. Mature achene with disc corolla attached. F. Distribution; Utah.

12343 (BRY), Lewis 6124 (BRY); Boulder Mt., Welsh 19336 (BRY), Welsh 19333 (BRY), SE of Hells Backbone, Neese & White 3942 (BRY); Hells Backbone Bridge Rd, Holmgren, Reveal & La France 2539 (GH, KANU, MIN, NY, UBC, WTU); Hells Backbone Bridge, Hreha E 0317 (UT), Semple & Chmielewski 8898 (WAT). Kane Co.: Bryce Canyon N.P., Bristle Cone Loop Trail, Semple & Chmielewski 8903 (WAT; fragment), Under-the-Rim-Trail, Graybosch 924 (BRY). Zion N.P., Boyle Z 225 (UC); W side Checkerboard Mesa, Neese, Welsh, et al. 15718 (BRY, NY), Semple 8829 (WAT). Washington Co.: Canaan Mts., Shultz & Anderson 5355 (NY). Canaan Mt., mesa N of Colorado City Az., Albee & Shultz 3385 (UT). N of Rockville, E side Cave Knoll, Wolf Spring Wash, Higgins 18467 (NY). NW side of Pine Valley Pk., Higgins 18470 (UT). Zion N.P., Cave Valley, Clark & Charlesworth 23873 (NY).

16. *Heterotheca zionensis* Semple, Brittonia 39: 384. 1987. TYPE: U.S.A. UTAH. Washington Co., W of Leeds, 15 Sep 1985, Semple & Heard 7859 (Holotype: NY!; isotypes: ASU!, UTC!, WAT!)

Perennial from stout woody taproots, STEMS several to many, ascending-erect, (17)-23-39-55-(70) cm tall, moderately to densely hispid and strigose (spreading hairs many), sometimes becoming densely glandular and moderately pubescent above; (13)-22-38-53-(68) nodes below capitulescence. LOWER STEM LEAVES narrowly to broadly oblanceolate, (15)-20-30-38-(45) mm long, (5)-5.4-6.3-7.2-(8) mm wide, petiolate to sessile, cuneate, acute, densely hispid-strigose on both surfaces, sparsely to moderately glandular; margins entire, strigose, longer hispid hairs near base, flat. UPPER STEM LEAVES narrowly to broadly ovate to lanceolate or oblong, sessile, reduced upward, 10-15.0-20-(30) mm long, (2.5)-3.2-4.6-6.0-(7.3) mm wide, moderately to densely glandular, (0)-10-32-55-(80) glands/mm², densely to very densely hispid-strigose (32)

72-117-163-(180) hairs/mm², margins flat. CAPITULESCENCE corymbiform, branches ascending, heads (7)-9-18-27-(46); peduncles moderately to densely hispid-strigose and moderately to densely glandular, (9)-14-24-33-(41) mm long, bracts few, lower ones lanceolate, much reduced upward 1.5-3.2-4.6-(6) mm long, 0.2-0.4-0.6-(0.8) mm wide. INVOLUCRES cylindrical to turbinate when fresh, narrowly campanulate upon drying, (4.3)-5.2-6.3-7.5-(8.1) mm high; phyllaries in 5-6 imbricate series, outer 1/5-1/4 length of inner, mid series narrowly triangular, very sparsely to densely glandular, very sparsely to moderately strigose, margins hyaline, fimbriate-ciliate apically. RAY FLORETS (8)-9-14-18-(23), strap yellow, (6.5)-7.8-9.4-11.2-(13) mm long, 1-1.3-1.5-(1.7) mm wide. DISC FLORETS (11)-16-30-44-(62), yellow, corolla somewhat ampliate, (3.5)-4.5-5.4-6.3-(7) mm long, lobes (0.4)-0.5-0.6-0.7 mm long, sparsely pilose, hairs on lobes 0.1-0.3 mm long. ACHENES (1.4)-1.5-2.2-2.9-(3.9) mm long, moderately strigose; pappus off-white, double, outer whorl of a few linear scales 0.25-0.5 mm long, inner whorl of 25-40 barbellate bristles (3.4)-4.4-5.5-6.7-(7.3) mm long. Chromosome numbers: $2n = 18, 36$; many reports.

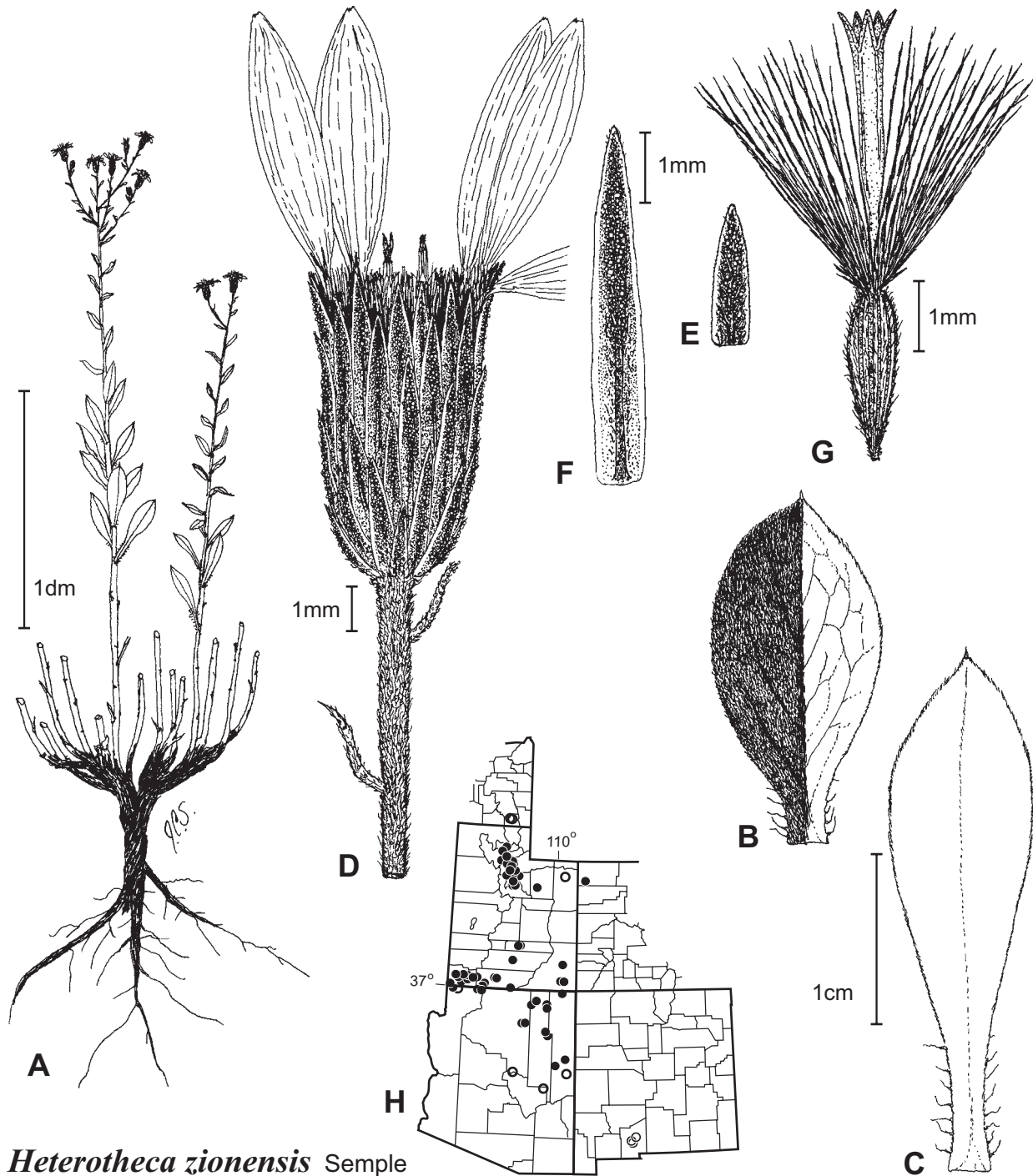
Flowering Period: JUNE-AUGUST-(October)

Distribution and habitat: Utah and northern and eastern Arizona (Fig. 38H); putatively introduced and now well established along interstate highways in the vicinity of Las Cruces, New Mexico; introduced into Moffat Co., Colorado and Franklin Co., Idaho and possibly not established; rocky, sandy or sandy loam soils, deep sand; edges of washes, roadsides, dry waste ground, open places, sand dunes, sandy ledges of rock outcrops; 950-2700 m (3000-8800 ft.) elevation.

Discussion: *Heterotheca zionensis* is characterized by its usually dense to very dense short-strigose indument on the stems and leaves, which can be white rather than silvery gray-green in appearance in the more densely pubescent forms (Figs. 38B-C). The phyllaries of *H. zionensis* vary from densely glandular and glabrate (Figs. 38 E-F) to densely strigose and nearly eglandular. The two forms can occur in the same population (e.g., *Semple & Heard 7914, 7915, 7916*). The whitish appearance of the stem and leaves readily distinguishes the species from *H. villosa* var. *scabra*, which frequently occurs sympatrically with *H. zionensis* in southern Utah and northern Arizona (Fig. 47).

The species could be confused with *H. villosa* var. *pedunculata* (Fig. 45) which has more hairs/mm² on its leaves and few or no glands on its phyllaries; the ranges of the two come into contact in eastern Arizona and western New Mexico. It could also be confused with narrow and smaller leaved forms of *H. fulcrata* var. *amplifolia* which have a few petiolate-ovate bracts subtending the heads (Fig. 30). These varieties generally lack glands. Individuals with more hairy, less glandular phyllaries might be confused with *H. villosa* var. *foliosa* (Fig. 43); the ranges of the two taxa do not overlap.

Plants looking in the field similar to *Heterotheca zionensis* were found to be very common (October 1995) along the interstate highways in the Rio Grande Valley in the vicinity of Las Cruces, New Mexico. Indument features of two collections examined in detail were atypical for the species: *Semple & Semple 10508* (WAT) had a very dense indument of hairs, but no glands; *Semple & Semple 10509* (WAT) had a very low number of hairs and more glands than expected for the species, but was a roadside plant with some stem damage. A collection from 1981 (*Ward 81-550* (NMC)) noted the commonness of plants like these at that time as well. Several interpretations of the origins of these plants are possible. These may have been introduced by humans via long distance dispersal from Utah with the marginal nature of the habitat accounting for the indument features. In northern Utah around Salt Lake City a number of collections with relatively few leaf hairs have been collected from range-margin populations. Alternatively, highway construction may have created or opened up suitable habits for the species, and these sites were subsequently colonized from atypical populations in eastern Arizona. Regardless, the plants are as weedy along the highway in Las Cruces as they are in Provo, Utah at the other end of the range of the species. In both cases, most herbarium collections seen were originally treated as *H. villosa* or *H. canescens* by the collectors. Experimental research may ultimately demonstrate that these New Mexican specimens are atypical members of *H. villosa* var. *pedunculata*. Both



Heterotheca zionensis Semple

Figure 38. Morphology and distribution of *Heterotheca zionensis*. A. Habit with only two shoots drawn; stem and leaf pubescence not indicated. B-C. Lower mid stem leaves from different plants; adaxial surface, hairs only drawn on left side in B; scale the same for both. D. Head with only some florets drawn. E-F. Typical outer and mid series phyllaries, respectively, with chlorophyllous zone dark; scale the same for both; phyllaries can be much more strigose and less glandular. G. Mature disc floret achene with corolla shown attached. H. Distribution in Utah, Arizona, New Mexico; introduced in western Colorado and southeastern Idaho (o aff. *H. zionensis*).

H. zionensis and *H. villosa* var. *pedunculata* can have such high densities of hairs that the leaves look whitish rather than some shade of green. The former usually has many glands on the upper stem and branch leaves while the latter is typically sparsely glandular or glandless.

The few collections from southeastern Idaho have large leaves for the species but the indument is rather typical on the leaves and phyllaries. Some of the collections come from hot springs, a habitat also occupied in northern Utah.

The original choice for the species epithet has turned out to be uninformative of the true distribution of this species. It is a common taxon distributed over parts of several states rather than a rare one confined to the vicinity of Zion National Park in southwestern Utah.

Specimens examined: U.S.A. ARIZONA. Apache Co.: Pipe Springs, *Kraus s.n.* (WIS). Coconino Co.: Flagstaff, *Jones 359* (POM). NE of Strawberry, *Semple & Heard 7914* (WAT). NE of Tuba City, *Gould & Phillips 4745* (UC). Mohave Co.: AZ-386, 6 mi from UT line, *Holmgren & Holmgren 4661* (ASU, MIN, NY, RM, RSA, TEX, UBC). W of Cedar Ridge, *Baker 4743* (ASU). W of Cone Beds, *Bundy 133* (ASU). Cottonwood Cyn., *Gierisch 4471* (ASU, BRY). NE of Jacobs Well, base of Black Rock Mt., *Bundy 171* (ASU, BRY). W of Pipe Springs, *Gierisch 3998* (ASU). Navajo Co.: Frazer's & Kaibito, *Shirley 90 & 91* (NMC). Kaibito, *Goodding 2135* (ARIZ), *Goodding 2136* (UT). Kaibito Plateau, *Love 84* (NMC). Keams Cyn., *Monson 2* (NY). SE of Kayenta, Black Mesa, *Howell & Eastwood 6626* (CAS, NY). COLORADO. Moffat Co.: US-40, *Baker 4833* (RM), *Baker 4833G* (LL). NEW MEXICO. Dona Ana Co.: 2 air km NNW of the top of Bishop Cap, *Worthington 17242* (NY). UTAH. WSW of Anderson's Ranch, *Moore N29194* (MIN(2)). Utah Valley, *Watson 516* (NY). Box Elder Co.: 8 mi S of Brigham City, US-89 & 91 S of Willard, *Roszbach 5560* (WTU). Davis Co.: Bountiful Peak, *Allan 224* (BRY). Farmington, *Holmgren 8258* (CAS, DS, POM, RM, UC, WS, WTU). N of Farmington, *Maguire 20117* (GH, NY, WTU). Great Salt Lake, Antelope Island, *Jones s.n.* (BRY). Garfield Co.: E of Boulder, between "The Gulch" and Deer Creek, *Albee 1151* (UT). Escalante, Deer Crk on Burr Trail, *Neese & White 3929* (BRY, NY, UT). Kane Co.: W of Glen Cyn City, *Atwood 2921* (UNCC). NE of Kanab, S of Mollie's Nipple, *Hester 1046* (RSA). NNE of Kanab, head of Dry Lake Cyn, *Welsh 21439* (BRY, NY). Vermillion, *Higgins 10956* (BRY). Zion N.P., E entrance, *Davies & Turner 79211* (TEX), *Kamb 632* (UC); E of N.P., *Semple & Heard 7877* (BRY, GH, JCS, MO, NY(2), RM, UC, WAT). Salt Lake Co.: Alta, *Jones s.n.* (NY). Between Big and Little Cottonwood Cyns., *Garrett 2653* (LL, NY, UT). City Creek Cyn., *Jones s.n.* (NY), *Arnou 1976* (UT), *Leonard 195* (NY), *Garrett 1703* (NY). Cottonwood Cyn., *Stokes s.n.* (DS). E of Draper, *Garrett 6619* (DS, KANU, LL), Corner Cyn, *Arnou 4230* (UT). Ft. Douglas, *Clemens s.n.* (RM, UC). SE of Holladay, *Arnou 790* (UT). Jordan Valley, *Leonard 265* (NY). Little Cottonwood Cyn., *Clemens s.n.* (CAS), below Brighton, *Shultz & Shultz 7233* (NY). Red Butte Cyn., *Arnou 2117* (BRY, UT). Salt Lake Cemetery, *Edwards 543* (NY), ridge N of City Cemetery, *Ludwig 580* (UT). Salt Lake City, *Garrett s.n.* (UT), *Garrett 3010* (NY), *Garrett 6847* (UC), *Garrett 6980* (KANU, LL, UT), *Howard s.n.* (POM), *Jones s.n.* (POM); North Bench, *Garrett 3079* (GH, NY, UT); S of Brighton High School, *Albee 503* (UT); near Salt Lake City, *Garrett 1709* (DS, GH, RM), *Garrett 2061* (NY, UT), *Redfield 162* (NY), *Moldenke & Moldenke 2106* (NY, mixed collection with *H. fulcrata*). S of Salt City, *Arnou 749* (UT), *Arnou 3271* (UT). Salt Lake Valley, *anon. s.n.* (UT). San Juan Co.: Abajo Mts, Grayson Mesa, *anon. s.n.* (BRY); near Bluffs, along San Juan River, *Rydberg & Garrett 9941* (CAN, NY), *Rydberg & Garrett 9996* (NY, UC, UT). Utah Co.: 1 mi S of Rotary Park, *Welsh s.n.* (BRY). E of Alpine, *Semple & Chmielewski 8884* (WAT). Diamond Fork Cyn, *Welsh, Murdock & Moore 6640* (NY). Lakeview, *Harrison 8387* (UC). Mt. Timpanogos, *Allred 366* (BRY). N Provo, *Semple & Chmielewski 8887* (WAT). Provo, *Jeppsen 422* (BRY), *Jones 5613* (NY, POM, UC), *Jones 185* (BRY), *Baird 216* (BRY), Rock Cyn., *Harrison 7552* (LL), "Y" Mt., *Morrill 44* (BRY); E Bench of Provo, *anon. 6123* (LL). NE of Provo, *Arnou 534* (GH, UT). S of Provo Cyn, *Jeppsen 158* (BRY). SE of Provo, mouth of Slate Cyn., *Replogle 13* (BRY). W of Provo, *Garrett 3350* (RM, UT). shore of L. Provo, *Semple et al, 5757* (ASU, BRY, CAN, JCS, MO, MT, RM, TEX, UC, WAT). Wasatch Co.: S of Farmington, *Kendrick K-1* (USFS(2)). Midway, *Harris C25174* (MIN(2)), Luke's Hot Pot, *Harris C27312* (PH, RSA), *Harris C29429* (GH, MIN), edge of "hot pots" along UT-220, *Semple & Chmielewski 8875* (WAT), near Midway, *Carlton & Garrett 6693* (NY, RM). Washington Co.: Beaverdam Mts., *Higgins 743* (NY). Dixie For., Leeds Div., Ash Crk Gate, *Storm 191* (USFS), Mill Creek, *Olsen 216* (BRY, USFS). Hurricane, N of Hwy-15 on Kolob Rd, *Foster 5628* (BRY). S of Ivins, *Higgins 14007* (BRY, NY). Kolob Reservoir Rd., below Sunset Cyn. Rd., *Moor Z1541* (NY). N of Leeds, *Warrick & Warrick 3127* (BRY), *Warrick & Warrick 3128* (BRY), *Warrick & Warrick 3211* (BRY), *Warrick 3222* (BRY, NY), *Welsh 14606* (BRY, NY). NE of Leeds, Grapevine Wash, *Higgins & Higgins 15633* (BRY). Pine Valley Mts., South Ash Crk, *Warrick 2717* (RM). Snow Cyn., *Coombs & Bundy 2982* (ASU, BRY). St. George, *Davis s.n.* (BRY). N of St. George, Dixie S.P., *Wiggins 20233* (DS), Snow Cyn, *Higgins 14439* (BRY, NY). Snow Cyn S.P., *Albee 6022* (UT). Santa Clara, *Cottam 1527* (UT). Toquerville, *Thorne & Hugie 161* (BRY), N of Toquerville, *Welsh 21423* (BRY). Zion N.P., Cave Valley, *Welsh, Clark & Charlesworth 23858* (NY). Wayne Co.: SE of Oak Crk. Campground, *Harrison 1275* (BRY). Weber Co.: N of Taylor Cyn, *Stewart 40* (USFS), Roy, *Clark 2238* (BRY).

H. aff. zionensis (most often pubescence density low for species)

U.S.A. IDAHO. Franklin Co.: SE of Cleveland, *Baker 9532* (NY(3), WTU(3)); leaves large for species). Maple Grove Hot Sprs., NE Preston, *Bright 61-46* (MIN, RM). NEW MEXICO. Dona Ana Co.: Las Cruces, *Semple & Semple 10509* (NMC, WAT). Grant Co.: Silver City, *Greene s.n.* (POM). UTAH. Davis Co.: Provo Terrace E of Bountiful, *Ludwig 1213* (UT). Salt Lake Co.: Big Cottonwood Cyn, *Ludwig 327* (UT). Little Cottonwood Cyn., *Cottam 6394* (UT). Oquirrh Mts., S of Harker's Cyn, *Cottam 14467* (UT). Uinta Co.: Vernal-Manila Hwy, *Garrett 7526* (UT).

H. aff. zionensis (approaching *H. villosa* var. *minor*)

U.S.A. UTAH. Davis Co.: Bountiful, N of Rock Cr, *Cottam & Anderson 15570* (DS, RSA, UT). Farmington, *Holmgren 8258* (CAS, DS, POM, RM, UC, WS, WTU). Utah Co.: Mt. Timpanogos, *Garrett 5780* (LL, UT).

H. aff. zionensis (approaching *H. villosa* var. *pedunculata*)

U.S.A. ARIZONA. Navajo Co.: US-180 E of Holbrook, *Semple & Heard 7906* (WAT). NEW MEXICO. Dona Ana Co.: S of Las Cruces, *Ward 81-550* (NMC). W of Las Cruces, *Semple & Semple 10508* (NMC, WAT). Mesa, Las Cruces, *Wooton s.n.* (GH).

- 17. *Heterotheca villosa* (Pursh) Shinnery**, Field & Lab. 29: 71. 1951. *Amellus villosus* Pursh, Fl. Amer. Sept. 2: 564. 1814. *Inula villosa* (Pursh) Nutt., Gen. N. Amer. Pl. 2: 151. 1818. *Diplopappus villosus* (Pursh) Hook., Fl. Bor. Amer. 27: 22. 1834. *Chrysopsis villosa* (Pursh) Nutt. ex DC., Prod. 5: 327. 1836. *Diplogon villosum* (Pursh) Kuntze, Rev. Gen. Pl. 1: 334. 1891. TYPE: U.S.A. Amer. septentrionalis. "on the Missouri", [1811], *Bradbury s.n.* (Holotype: lost/destroyed, not in K, LIV, PH). NEOTYPE, designated by Semple (1990): "Missouri", [1811], *Nuttall s.n.* (PH-001726!, shoot No.1).
Sideranthus integrifolius Nutt. in Fras. Cat. no.80. 1813. nom. nud.

Perennial from stout woody taproots, STEMS several to many, decumbent to erect, (5)-16-**28**-40-(71) cm tall, sparsely to densely hispid-strigose, long hispid hairs very few to numerous; (8)-12-**22**-32-(68) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (9)-22-**31**-40-(60) cm long, (2)-4.1-**6**-8-(13) mm wide, petiolate, cuneate, sometimes mucronate, indument highly varied, sparsely to very densely hispid-strigose and eglandular to densely sparsely glandular on both surfaces; margins entire or very rarely with 1-2 teeth apically, strigose, few to many longer hispid hairs along margins. UPPER STEM LEAVES oblanceolate, oblong, lanceolate or rarely ovate, (4)-15-**22**-28-(42) mm long, (1.5)-3.5-**5.3**-7-(12.5) mm wide, sessile, often reduced upward, acute to obtuse, indument similar to lower or becoming less or more dense, 0-**10**-22-(50) glands/mm², (1)-7-**50**-93-(270) hairs/mm², margins flat or rarely very remotely undulate, some longer hispid hairs along margins basally. CAPITULESCENCE open cymose-corymbiform, rarely paniculiform, heads 1-**8**-16-(42); peduncles sparsely to densely hispid-canescens and eglandular to densely glandular, (4)-15-**28**-41-(98) mm long; bracts few, linear-oblanceolate, usually greatly reduced, rarely foliar and linear-oblanceolate, indument like leaves. INVOLUCRES narrowly cylindrical to campanulate when fresh, campanulate-hemispheric upon drying, (5)-6.2-**7.8**-9.5-(13) mm high; phyllaries in 4-5 imbricate series, outer ones 1/5-1/3 the length of the inner, narrowly triangular-lanceolate, sparsely to densely strigose, eglandular to moderately glandular, margins hyaline narrow, fimbriate-ciliate and sometimes anthocyanotic apically; inner ones similar. RAY FLORETS (5)-10-**15**-20-(38), strap yellow, (3.5)-6.6-**9**-11-(20) mm long, (0.5)-0.9-**1.4**-1.8-(3.1) mm wide, tube glabrous to glabrate. DISC FLORETS (10)-19-**35**-51-(83), yellow, glabrous or a few minute hairs, corolla barely ampliate, (4.1)-4.9-**5.5**-6.2-(7.7) mm long, lobes (0.4)-0.5-**0.65**-0.75-(1) mm long, hairs absent or few, 0.1-**0.2**-0.35 mm long. ACHENES 1.7-**2.2**-2.7-(3.4) mm long, sparsely to moderately strigose; pappus off-white, double, outer whorl of linear scales 0.25-1 mm long, inner whorl of 30-45 barbellate bristles (4.1)-5.0-**5.8**-6.5-(8.6) mm long. Chromosome numbers: $2n = 18, 36$; numerous reports.

Flowering Period: (May)-JUNE-OCTOBER-(November in southern part of range).

Distribution: Western mountains from British Columbia in Canada to New Mexico, Arizona and California in the United States, great plains from Alberta to western Ontario in Canada south to New Mexico and Nebraska in the United States (Figs. 39 and 40); a wide variety of soil types in pine forests, grasslands and badlands; 330-2900-(3200) m (1100-9500-(10,500) ft.) elevation.

Discussion: *Heterotheca villosa* is very variable in stem height, leaf base shape, stem and leaf indument traits, numbers of heads per capitulescence and florets per head. Thus, it is difficult to define as a species, although each infraspecific taxon has a diagnostic suite of traits. Usually the individuals lack large bracts subtending the heads (except var. *ballardii*, Fig. 42), the upper leaves are narrowly cuneate-oblanceolate (except var. *ballardii*, var. *foliosa* and var. *nana* which have oblong leaves with rounded bases (Figs. 42, 43 and 48, respectively). Numerous local races occur that are sometimes quite distinct in the extreme, but all of these

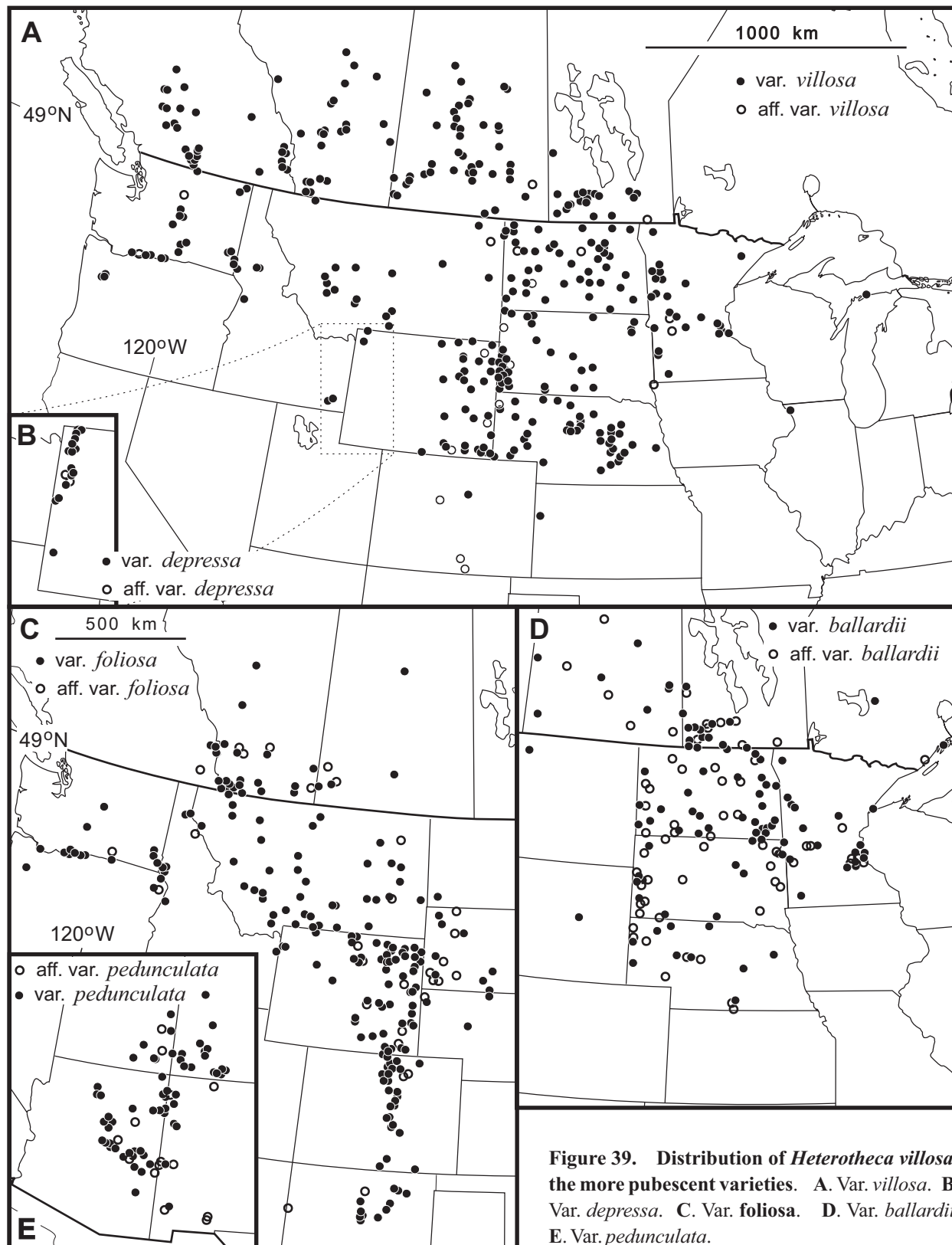


Figure 39. Distribution of *Heterotheca villosa*: the more pubescent varieties. A. Var. *villosa*. B. Var. *depressa*. C. Var. *foliosa*. D. Var. *ballardii*. E. Var. *pedunculata*.

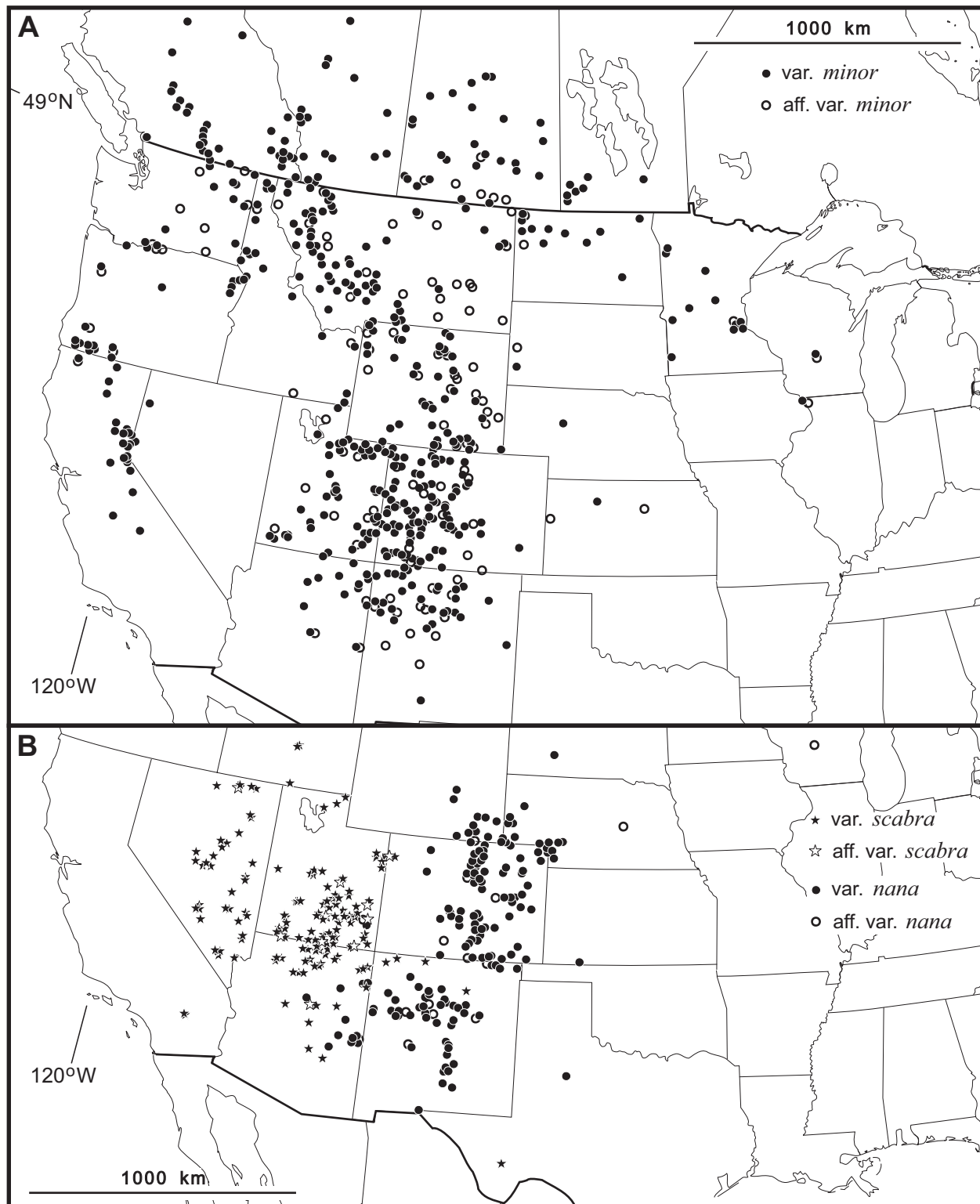


Figure 40. Distribution of *Heterotheca villosa*, the more glandular varieties. A. *Var. minor*. B. *Var. nana* and *var. scabra*. C. *Var. sierrablancensis*.

intergrade with one or more other races (Cronquist 1994; Harms 1963; Semple 1990, 1994). In this treatment, the species is divided on the bases of indument features, leaf shape and stem height paralleling the infraspecific treatments of *H. fulcrata* and *H. sessiliflora*. Cronquist (1955, 1994) acknowledged the variability of the species and the existence of many local races, but lumped most of these into var. *villosa* and var. *hispid*, both of which encompassed a great range in indument forms. He continued to treat sect. *Phyllothea* as part of *Chrysopsis*, but acknowledged that its placement in *Heterothea* was a defensible alternative (Cronquist 1994). He also lumped *H. camporum*, *H. fulcrata*, *H. pumila*, *H. visicida* and *H. zionensis* into his *Chrysopsis villosa* (Cronquist 1991, 1994). He did find *H. jonesii* sufficiently distinct to be treated as a species. Such lumping of taxa results in a taxon so variable in features that it would be impossible for any \hat{a} -level taxonomist to sort out phylogenetic patterns, since the Cronquist scheme offers no means of distinguishing and identifying many of the species in sect. *Phyllothea*. Dr. Cronquist remained steadfast to the traditional uninformative treatment of the *villosa* complex.

The species is more defined by what it lacks rather than what it possesses. This is, of course, a very unsatisfactory situation from a cladistics point-of-view. The problem may arise from the fact that the species is the most widespread of any in the genus and is highly variable in diagnostic features. Tetraploids are more common than diploids in *H. villosa*, and this has led to a "pillar complex" problem for taxonomists. The diploid races are usually distinct from each other, but each has given rise to one (or more) tetraploid lines. Tetraploids tend to look more alike because the diploid traits are less pronounced and because the tetraploids are more likely to have hybridized, thus further blurring the distinctions between the races. Possible occasional hybridization with tetraploids in other species may also have further buffered the distinctive morphology of the tetraploid level of the pillar complex. The details can undoubtedly be resolved via macromolecular biochemical analyses and great effort and expense. Flavonoid data have not provided the kind of phylogenetic information necessary.

A number of morphotypes appear sufficiently distinct to warrant recognition. These separated from each other to varying degrees in an unpublished discriminant analysis; all races have well defined geographic distributions which overlap to a considerable degree in some cases (Figs. 39-40). The highly plastic nature of the species and undoubted hybridization make identification to variety difficult in numerous cases. Nonetheless, 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. Some taxa have sufficiently non-overlapping ranges that subspecies status might be considered (following the definitions discussed in Semple 1974). Each variety most likely evolved in isolation and adapted to a different set of habitat parameters, but by and large no variety now occurs in isolation. The new var. *sierrablancensis* is the most restricted in distribution within the species (Fig. 40C). Other distinctive local races warranting variety level recognition might also be discovered in the future. The range of the species is so large that even an examination of several thousand collections is not considered sufficient to clarify all the varietal level problems in this most difficult species complex. Nine varieties are recognized in this treatment; these are distinguished on the basis of indument and leaf shape features.

17.1 *Heterothea villosa* (Pursh) Shinnery var. *villosa*

Chrysopsis mollis Nutt., Trans. Amer. Phil. Soc. 2.7: 316. 1841. TYPE: U.S.A. "Rocky Mts.", *Nuttall s.n.* (Holotype: BM! with Baker et al. 674; isotype: PH!).

STEMS several to many, decumbent to erect, (16)-22-27-33-(39) cm tall, moderately to densely hispid-strigose, long hispid hairs few to numerous; 10-20-31-(52) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (25)-27-35-43-(52) mm long, (3.4)-3.8-5.2-6.5-(7.5) mm wide, petiolate, cuneate, sometimes slightly mucronate, moderately to densely hispid-strigose and eglandular on both surfaces; margins entire, strigose, longer hispid hairs along margins basally. UPPER STEM LEAVES oblanceolate, (15)-21.5-26-31-(35) mm long, (3.5)-4.1-4.9-5.8-(6) mm wide, sessile, somewhat reduced upward, acute, indument

similar to lower, (20)-27-38-48-(50) hairs/mm², margins flat, a few longer sprading hairs along margins basally. CAPITULESCENCE open cymose-corymbiform, heads 1-6.7-12-(25); peduncles sparsely to densely hispid-canescens and eglandular, (5)-12-30-47-(67) mm long; bracts few, linear-oblongate, usually greatly reduced, rarely foliar and linear-oblongate, indument like leaves. INVOLUCRES narrowly cylindrical to campanulate when fresh, campanulate-hemispheric upon drying, (5)-6.1-7.5-9-(11) mm high; phyllaries in 4-5 imbricate series, outer ones 1/5-1/4 the length of the inner ones, narrowly triangular-lanceolate, moderately to densely strigose, eglandular, margins hyaline narrow, fimbriate-ciliate and usually antho-

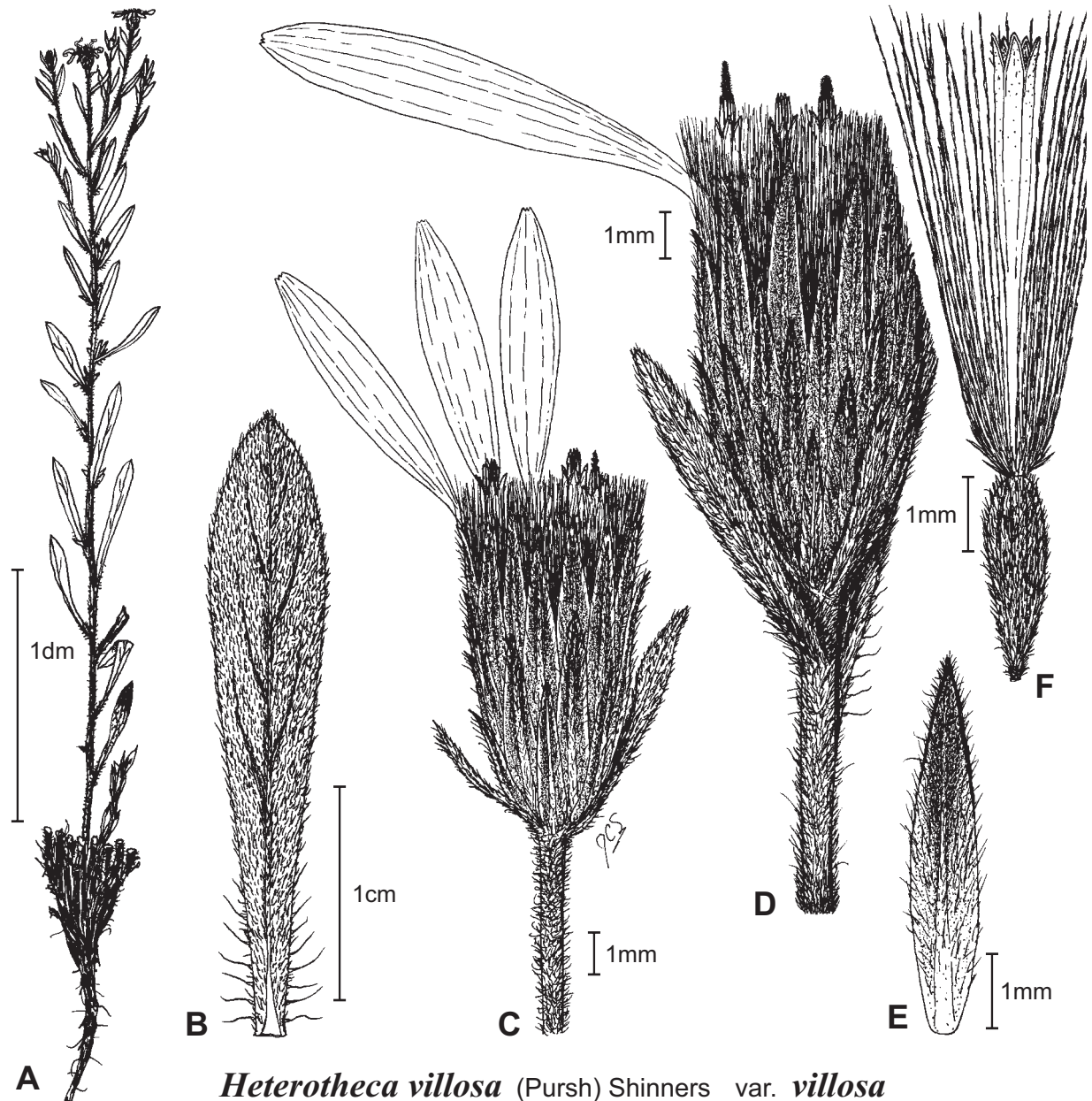


Figure 41. Morphology of *Heterotheca villosa* var. *villosa*. **A.** Habit. **B.** Upper stem leaf, adaxial surface. **C-D.** Heads with only some florets drawn; diploid and tetraploid plants, respectively. **E.** Mid series phyllary with chlorophyllous zone dark; apical margins anthocyanotic. **F.** Mature achene with disc corolla attached.

cyanotic apically; inner ones similar. RAY FLORETS (10)-12-19-27-(38), strap yellow, (6.5)-8.5-11.6-15-(20) mm long, (0.9)-1.1-1.4-1.8-(2) mm wide, tube glabrate. DISC FLORETS (15)-17-34-51-(83), yellow, glabrous or a few minute hairs, corolla barely ampliate, (4.7)-5.1-5.7-6.4-(6.9) mm long, lobes (0.5)-0.6-0.7-0.8 mm long, hairs absent or few, 0.1-0.2-0.25 mm long. ACHENES 1.5-2.1-2.6-(3.1) mm long, sparsely to moderately strigose; pappus off-white, double, outer whorl of linear scales 0.25-1 mm long, inner whorl of 35-45 barbellate bristle (4.7)-5.3-6.3-7.3-(8.6) mm long. Chromosome numbers: $2n = 18, 36$; numerous reports.

Flowering Period: (May-) JUNE-OCTOBER (-November in south).

Distribution and habitat: Western mountains at lower elevations and northern Great Plains (Fig. 39A); sandhill prairies, pastures, grasslands, roadsides, railroad rights-of-way; silty, sandy loam or clay soils, chalk, or granitic soils, gravel soils, dry shale-limestone soils, red sandstone soils, travertine soils; 330-2300-(2900) m (1100-7500-(9500) ft.) elevation.

Discussion: Variety *villosa* is distinguished from other races of the species by its narrow oblanceolate, narrowly tapered upper stem leaves that have an indument of moderately dense hairs (25-50 hairs/mm²) and no glands, a few headed capitulescence that generally lacks large bracts subtending the short to long pedunculate heads, and pubescent glandless phyllaries that have anthocyanotic pigment at the tip and often along the upper margins (Fig. 41). The stems usually have only a few longer spreading hairs and the shorter appressed primary hairs; rarely such long hairs are more abundant.

The upper leaf indument density of the neotype is moderately high for a western goldenaster but does not totally obscure the leaf surface from view as var. *pedunculata*, which generally has many more hairs/mm² and some glands. As treated here var. *villosa* is found only in the northern half of the range of the species. Other authors have lumped into the variety any member of the species (and often members of other species) that had numerous hairs on the leaves and were not obviously glandular and hispid.

Specimens examined: CANADA. ALBERTA. Nagy 2743 (CAN). Banff, *Farr s.n.* (PH). Calgary, *Jenkins 7279* (DAO), *Kerr 324* (UBC). Near Banff, *Macoun s.n.* (MIN). East Calgary, *McCalla 11800* (UBC). Near Clyde, *Moss 4433* (CAN, WIS). N of Consort, *Scott 1222* (CAN). near Ft. MacLeod, *Deneka 35* (WAT). Ft. Saskatchewan, *Turner 7402* (CAN, DAO). W of Gatine, *Pinel & Wallis V-568* (DAO). Gem, *Kieth s.n.* (WIS). Hesketh, *Pinel & Wallis V-534* (DAO). Jasper, *Scamman 3397* (GH). Lacombe *O'Brian 972* (DAO). Lethbridge, *Boivin & Perron 12148* (DAO). W of Mannville, *Semple & Brouillet 4282* (WAT). Milk R., S of Sage Cr, *Macoun 10822* (CAN). Nevis, *Calvert s.n.* (WAT). W of Pincher, *Malte & Watson 2386* (CAN, WTU). N of Pincher, *Moss 286* (GH, WIS). SW of Pincher Cr, *Moss 19* (DAO, GH, WIS). Okotoks, *Anderson 1041* (DAO). Oldman R., middle fk of N branch, *Dawson 9881* (CAN). N of Oyen, *Harms 27557* (DAO). Red Deer, *Malte & Watson 1742* (CAN), *Nelson & Nelson 4768* (DS, RM, UC). Waterdon Lakes, *Hunnell 15651* (GH). E of Waterdon Lakes N.P., *Kojima 770294* (DAO). S of Wetaskawin, *Coneybeare 443* (DAO). BRITISH COLUMBIA. S of 100 Mile House, *Turner 474* (UBC). SSW of Alkali L. P.O., *Calder & Parmelee 17099* (DAO). Botanie Valley, *Krajina s.n.* (DAO, UBC), *Perry s.n.* (UBC). Canoe Cr Indian Cr, *Calder & Parmelee 17816* (DAO). Chilcotin country, Gang Ranch, *Tisdale s.n.* (DAO). Columbia Valley, Canal Flats, *Eastham s.n.* (UBC). E of Cranbrook, *Littlewood & MacRae 30* (NY(2)). NE of Cranbrook, *Calder & Savile 9084* (DAO). Fairmont Hot Springs, *Eastham s.n.* (UBC). Confluence of Fraser R. and Chilcotin R., *Hyne 49* (UBC), *Jones 253* (UBC). W side of Fraser R, Sword Cr, *Calder & Parmelee 17976* (DAO). Glacier, *Dudley s.n.* (DS). Hedley, *Cornish* (UBC). N of Hedley, *Calder & Parmelee 17499* (DS, UC, WTU). NW of Hedley, *Grant 64-86* (DAO). Hells Gate, *Newcombe 261* (UBC). S of Invermere, *McLean s.n.* (DAO). Kamloops, *Groh 228* (DAO), *Malte s.n.* (CAN). N of Kamloops, *Calder & Savile 10361* (DAO, UC). Keremeos, *Scoggan 15960* (CAN, MIN). opposite Keremeos, *Calder & Savile 9903* (DAO). Kinbasket Mt., *Calder & Savile 11977* (DAO, GH), *Eastham s.n.* (UBC). Kooteney L. near Sanca Cr, *Calder & Savile 9345* (CAS, DAO). NE of Lillooet, *Calder & Parmelee 17652* (DAO). Lower Arrow L., *Macoun 979* (DAO). Lytton, *Henry s.n.* (UBC), *Krajina 1226* (DAO, GH, UBC), *Pinder-Moss s.n.* (UBC). N of Lytton, *McCabe 187* (UC). Marysville, *Fodor 263* (UBC). Oliver, *Krajina s.n.* (DAO, GH(2)), *Taylor s.n.* (UBC). near Oliver, *Beamish 610430* (CAN, UBC). Penticton, *Eastham s.n.* (DAO), *Stonor s.n.* (UBC). South Penticton, *Eastham s.n.* (UBC). Seton Lake, *Taylor, Krajina & Tusco 16* (UBC). S of Skookumchuck bridge over Kootenay R, *Taylor & Ferguson 1222* (DAO). Spences Bridge, *Brink s.n.* (UBC), *Davidson s.n.* (UBC), *Scagel 82-16* (UBC). SE of Spences Bridge, *Pojar s.n.* (UBC). Summerland Expt. Stn., *Calder & Savile 9699* (DAO, NY, WTU). S of Summerland, *Beulah s.n.* (UBC), *Cannings s.n.* (DAO). Thompson R, E of Cache Cr, *Douglas & Douglas 5247* (BRY, DAO). Thompson R., between Spences Bridge and Cache Cr., *Scoggan 15592* (CAN). ENE of Wasa, *Taylor & Ferguson 1945* (DAO). N of West Bank, Okanagon, *Krajina s.n.* (UBC). Windermere, *Eastham s.n.* (UBC), *Taylor & Ferguson 2605* (DAO). MANITOBA. *Denike 1862* (DAO). E of Austin, *Hainault & Tanguay 6286* (DAO). Aweme, *Groh s.n.* (DAO), *Criddle s.n.* (CAN). Birds Hill, *Neatby s.n.* (DAO). Brandon, *Marshall 10* (DAO), *Stevenson 508* (DAO), *Stevenson 509* (DAO). ESE of Brandon, *Dugal 218* (BRY). Carberry, *Baldwin & MacPherson 10789* (CAN). Crystal City, *Bassett & Kemp 3512* (DAO). Douglas, *Scoggan 10939* (CAN). Grande Clariere, *Scoggan 10090* (CAN).

Melita, *Senn & Gordon 3101* (DAO). Lake Metigoshe, *Nielsen 1264* (MIN). Pine Ridge, *Boivin 6467* (DAO, NY). Between Oak Lake and Griswold, *Morton NA2258* (WAT). Qu'appelle, Assin., *Llyod s.n.* (NY). NE of Melita, *Dore & Breitung 12663* (DAO). Rivers, *Knowlton s.n.* (GH). C.F.B. Shilo, *Bell 47* (DAO), *Keheler 499* (CAN). Spruce Woods For. Res., *Scoggan 9728* (CAN). Stephenfield Reservoir, *Keleher 429* (CAN, DAO). Stony Mt., *Garton 3546* (DAO). Treesbank, *Fyles s.n.* (DAO). Virden, *Krivda V297* (DS, NY). Winnipeg, *Garton 3110* (CAN). W of Winnipeg, *Morton NA 2258* (WAT). SASKATCHEWAN. *Bourgeau s.n.* (GH). Junction of Hwy-6 and Big Bear Rd, *Hainault & Tanguay 6333* (DAO). Bare Hills, *Macoun & Herriot 72879* (CAN, NY). Beverly, *Breitung 5855* (DAO, RM). S of Biggar, *Gillett 10458* (DAO, GH). Big Muddy Valley, *Shevkenek 7* (DAO). Big River, *Hudson 3838*(DAO). Breakmore, *Macoun & Herriot 72878* (CAN, GH), *Macoun & Herriot 42848* (NY, POM). Brownlee, *Johnson 1237* (NY). E of Calderbank, *Wiehler 6986* (WIS). Canwood, *Groh 1176* (DAO). SE of Chamberlain, *Harms 2529* (SASK). N of Chaplin, *McAndrews s.n.* (MIN). Crane L, *Macoun 5017* (CAN, GH). E of Craven, *Ledingham 48-474* (DAO). Cypress Hills, *Carmichael 376* (DAO), *Shevkenek s.n.* (DAO). S of Dana Rosthern Dist, *Senn & Groh 2760* (DAO). NW of Duck L., *Senn & Groh 2881, 2882* (DAO). Dundurn, *Heyes 75-9* (UBC). Eagle Cr, *Macoun 9890* (CAN). Elbow, *Hudson 2126* (DAO). SE of Elbow, *Gray 1902* (CAN), *Gray 1975* (CAN), *Gray 1844* (CAN). Findlator near Regina, *Morton NA 1822* (WAT). Ft Walsh Natl Historic Site, W Cypress Hills, *Ledingham 8944* (CAN). Humbolt, *Breitung 1164* (DAO, LL). S of Humbolt, *Breitung 1164* (DAO, GH). S of Indian Head, *Jones 465* (DAO). Katopwe, *Russell S3933* (DAO). Kisbey, *Hudson 3394* (DAO). L. Katopwa region, *de Vries 824* (DAO). Landing Prov. Pk, *Hainault 7150* (DAO). Langham, *Anderson 915* (DAO). E of Hanley, *Taylor s.n.* (DAO). E of Maple Cr., *Boivin 6646* (DAO). S of Maple Cr., *Semple & K.Shea 1943* (CAN, WAT). Moose Jaw, *Johnson 964* (NY), *Knowlton s.n.* (GH). S of Moose Jaw, *Hamilton s.n.* (DAO). E of Mortlach, *Hudson 2280* (DAO). E of Nipawin, *Rowe 389* (DAO). Nipawin, *Breitung 6057* (DAO). NE of Parkberg, *Coupland 143* (DAO), *Selleck 103* (DAO). Pike L., *Anderson s.n.* (CAN). Product P.O., Touchwood Hills, *Russell & Russell 3772* (DAO). Qu'Appelle Valley, *Shevkenek 82* (DAO). Qu'Appelle Valley, *Calvert s.n.* (WAT). Quill L., *Breitung s.n.* (DAO), *Breitung 1633* (DAO, GH). Regina, *Carmichael 1090* (DAO). Saskatchewan Landing, *Russell S58097* (DAO). Saskatoon, *Frankton & Bibbey 400* (DAO), *Fraser s.n.* (DAO), *Fraser s.n.* (WIS). SW of Saskatoon, *Coupland 190* (DAO). Shevlin, *Rowe 886* (DAO). Swift Current, *Breitung 5791* (DAO, RM). Touchwood Hills, Punnichy, *Russell 3837* (DAO). Webb S.C.C.P., *Buchanan s.n.* (UBC). N of White City, *Bere 58* (WIS). U.S.A. "Long's 1st Expedition", *James s.n.* (NY ex Columbia U.). "N.W. Territory," *Dr. Houghton* (WIS). COLORADO. *Johnson 489* (RM). "Rocky Mountains," *Hall & Harbour* (PH). Arapahoe Co.: Denver, *Eastwood s.n.* (DS). Costillo Co.: W of La Veta Pass, *Harms 2046* (KANU, SASK). Las Animas Co.: Stonewall, *Beckwith 229* (CAN), *Beckwith 231* (DS). IDAHO. Franklin Co.: SE of Cleveland, *Baker 9532* (NY(3), WTU(3)). Idaho Co.: 2 mi. S of Pollock, *Baker 11975* (WTU). Riggins, *Christ 8500* (NY). Kootenai Co.: *Sandberg s.n.* (WTU). Nez Perce Co.: Clear Water, *Ridout s.n.* (WS), *Spalding s.n.* (NY). Lewiston, *Christ 4260* (NY). KANSAS. Sherman Co.: Goodland, 10.0 mi S, *McGregor 15223* (KANU). MICHIGAN. Schoolcraft Co.: along Soo R.R. *Henson 1469* (WIS). MINNESOTA. *Aiton s.n.* (MIN). Lake Brenton, *Sheldon s.n.* (MIN, NY). Winnipeg Junction, *Lloyd s.n.* (NY). Anoka Co.: Allison Savanna, *Heitlinger 724* (MIN), *Heitlinger 753* (MIN). Bethel Twp., *Wertman 234* (MIN). Fridley, *Smith 1109* (MIN). W of Fish L., *Archer & Bray 25136* (MIN). N of Minneapolis, *Lakela 1174* (MIN). Moore Lake, *Rosendahl 3617* (MIN), *Rydberg 9657* (NY). Big Stone Co.: S of Ortonville, *Johnson 402* (GH, NY, WTU), *Moore 13178* (MIN, UC). SE of Ortonville, *Nietering 210* (MIN). , *Wheeler 4364* (MIN). Clay Co.: E of Barnesville, *Moore 22682* (MIN). Buffalo River S.P., *Forster 81* (KANU), *Forster 188* (KANU), *Moore 22602* (MIN), *Smith 1411* (MIN). E of Moorehead, Bluestem Prairie, *Severson 360* (MIN). SE of Felton, *Ottoson 51* (MIN). Dakota Co.: 2 mi SE Hastings., *Smith 1346* (MIN). Douglas Co.: Lake Christina Prairie (NW corner of county), *Sperling 279* (MIN). Hennepin Co.: *T.H.B. 55* (WTU). Minneapolis, *Herrick s.n.* (MIN), *Kassube s.n.* (MIN). , *Sandberg s.n.* (POM). St. Anthony, *Houghton 540* (NY), *Shuette s.n.* (GH). Kandiyohi Co.: S of Sibley S.P., *Clemants 1466* (MIN). Spicer, *Frost s.n.* (RM), *Frost 376* (MIN). W of Spicer, *Richter s.n.* (MIN). Kittson Co.: NE of Halma, *Smith 6824* (MIN). NW of Halma, *Moore & Heig 24113* (MIN). Norway Dunes, *Boe 1968* (MIN). Lac Qui Parle Co.: E of Nassau, *Smith 1273* (MIN). Lincoln Co.: E of Verdi, *Moore & Moore 10545* (MIN, TEX). Mahanomen Co.: S of Syre, *Green 366* (WIS). Nobles Co.: Adrian, *Carr s.n.* (GH). Norman Co.: N of Flom, Frenchman's Bluff, *Farrell 65* (MIN), *Stevens & Johnson 2429* (MIN). Lockhart, *Moore 22924* (KANU, MIN). E of Syre, *Churchill 6409* (KANU). ENE of Syre, *Thorne 30694* (RSA). Twin Valley Prairie, *Herman 183* (MIN). Ottertail Co.: Pelican L., *Sheldon 3805* (MIN). Polk Co.: SE of Crookston, Pankratz Prairie North, *Farrell 136* (MIN). S of Fertile, *Churchill 6416* (KANU), *Green 367* (WIS). W of Fertile, *Ownbey 4665a* (MIN). E of Harold, *Schmidt & Severson 334* (MIN). St. Louis Co.: Ely, *Jones 18729* (NY). Scott Co.: 0.2 mi W of Hwy-13, 0.5 mi S of Hwy-101, *Smith 1787* (MIN). Sherburne Co.: Co.Rd-1 NNW of Elk R., *Smith 4721* (MIN). Stearns Co.: East St. Cloud, *Campbell s.n.* (MIN, NY(2)). Ely, *Lakela 9307* (MIN). Washington Co.: N of Afton, *Ownbey 4354* (MIN). 1 mi S of Hwy-61, S of Co.-Rd-19 at Hwy-61, *Lindayen 189* (MIN). MONTANA. Carbon Co.: Beartooth N.F., *Baum 20622* (USFS), *Lockhart 623* (USFS). Daniels Co.: E of Flaxville, *Stephens 67854* (KANU). Dawson Co.: NW of Glendive, *Stephens & Brooks 23514* (KANU). Deerlodge Co.: *Fleming 66* (USFS). Fergus Co.: W of Lewistown, *Stephens 68812* (KANU). Gallatin Co.: Bozeman, *Cull s.n.* (WIS). S of Gallitan Gateway, *Schreiber 1284* (DS, UC). Garfield Co.: NW of Jordan, *Woodland 1204* (DS). Glacier N.P.: Many Glacier, *McLaughlin 3285* (WIS). Jefferson Co.: Deerlodge N.F., Kilborn Gulch, *Park 24* (USFS). Lewis & Clark Co.: N of Silver City, *Hitchcock 17933* (RSA, UC, WS, WTU). Missoula Co.: Lusk, *Render s.n.* (WIS). Powell Co.: Deer Lodge Valley, *Jones s.n.* (POM). W of Deer lodge, *Semple & K.Semple 2015* (WAT). Roosevelt Co.: S of Bainville, *Lackschewitz 9288* (RM). Stillwater Co.: Absarokee, *Hawkins s.n.* (WIS). Beehive, *Hawkins s.n.* (WIS). Valley Co.: NW of Glasgow, *Stephens 68138* (KANU). NEBRASKA. Blaine Co.: E of Brewster Valley, *Stephens & Brooks 24374* (KANU). W of Dunning, *Stephens 28212* (KANU). Boone Co.: S of Petersburg, *Stephens & Brooks 11822* (KANU). Box Butte Co.: N of Alliance, *Harms 18501* (KANU, SASK), *Stephens & Brooks 24506* (KANU). Brown Co.: S of Ainsworth, *Stephens & Brooks 24406* (KANU), *Stephens 29383* (KANU). Cherry Co.: W of Merriman, *Stephens & Brooks 17050* (KANU). E of Nenzel, *Barker 3398* (KANU). S of Valentine, *Stephens 36910* (KANU). Cheyenne Co.: Sidney, *Nelson 9276* (RM, UC).

NE of Sunol, *Stephens & Brooks 16049* (KANU). Dawes Co.: S of Chadron, *Stephens & Brooks 16987* (KANU). Garden Co.: SSE of Broadwater, *Harms 18500-A* (KANU, SASK). SW of Goose Lake, *Richardson & Robertson 1778* (KANU). N of Oshkosh, *Stephens & Brooks 41257* (KANU). Garfield Co.: E of Burwell, *Stephens & Brooks 24314* (KANU), *Stephens 48698* (KANU). Greeley Co.: N of Greeley, *MacGregor 19347* (KANU). Greeley Co.: SW of Scotia, *Stephens 29390* (KANU). Hall Co.: SE of Wood River, *Stephens 48583* (KANU). Hamilton Co.: W of Hordville, *Stephens 18972* (KANU). NE of Marquette, *Stephens 60347* (KANU). Howard Co.: N of Dannebrog, *Stephens & Brooks 15757* (KANU). Kearney Co.: S of Minden, *Birkholz 2365* (KANU). Perkins Co.: N of Grant, *Stephens 45585* (KANU). Platte Co.: S of Columbus, *Stephens 49030* (KANU). Rock Co.: W of Newport, *McGregor & Bare 509* (KANU). Sheridan Co.: E of Ellsworth, *Semple & K.Semple 2263* (CAN, WAT). Sioux Co.: S of St. Agate, *Stephens & Brooks 16190* (KANU). Thomas Co.: W of Halsey, *Stephens & Brooks 25126* (KANU). SE of Thedford, *Stephens 28221* (KANU). Valley Co.: *Barker 2929* (KANU). N of Ord, *Barker 2912* (KANU). Wheeler Co.: N of Bartlett, *McGregor & Bare 466* (KANU). NW of Bartlett, *Stephens 62039* (KANU). **NORTH DAKOTA.** Grebs, *Lunell s.n.* (NY). Barnes Co.: S of Luverne, *Seiler 1854* (KANU). Valley City, *Bergman 1126* (UC), *Bolley s.n.* (RM), *Stevens s.n.* (DAO). Benson Co.: Devils Lake, *Lunell s.n.* (NY). Leeds, *Facey 109* (TEX), *Lunell s.n.* (GH), *Lunell s.n.* (MIN), *Lunell 3659* (GH). Pleasant Lake, *Lunell s.n.* (MIN). N of Warwick, *Seiler 1985* (KANU). Billings Co.: Roosevelt Nat. Mem., Medora, *Facey 149* (TEX). Burk Co.: SW of Sowbelle, *Stephens & Brooks 13106* (KANU). Cavalier Co.: N of Langdon, *Stephens 28903* (KANU). Dickey Co.: S of Monango, *Stephens 61426* (KANU). Divide Co.: W of Fortuna, *Harms 18512* (KANU, SASK). Dunn Co.: W of Dodge, *Larson 5370* (KANU). SW of Manning, *Rohde & Fulton 3614* (KANU). Eddy Co.: E of New Rockford, *Seiler 2548* (KANU). Foster Co.: SE of Carrington, *Stephens 61553* (KANU). Grant Co.: *Bell 1376* (UC(2)). Pretty Rock, *Bell 1239* (DAO, PH). Kidder Co.: E of Crystal Lake, *Hickey 14* (WIS). S of Pettibone, *Williams 1387* (KANU). W of Tuttle, *Stephens & Brooks 15055* (KANU). Logan Co.: S of Napoleon, *Stephens & Brooks 15111* (KANU). McKenzie Co.: SW of Keene, *Rohde & Fulton 3511* (KANU). Morton Co.: Mandan, *Lee s.n.* (WIS). Mountrail Co.: E of New Town, *Stephens 28710* (KANU). Nelson Co.: Stump L., *Tufte 186* (RM). Tolna, *Tufte 183* (RM), *Tufte 294* (RM). Nettinger Co.: W of Regent, *Stephens 50083* (KANU). Pembina Co.: W of Cavalier, *Seiler 1140* (KANU). Ramsey Co.: Devils L., *Palmer 36893* (GH), S of lake, *Stephens 29017* (KANU). Ransom Co.: E of Lisbon, *Stephens & Brooks 33484* (KANU), *Stephens 36657* (KANU). Roulette Co.: Dunseigh, *Bergman s.n.* (LL). Sheridan Co.: W of Pickardville, *Stephens 49698* (KANU). Slope Co.: NW of Amidon, *Stephens & Brooks 35878* (KANU). Marmarth, *Moyer 715* (MIN, NY). Stark Co.: Dickinson, *Kraus s.n.* (WIS). Stutsman Co.: Jamestown, *Sister St. Lawrence 514* (NY). Ward Co.: Black Butte, *Lautenschlager 583* (MIN). W of Des Lacs, *Stephens 49860* (KANU). N of Riverdale, *Carufel s.n.* (ASU). W of Minot, *Lautenschlager 790* (CAN, MIN). Williams Co.: S of Grenore, *Stephens & Brooks 13288* (KANU). W of Grenore, *Stephens & Brooks 13248* (KANU). Williston, *Bell 409* (NY) N of Williston, *Harms 18510* (KANU). **OREGON.** *Wilkes Expedition 534* (NY). Hood River Co.: Hood River, *Howell s.n.* (NY), *Howell s.n.* (WTU). Melamoose Pt., *Jepson 18490* (JEPS). Marion Co.: E of Independence, *Nelson 3261* (WS). W of Keizer, *Nelson 4613* (GH, PH). W of Orville, *Nelson 4399* (WS, WTU). Wasco Co.: E of Moster, *Brooks & Kuhn 20201* (KANU). Rowena Pt., *Johnston s.n.* (CAS). **SOUTH DAKOTA.** Baugor, *Griffiths & Schlossen s.n.* (GH). Black Hills N.F., *Pilcher 6007* (USFS); Bald Hills, *Murdoch 4300* (CAS, GH, NY); North Castle Cr., *Murdoch 4359* (CAN, CAS); Sylvan L., *Hayward 412* (NY). Medicine Cr., *Williams 137* (POM). Mud Root Cr, *Wallace s.n.* (RM). Bennett Co.: E of Martin, *Stephens 49385* (KANU). Buffalo Co.: W of Ft. Thompson, *Stephens 52234* (KANU). Campbell Co.: S of Mound City, *Semple et al. 6663* (WAT). Custer Co.: *Degener & Peiler 16273* (GH, NY). NW of Custer, *Stephens & Brooks 35336* (GH, KANU). NE of Dewey, *Stephens & Brooks 16538* (KANU). Harney N.F., *Gierisch 1539* (USFS). N of Hot Springs, *Harms 2141* (KANU, SASK). Piety Hill, *Ginter 65* (USFS). E of Prairie Dog Springs, *Marriott 9819* (RM). N of Pringle, *Stephens 28430* (KANU). S of Pringle, *Stephens & Brooks 13794* (KANU). Pringle Prairie Dog Town, *Painter 265* (ASU). Redbird Cyn., *Gould 22* (USFS). Stockade Lake, *Jones & Jones 14476* (NY). Wind Cave Cyn., *Degener 16609* (NY). Day Co.: Blue Dog L., *Harms 2880* (KANU). Enemy Swim L, *Thorne 19700* (RSA). Day Co.: SE of Haubay, *Monserud 872* (MIN). Fall River Co.: E of Edgemont, *Hayward 2505* (RM). NE of Edgemont, *Stephens & Brooks 16499* (KANU). Hot Springs, *Hayward 505* (NY). S of Hot Springs, *Stephens 28398* (KANU). Gregory Co.: N of Gregory, *Stephens & Brooks 34058* (KANU). Haackson Co.: N of Kirley, *Stephens & Brooks 33888* (KANU). Harding Co.: *Visher 352* (RM). N of Buffalo, *Stephens 7894* (KANU). Lawrence Co.: Black Hills N.F., *Anderson 30* (USFS, TEX). SW of Cheyenne Crossing, *Stephens & Brooks 16844* (KANU). W of Nahant, *Stephens & Brooks 35906* (KANU). Spearfish Cyn., *Hayward 193* (RM). Lyman Co.: 38 mi W of Lower Brule, *Barker 3136* (KANU). Marshall Co.: Piyas Lake, *Harms 2943* (KANU). McPherson Co.: E of Eureka, *Stephens & Brooks 15199* (KANU). Meade Co.: Faith, *Moyer 153* (RM). Minnehaha Co.: *Duncan s.n.* (MIN). Pennington Co.: N of Deerfield, *Stephens & Brooks 35561* (KANU); NE of town, *McIntosh 846* (RM), *Stephens & Brooks 16741* (KANU), *Stephens 28497* (KANU); NW of town, *Stephens & Brooks 35950* (KANU); SE of town, *Stephens & Brooks 35449* (KANU), *Stephens & Brooks 41772* (KANU). E of Hill City, *Stephens & Brooks 16630* (KANU); NE of city, *Stephens & Brooks 35247* (KANU), *Stephens & Brooks 41629* (KANU); SW of city, *Stephens & Brooks 7261* (KANU), *Stephens 7272* (KANU), *Stephens & Brooks 35277* (KANU). Prairie Cr, *Lee 457* (RM), *Lee 484* (RM). S of Rapid City, *Harms 18505* (KANU). W of Rockford, *Stephens & Brooks 35636* (KANU). SW of Wall, *Stephens 7028* (KANU). Perkins Co.: SE of Bison, *Stephens 8000* (KANU). Custer N.F., *Harris & Lockhart 75* (USFS). S of Lodgepole, *Stephens 45369* (KANU). Stanley Co.: SE of Fort Pierre, *Stephens & Brooks 33967* (KANU). Todd Co.: E of Okreek, *Stephens & Brooks 34165* (KANU). **WASHINGTON.** Asotin Co.: Asotin, *Eastwood & Howell 3206* (CAS). S of Asotin, *Hichcock & Muhlick 8337* (NY, WTU). Benton Co.: Hanford Works, *Baird 997* (BRY, NY). East Prosser, *Smith s.n.* (WS). Chelan Co.: Menachee, *Whited 7* (WS). Garfield Co.: Iliia, *St. John, English, Jones, & Palmer 9231* (LL, WS). Kittitas Co.: Ellensburg, *Whited 575* (WS). N of Vantage, *Ogilvie s.n.* (UBC). Okanogan Co.: Oroville, *Jones s.n.* (POM). Pend Oreille Co.: Pend d'Oreille R., *Kreuger 397* (UC). Whitman Co.: Snake R. Cyn., *Bottorf & Lindon 11* (WS); opposite Clarkston, *Clarke s.n.* (WTU). Wawawai, *Elmer 1017A* (MIN), *Piper s.n.* (NY), *St. John 6727* (WS). Yakima Co.: Naches R. E of Naches, *Hoover 6001* (CAS, OBI). Yakima, *Jones 1792* (WTU). North Yakima, *Piper s.n.* (NY), *Watt s.n.* (WS). **WYOMING.** Albany Co.: W of Eagle Rock, *Aslamy 112* (RM). Happy Jack Area, *Crawford 213* (SASK). E of Laramie, *Lepper 52* (WIS).

W of Laramie, *Denniston s.n.* (WIS). Sherman and Buford, *Macbride 2552* (RM). Strouss Hill Deer Area, *Goodwin s.n.* (RM). Tie Siding *Osterhout 5528* (RM(2)). S of Tie Siding, *Osterhout 5683* (NY, RM). Big Horn Co.: *Nelson 3415* (RM). Campbell Co.: *Sanguinetti & Dueholm 385* (RM). Black Thunder Strip Mining Area, *Ries & Sabinske 57* (RM). NNE of Gillette, *Nelson 2182* (BRY). NNW of Gillette, *Dueholm & Sanguinetti 3728* (RM). S of Gillette, *Stephens 78874* (KANU). SW of Gillette, *Saulea & Saulea 6247* (WAT). NNW of Hilight, *Dueholm & Sanguinetti 4404* (KANU, RM). SE of Montana, *Dueholm, Hartman & Sanguinetti 2665* (RM). W of Pine Tree, *Dueholm & Sanguinetti 4187* (RM). N of Recluse, *Dueholm & Sanguinetti 3816* (RM). NW of Weston, Horse Creek Ranch, *Dueholm & Sanguinetti 3524* (RM). Carbon Co.: Arlington Snow Fence 271.3, *Goodwin s.n.* (USFS). N of Medicine Bow, *Stephens 70394* (KANU). Sierra Madre Mts., *Mastrella 138* (RM). Converse Co.: *Sanguinetti & Dueholm 8* (RM), *Sanguinetti & Dueholm 58* (RM). Douglas, *Pfadt s.n.* (RM). Crook Co.: SE of Hawk Springs, *Nelson 2529* (RM). NW of Hulett, *Ownby 479* (RM). NW of Inyan Kara Mt, *Hartman 18281* (BRY), *Marriott 9196* (NY). NW of Moorcroft, *Rosbach 5708* (UC). Johnson Co.: *Hartman & Sanguinetti 7399* (KANU). Laramie Co.: WSW of Albin, *Nelson 2317* (RM). Cheyenne *Davis s.n.* (RM), *Nelson 2718* (GH, NY, RM). NE of Cheyenne, *Hammel 745* (RM). NW of Cheyenne, *Current 187* (RM). Otto, *Edwards s.n.* (NY). E of Pine Bluffs, *Lepper s.n.* (WIS). Park Co.: Yellowstone N.P., Mammoth Hot Springs, *Oleson 101* (RM); West Thumb, *Payson & Payson 3093* (RM). Platte Co.: Hartville, *Nelson 533* (GH, MIN, NY, RM). Sheridan Co.: hills E of Sheridan *Sharp 134* (RM). Weston Co.: Boyd, *Nelson 9469* (GH, MIN, RM). Horton, *Nelson 9512* (RM). E of Newcastle, *Marriott 8068* (KANU). W of Upton, *Dueholm 4742* (NY, RM).

aff. var. villosa

U.S.A. IDAHO. Casper, *Render s.n.* (WIS). MINNESOTA. Chippewa & Swift Co.: Chippewa Prairie, *Converse 1076* (MIN). Pope Co.: Ordway Prairie, *Converse 1594* (MIN). WASHINGTON. Klickitat Co.: Bingen, *Jones 2427* (WTU).

aff. var. villosa (approaching var. *ballardii* or mixed collection of both varieties)

CANADA. MANITOBA. Indian Res. 2A, *Löve & Löve 5917* (DAO, GH). U.S.A. MINNESOTA. Hubbard Co.: near Badoura, *Mayle 1302* (MIN, NY, PH, UC, WIS). Pope Co.: E of Glennwood, *Jacobs 14648* (MIN, NY, WS). NEBRASKA. Sioux Co.: E of Agate, *Stephens & Brook 24721* (KANU). NORTH DAKOTA. Benson Co.: Butte, *Lunell s.n.* (NY, UC). Kidder Co.: N of Steele, *Keil 17699* (OBI). McKenzie Co.: NE of Watford City, *Rohde 1338* (KANU). Pierce Co.: SE of Orrin, *Stephens & Brooks 14997* (KANU). Stark Co.: Dickinson, *Holgate s.n.* (GH, NY). SOUTH DAKOTA. Fall River Co.: Erskine, Hot Springs, *McIntosh 503* (RM).

aff. var. villosa (approaching var. *foliosa* or mixed collection of both varieties)

CANADA. ALBERTA. Waterdon Lakes Pk, gravel flats of Blakiston Branch, *Moss 667* (DAO, GH, NY, WIS). U.S.A. IDAHO. Franklin Co.: NE Preston, *Bright 61-46* (MIN, RM). ILLINOIS. Carroll Co.: S of Savanna, *Hermann 8867* (F, NDG, NY). MONTANA. Roosevelt Co.: 2 mi N of Culbertson, *anon.* (KANU). OREGON. Franklin Co.: Fish Hook Ferry, *Leiberg 931* (GH, NY, UC). SOUTH DAKOTA. Custer Co.: Custer, *Rydberg 758* (NY(2)). Fall River Co.: NE of Edgemont, *Harms 2135* (KANU, SASK). Pennington Co.: N of Deerfield Lake Dam, *Stephens & Brooks 16769* (KANU). S of Rapid City, *Harms 18504* (KANU, SASK). WASHINGTON. Chelan Co.: Columbia R at Entiat, *Thompson 6899* (DS, GH, LL, WTU). Kittitas Co.: E of Ginkgo Petrified Forest St.Pk., *Smith 1243* (DS, WTU), *Smith 2003* (DS, WS). Klickitat Co.: Columbia R., *Suksdorf s.n.* (CAN, DS, PH). WYOMING. Campbell Co.: N of Adon, *Hartman & Dueholm & Sanguinetti 6901* (MIN, RM). S of Little Powder R., *Dueholm & Sanguinetti 3475* (KANU, RM). Crook Co.: S of Devil's Tower, *Stephens 7637* (KANU). Goshen Co.: N of Jay Em, *Harms 2127* (KANU, SASK, WAT). S of Jay Em, *Harms 2126* (KANU, SASK(2), WAT).

aff. var. villosa (approaching var. *minor* or mixed collection of both varieties)

CANADA. SASKATCHEWAN. W of Delmas, *Harms 17066* (KANU(2), SASK(2)). Qu'Appelle R Valley, *Shchepanek & Dugal 4952* (CAN). U.S.A. IDAHO. Idaho Co.: below Kooskia, *Constance & Rollins 1697* (LL, WTU). Nez Perce Co.: Clear Water, *Spalding s.n.* (GH). MONTANA. Meagher Co.: NW of White Sulphur Springs, *Hitchcock & Muhlick 12202* (NY, WS, WTU). Silver Bow Co.: Pipestone Pass, *Brenckle & Shinnars 41-052* (WIS). OREGON. Marion Co.: 2 mi W of Keizer, *Nelson 4613* (GH, PH). WASHINGTON. Stevens Co.: near Colville, *Lyll s.n.* (GH). WYOMING. Albany Co.: W of Laramie, *Brenckle, Solheim & Shinnars s.n.* (WIS).

aff. var. villosa (approaching *H. stenophylla* var. *angustifolia*)

U.S.A. NEBRASKA. Antelope Co.: Neligh, *Harper s.n.* (WIS). Thomas Co.: E of Thedford, *Semple & K.Shea 2268* (CAN, WAT). SOUTH DAKOTA. Harding Co.: S of Camp Creek, *Stephens 7851* (KANU).

aff. var. villosa (approaching *H. stenophylla* var. *stenophylla*)

U.S.A. IOWA. Lyon Co.: Gitchie Manitou S.P., *Shimek s.n.* (UC). NEBRASKA. Saunders Co.: Meadville, *Clements 2954* (MIN, NY, UC).

17.2 *Heterotheca villosa* (Pursh) Shinnars var. *ballardii* (Rydb.) Semple, Novon 4: 53. 1994.

Chrysopsis ballardii Rydb., Brittonia 1: 100. 1931. TYPE: U.S.A. MINNESOTA. Carver Co.: Chaska, Jul 1891, *Ballard 640* (Holotype: MIN!)

STEMS several to many, ascending-erect, (22)-27-34-42-(50) cm tall, moderately to densely hispid-strigose, long hispid hairs few to numerous; (16)-19-23-27-(32) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (26)-29-37-45-(57) mm long, (5.3)-6.2-8.2-10.2-(11) mm wide, petiolate, cuneate, sometimes slightly mucronate, moderately to densely hispid-strigose and eglandular on both surfaces; margins entire, strigose, longer hispid hairs along margins basally. UPPER STEM LEAVES oblong, (18)-22-28-34-(42) mm long, (4.3)-5-7.1-9.3-(12.5) mm wide, sessile, little reduced upward, broadly acute to obtuse, indument

similar to lower, (19)-28-**42**-56-(70) hairs/mm², margins flat, a few longer hispid hairs along margins basally. CAPITULESCENCE congested to open cymose-corymbiform, heads (2)-4-**10**-16-(24); peduncles moderately to densely hispid-canescens, eglandular, (9)-16.5-**28**-41-(52) mm long; bracts few, linear-oblong, usually reduced, often foliar, indument like leaves. INVOLUCRES campanulate when fresh, campanulate-hemispheric upon drying, (5.5)-6.5-**7.5**-8.5-(9.3) mm high; phyllaries in 4-5 imbricate series, outer ones about 1/4 the length of the inner ones, narrowly triangular-lanceolate, moderately to densely strigose, eglandular to very sparsely glandular, margins hyaline narrow, fimbriate-ciliate and often anthocyanotic apically; inner ones similar. RAY FLORETS (12)-17-**21**-26-(30), strap yellow, (8.5)-9.9-**11.5**-13.2-(14.5) mm long, 1-**1.5**-1.9-(2.8) mm wide, tube glabrate. DISC FLORETS (18)-22-**31**-40-(43), yellow, glabrous or a few minute hairs, corolla barely ampliate, (4.2)-4.9-**5.7**-6.4-(7.2) mm long, lobes (0.5)-0.6-**0.7**-0.75 mm long, hairs absent or few, 0.1-**0.12**-0.25 mm long. ACHENES 1.5-**2.1**-2.6-(3) mm long, sparsely to moderately strigose; pappus off-white, double, outer whorl of linear scales 0.25-1 mm long, inner whorl of 35-45 barbellate bristle (4.7)-5.3-**6.2**-7.1-(8.1) mm long. Chromosome numbers $2n = 36$; many reports.

Flowering Period: (June)-JULY-AUGUST-(October).

Distribution: Northern Great Plains from Alberta to Manitoba and south to Nebraska and Minnesota, probably introduced in northwestern Ontario (Fig. 39D); prairies, fields, roadsides, railroad rights-of-way; dry sandy clay and gravel soils, dry rocky granite gravel soils, thin silt loam or sandy loam soils; 330-2300 m (1100-4500 ft.) elevation.

Discussion: Variety *ballardii* is distinguished by the combination of its rounded leaf bases, its indument of short hairs and no glands, and large many-rayed heads often subtended by one or more large narrow foliar peduncular bracts (Fig. 42). Narrower leaved specimens are difficult to distinguish from var. *villosa* (Fig. 41). The collections listed below as "aff. var. *ballardii*" undoubtedly include hybrids and backcrosses involving var. *villosa* as well as specimens that are only phenotypically close to var. *villosa*. 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*. In its typical larger-leaved and many-rayed form, var. *ballardii* is quite distinct. Harms (1963) ultimately opted not to recognize the variety and placed its members in his var. *villosa*, although based on annotation label data, he had considered accepting varietal status. After some hesitation, I chose to recognise that taxon in order to include in the nomenclature acknowledgement of the existence of a northeastern prairie race of the species that would otherwise remain buried in synonymy. If the diagnostic rounded leaf bases character is viewed as insufficient grounds for recognizing the taxon, then the same position becomes logical in merging var. *foliosa* into var. *villosa*, and var. *nana*, and var. *scabra* into var. *minor*. It then would be logical to merge all other varieties together with no infraspecific taxa being recognized in *H. villosa*. 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. Splitting seems justifiable in this case, and it maintains a nomenclature that parallels what has been adopted with less hesitation for other species in the the section.

Specimens examined: CANADA. ALBERTA. SW of Dorion P.O., *Garton 18348* (CAN). W of Ft. Saskatchewan, *Turner 5811* (DAO). Near Red Deer, *Nelson & Nelson 4765* (RM). MANITOBA. Birtle, *Scoggan 10222* (CAN, MIN). Brandon, *Macoun 5018* (CAN, GH), *Macoun 12166* (CAN, NY), , *Baldwin & MacPherson 10789* (WAT). N Brandon, *Hermann 13562* (CAN). 1 mi S of Morden, *Marshall 8* (DAO, NY). 2 mi NW of Pilot Mt., *Alex 102* (DAO). Coulter, SW corner of Man, *Scoggan 9828* (CAN). S of Delta, *Mosquin s.n.* (DAO). Dropmore, *Scoggan 10338* (CAN). Macgregor, *Scoggan 9649* (CAN). Melita, *Wallace s.n.* (DAO). N of Minto, *Scoggan 9747* (CAN). Morden, S of Exp. Station, *Frankton 1005* (DAO). Portage la Prairie, *Denike 1342* (DAO), *Kraclewing (?) s.n.* (NY). S of Portage-la-Prairie, *Keleher 395* (CAN, DAO). Sidney, *Scoggan 9667* (CAN, GH). E of Sidney, *Rosbach 85* (DAO). NW of Snowflake, *Alex 92* (DAO). Souris, below along Souris R., *Garton 15548* (CAN, UC). Turtle Mt. Depot, *Dawson s.n.* (GH). Virden, *Krivda V307* (DS). Wawanessa, *Scoggan 11413* (CAN, GH). Dirt rd parallel to MB-1 at MB-242, *Semple & Brouillet 4171* (CAN, WAT). Whitewater Lake, *Bossenmeier 170* (MIN). ONTARIO. W of Thunder Bay, *Garton 19550* (CAN). Sioux Lookout, *Baldwin 9561* (CAN).

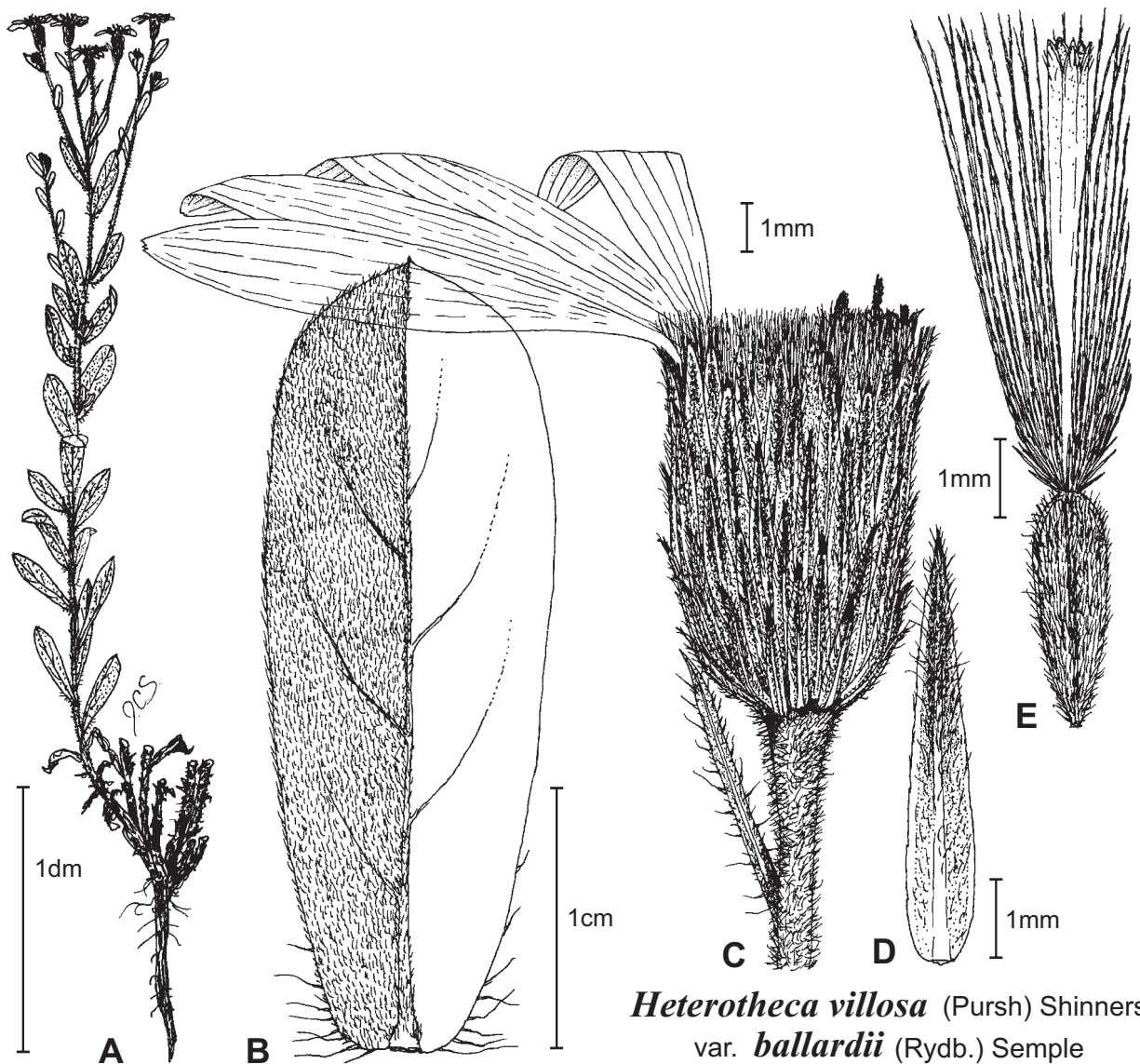


Figure 42. Morphology of *Heterotheca villosa* var. *ballardii*. A. Habit. B. Mid stem leaf, hairs shown only on left side. C. Head with only some florets drawn. D. Mid series phyllary with chlorophyllous zone dark. E. Mature achene with disc corolla attached.

SASKATCHEWAN. SW of McKague, *Breitung* 371 (CAN, DAO, NY, UC). Cypress Hills, *Anderson s.n.* (CAN). Douglas Prov. Pk., *Gray* 1816 (CAN). Deer Cr Bridge, Hwy-3 on N Saskatchewan R, *Wise* 388 (DAO). NW of Hoosier, *Jenkins* 951 (DAO). Indian Head, *Malte s.n.* (CAN). Macdowall, *Hudson* 2116 (DAO). McKague, *Breitung s.n.* (DAO, UBC). SW of McKague, *Breitung* 371 (CAN, DAO, NY, UC). Yorkton, *Shaw* 145 (DAO). **U.S.A. KANSAS.** Clark Co.: prairie, *McGregor* 40026 (KANU(2)). **MINNESOTA.** Ft. Snelling Reservation, *Rosendahl* 2181 (MIN). Chisago Co.: Amador, *Taylor s.n.* (NY), *Taylor* 1596 (MIN). Crow Wing Co.: Brainerd, *Sheldon et al.* 46 (MIN). Hennepin Co., *Hapeman s.n.* (RM), *Sandberg s.n.* (PH). E of Bethel, Cedar Bog Cr., *Malone* 35 (MIN). Minneapolis, *Oestlund s.n.* (MIN). Kittson Co.: W of Two Rivers St.P., *Johnson* 593 (NY). Lac Qui Parle Co.: SW of Dawson, Antelope Hills, *Smith* 5069 (MIN). E of Nassau, *Wheeler* 4725 (MIN). Murray Co.: *Holzinger s.n.* (MIN, NY). Norman Co.: NE of Sayre, *Hamilton* 286 (ASU). Norman Co.: NW of Flom, *Moore* 22650 (MIN). Ottertail Co.: Battle L., *Sheldon s.n.* (GH). Michdale, *Chandonnet s.n.* (GH, PH, RM). Polk Co.: W of Fertile, *Moore* 15556 (MIN, TEX). St. Louis Co.: Duluth, *Lakela* 2775 (GH, MIN). Stearns Co.: Saux Centre, *Blanchard s.n.* (GH, NY). Washington Co.: Stillwater, *Holzinger* 2047 (CAS). **MONTANA.** Hill Co.: W of Havre, *Stephens* 68453 (KANU). Chouteau Co.: W of

Ft. Benton, *Harms 19144* (KANU, SASK). **NORTH DAKOTA.** Benson Co.: Leeds, *Lunell s.n.* (MIN, RM), *Lunell 1042* (MIN). Cass Co.: Kindred, *Solhiem s.n.* (RM), *Solheim 250* (RM). Emmons Co.: N of Linton, *Stephens 61626* (KANU). Golden Valley Co.: S of Sentinel Butte, *Semple & K. Semple 2028* (WAT). Grand Forks Co.: *Semple & Brammall 2681* (WAT). N of Larimore, *Stephens & Brooks 14654* (KANU). Grant Co.: Pretty Rock, *Bell 1165* (RM). McHenry Co.: N of Towner, *Boivin & Dore 8157* (DAO). Mercer Co.: E of Pick City, *Stephens & Brooks 12607* (KANU). Morton Co.: *Bell 1137* (WIS). W of Bismarck, *Semple & K. Shea 2029* (WAT). Mandan, *Sarvis s.n.* (LL). Pembina Co.: W of Cavalier, *Seiler 1010* (ASU), *Willenbring 279* (KANU). S of Walhalla, *Semple & Brammall 2680* (JCS, WAT). W of Walhalla, *Stephens 28969* (KANU). Ramsey Co.: S of Devils Lake, *Stephens & Brooks 14856* (KANU). Montpelier, *Bergman s.n.* (MIN, NY). Ransom Co.: S of Ft. Ransom, *Stephens 36550* (KANU). E of Lisbon N. Grassland, *Stephens 90810* (KANU). McLeod, *Bell 328* (RM). Richland Co.: N of Wyndmere, *Stephens & Brooks 14585* (KANU). Sargent Co.: W of Brampton, *Seiler 2331* (KANU), *Seiler 3492* (KANU). W of Genesco, *Semple & Brammall 2691* (WAT). Sioux Co.: SE of Salfridge, *Stephens 29180* (KANU). Slope Co.: SW of Amidon, *Stephens 28565* (KANU). Marmarth, *Moyer 712* (MIN, NY). Stark Co.: Dickinson, *Holgate s.n.* (CAS). Steele Co.: NE of Finley, *Stephens 45150* (KANU). William Co.: W of Williston, *Harms 18509* (KANU(2), SASK). **NEBRASKA.** Cherry Co.: 22 mi W of Merriman, *Barker 3359* (KANU). Greeley Co.: Tribune, *Reed s.n.* (UC). Hooker Co.: E of Mullen, *Stephens 28252* (KANU). Kearney Co.: Minden, *Hapeman 892* (GH). Keya Paha Co.: NW of Norden, *Stephens & Brooks 34281* (KANU). Scotts Bluff Co.: Wildcat Hills Rec. Area, *Richardson & Robertson 1510* (KANU). Sheridan Co.: N of Hay Springs, *Nixon 225* (RM). Sioux Co.: *Kramer 105* (RM). S of Agate, *Stephens 45489* (KANU). Stanton Co.: S of Pilger, *Stephens & Brooks 14117* (KANU). Thomas Co.: E of Mullen, *Jones s.n.* (WIS). **SOUTH DAKOTA.** *Black s.n.* (NY). Brown Co.: W of Hecla, *Stephens 51685* (KANU). Custer Co.: Sylvan Lake, *English s.n.* (WIS). Faulk Co.: E of Faulkton, *Stephens 61310* (KANU). Harding Co.: SE of Buffalo, *Stephens 36852* (KANU). Lawrence Co.: SW of Cheyenne Crossing, *Stephens 7377* (KANU). Deadwood, *Carr 169* (CAN, GH), *Rydberg 169* (MIN, WIS). Meade Co.: Sturgis, *Hayward 2617* (RM). Roberts Co.: Big Stone Lake, *Ailts 266* (ASU). SE of Wilmot, *Stephens & Brooks 14399* (KANU). Spink Co.: Redfield, *Ricksecker 62* (MIN, POM, UC). N of Tulare, *Semple & Brammall 2692* (WAT). Tripp Co.: S of Colome, *Stephens 29276* (KANU). **WISCONSIN.** St. Croix Co.: S of Hudson, *Fassett 16939* (GH). St. Croix *Hale s.n.* (GH, NY). **WYOMING.** Converse Co.: SW of Douglas, *Stephens & Brooks 23981* (KANU).

var. *ballardii* (generally narrower leaved forms close to var. *villosa*)

CANADA. MANITOBA. NE of Birtle, *Scoggan 11274* (CAN). Brandon, *Guisso 939* (DAO), *Malte s.n.* (CAN). Carberry, *Baldwin & MacPherson 10768* (CAN, WAT). Delta, *Löve 5204* (DAO). Indian Res. 2A, *Löve & Löve 5953* (DAO, GH), *Löve & Löve 5917* (DAO, GH). Lauder, *Scoggan 9967* (CAN). Morden, *Groh s.n.* (DAO). Neepawa Twp., *Bassett & Kemp 3782* (DAO). Rock L., *Groh s.n.* (DAO). Sidney, *Gordon s.n.* (DAO). **NORTHWEST TERRITORIES.** Moose Mts., *Macoun s.n.* (GH). **SASKATCHEWAN.** Battleford *Robbins s.n.* (DAO). Devils L (Good Spirit L), *Shaw 75* (DAO). Ft. Qu'Appelle, *de Vries 490* (DAO). Ganora, *Shaw 73* (DAO). NW of Glen Kerr, *Coupland 158* (DAO). SE of Kyle, *Skoglund 169* (CAN, DAO, GH). Moose Jaw, *Groh 150* (DAO). Porcupine Hills, 1525 m, *McGillis 53* (DAO). N of Prince Albert, *Macoun 12215* (CAN). Sifton, *Clokey 1833* (UC). Theodore, *Shevkenek s.n.* (DAO). **U.S.A. MINNESOTA.** Benton Co.: SE of Rice, *Dorio 144* (MIN). Dakota Co.: SE of Hastings, *Smith 1354* (MIN). Hennepin Co.: *Sandberg 5062* (GH, MIN). Near Minneapolis, *Aiton s.n.* (WIS). Pope Co.: *Moyer s.n.* (MIN). Glenwood, *MacMillan 7* (MIN), *MacMillan 5887* (NY, WIS). Stearns Co.: Sauk Center, Sauk R., *Moore 15642* (MIN). Travers Co.: S of Boisberg, *Moore & Moore 10476* (UC, MIN, NY). **NEBRASKA.** Box Butte Co.: S of Chadron, *Harms 18502* (KANU, SASK). Chase Co.: E of Enders, *McGregor 18852* (KANU). Cherry Co.: W of Nenzel, *Barker 3386* (KANU). Dawes Co.: S of Chadron, *Stephens 28352* (KANU). Franklin Co.: N of Franklin, *Bare & McGregor 1721* (KANU). Garden Co.: SE of Lewellen, *Harms 18498* (KANU, SASK). Hooker Co.: W of Mullen, *Stephens & Brooks 17171* (KANU). Kearney Co.: Minden, *Hapeman s.n.* (RM). Sioux Co.: S of Agate, *Stephens & Brooks 16130* (KANU). S of Harrison, *Stephens & Brooks 24690* (KANU). Thomas Co.: S of Thedford, *McGregor 19644* (KANU). **NORTH DAKOTA.** Benson Co.: Butte, *Lunell s.n.* (NY(3)), *Lunell s.n.* (MIN, RM). Billings Co.: Roosevelt N. Mem. P., *Harms 18507* (KANU, SASK). Bowman Co.: W of Rhame, *Stephens 90060* (KANU). Emmons Co.: SW of Strasburg, *Williams 663* (KANU). McKenzie Co.: S of Watford City, *Harms 18508* (KANU, SASK). Morton Co.: *Bell 1165 A* (MIN, WIS). Pembina Co.: SW of Cavalier, *Larson 2383* (KANU). Crystal Springs, *Harms 6351* (KANU, SASK). N of Mountain, near Tongue R., *Stephens & Brooks 14771* (KANU). Pierce Co.: Rugby, *Bergman 2590* (MIN, NY). Ramsey Co.: Devils L. *Tufte 184* (RM). S of Devils L., *Bartlett & Grayson 354* (NY). Stutsman Co.: NE of Jamestown, *Stephens 61519* (KANU). Ward Co.: E of Berthold, *Stephens 28768* (KANU). Kenmare, *Bergman 2704* (MIN). **SOUTH DAKOTA.** Little White River, *Wallace 86* (NY). Lower White R, *Williams 86* (CAS, GH). Medicine Creek, *Wallace s.n.* (NY). Missouri R. bottoms, *Moyer 3656* (MIN). Brookings Co.: Brookings, *Carter s.n.* (NY). S of Lake Poinsett, *Barker 2682* (KANU). Butte Co.: Belle Fourche, *Hayward 41* (RM). Carson Co.: NW of Wakpala, *Stephens 29166* (KANU). Codington Co.: NW of Watertown, *McGregor 18686* (KANU). Custer Co.: E of Custer, *Stephens & Brooks 35163* (KANU). Near Custer, *McIntosh 1223* (RM). Day Co.: Egeland Twp., *Monserud 996* (MIN). Fall River Co.: Cheyenne R, *McIntosh 954* (RM). Haakon Co.: N of Billsburg, *Stephens 29223* (KANU). Harding Co.: S of Redig, *Stephens 28551* (KANU). Hutchinson Co.: W of Freeman, *Harms 18484* (KANU, SASK). Lawrence Co.: Piedmont, *Lee s.n.* (RM). Marshall Co.: NE of Britton, *Stephens 29096* (KANU). Pennington Co.: S of Rapid City, *Harms 2144* (KANU, SASK). Roberts Co.: *Over 14355* (GH). Shannon Co.: SE of Wounded Knee, *Stephens 49472* (KANU). **WISCONSIN.** St. Croix Co.: N of falls of St. Anthony, *Houghton s.n.* (GH), *Thurber s.n.* (GH).

aff. **var. *ballardii*** (close to var. *foliosa* or merely smaller var. *ballardii*)

U.S.A. NORTH DAKOTA. Grant Co.: Pretty Rock *Bell 1401* (CAN, MIN, WIS). **SOUTH DAKOTA.** Custer Co.: Black Hills', *Pase 666* (USFS). Perkins Co.: Custer N.F., *Klebenow & Avants DAK-26* (RM).

aff. var. *ballardii* (close to var. *minor*; somewhat glandular)

U.S.A. MINNESOTA. Anoka Co.: Moon Lake, *Rydberg 9650* (NY, WIS). Ramsey Co.: St. Paul, *Seim 9* (MIN). NORTH DAKOTA. McKenzie Co.: dry stony hillside, *Bell 814* (LL). Williams Co.: Williston, *Bell 63* (MIN, NY, UC). SOUTH DAKOTA. Custer Co.: *Demaree 54157* (MIN). Harding Co.: S of Buffalo, *Harms 18506* (KANU, SASK). Shannon Co.: Pine Ridge Res., *Visher 2155* (NY).

aff. var. *ballardii* (close to *H. stenophylla* var. *angustifolia* in indument)

U.S.A. KANSAS. Geary Co.: SE of Milford, *Gates 18511* (TEX, UC). NEBRASKA. Kearney Co.: Minden, *Hapeman s.n.* (PH, WIS). Wheeler Co.: NE of Bartlett, *Stephens & Brooks 24225* (DS, KANU).

17.3 *Heterotheca villosa* (Pursh) Shinnery var. *foliosa* (Nutt.) Harms, Wrightia 4: 15. 1968.

Chrysopsis foliosa Nutt., Trans. Amer. Philos. Soc. 2.7: 316. 1841. *Chrysopsis villosa* (Pursh) Nutt. var. *foliosa* (Nutt.) Cronq., Bull. Torrey Bot. Club 74: 150. 1947. *Heterotheca foliosa* (Nutt.) Shinnery, Field & Lab. 29: 71. 1951. TYPE: [U.S.A. WYOMING.] Rocky Mts, [Jun-Jul 1834] *Nuttall s.n.* (Holotype: K!; isotypes: GH!, GH ex Lowell!). Nuttall gives the habitat as "near the banks of the Platte. Flowering in August," but he was in the Platte region in SE Wyoming in very early June, which is extremely early in the season for *H. villosa*.

Chrysopsis imbricata A. Nels., Bot. Gaz. 37: 263. 1904. *Chrysopsis foliosa imbricata* (A. Nels.) A. Nels. in Coult. & Nels., Man. Bot. Rocky Mts., 493. 1909. TYPE: U.S.A. COLORADO. El Paso or Teller Co.: Pike's Peak, open slopes, 1 Sep 1901, *Nelson 8616* (Holotype: RM!)

Chrysopsis butleri Rydb., Bull. Torr. Bot. Club 37: 129. 1910. TYPE: U.S.A. MONTANA. Gallatin Co.: Gateway, 17 Aug 1908, *Bulter 620* (Holotype: NY!)

STEMS several to many, ascending-erect, 22-**32**-41-(58) cm tall, moderately to densely hispid-strigose, long spreading hairs numerous; (13)-15-**21**-26-(32) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (21)-25-**30.5**-36-(38) mm long, (5.3)-5.8-**6.9**-8-(9) mm wide, petiolate, cuneate, sometimes mucronate, moderately to densely hispid-strigose and eglandular to sparsely glandular on both surfaces; margins entire, strigose, longer spreading hairs along margins basally. UPPER STEM LEAVES oblong, rarely ovate, (11)-17.8-**23**-28-(33) mm long, (3.5)-5.7-**7.1**-8.5-(9.7) mm wide, sessile, sometimes little reduced upward, broadly acute to obtuse, indument similar to lower, 0-**1**-2.2-(6) glands/mm², 25-**42**-59-(90) hairs/mm², margins flat, a few longer spreading hairs along margins basally. CAPITULESCENCE congested to open cymose-corymbiform, heads 4-**13**-24-(35); peduncles moderately to densely hispid, eglandular, (9)-17.3-**26**-37-(39) mm long; bracts few, linear-oblong, usually reduced, sometimes foliar, indument like leaves. INVOLUCRES narrowly campanulate when fresh, campanulate-hemispheric upon drying, (5.9)-6.2-**6.9**-7.6-(8.6) mm high; phyllaries in 4-5 imbricate series, outer ones 1/5-1/4 the length of the inner, narrowly triangular-lanceolate, moderately to densely strigose, eglandular to very sparsely glandular, margins hyaline narrow, fimbriate-ciliate and often anthocyanotic apically; inner ones similar. RAY FLORETS (7)-13-**17**-20-(22), strap yellow, (8)-8.9-**10.2**-11.4-(12.4) mm long, (0.7)-0.9-**1.2**-1.6-(2) mm wide, tube glabrate. DISC FLORETS (19)-21-**28**-34-(44), yellow, glabrous or a few minute hairs, corolla barely ampliate, 5-**5.5**-6-(7) mm long, lobes 0.5-**0.6**-0.7-(0.75) mm long, hairs absent or few, 0.1-**0.11**-0.25 mm long. ACHENES (1.5)-1.7-**2.2**-2.7-(3.3) mm long, sparsely to moderately strigose; pappus off-white, double, outer whorl of linear scales 0.25-1 mm long, inner whorl of 35-45 barbellate bristle (5)-5.3-**5.9**-6.4-(7.1) mm long. Chromosome numbers: 2n = 18, several reports; 36, many reports.

Flowering Period: JULY-SEPTEMBER-(October).

Distribution and habitat: Western Great Plains and foothills and lower elevations of Rocky Mts. from southern British Columbia to north central New Mexico (Fig. 39C); dry short-grass and semi-barren prairies, grassy areas with scattered sagebrush, ponderosa pine, aspen and *Cercocarpus*, stabilized dunes, dry coulees and flood plains, roadsides, loose talus slopes, grassy roadsides, lava reefs; sandy shale and clay soil, sandy loam on sandstone, gypsum soils, crevices in granite and sandstone; 650-2600 m (2200-8500 ft.) elevation.

Discussion: Variety *foliosa* is distinguished by its upper stem leaves that are oblong, eglandular and have

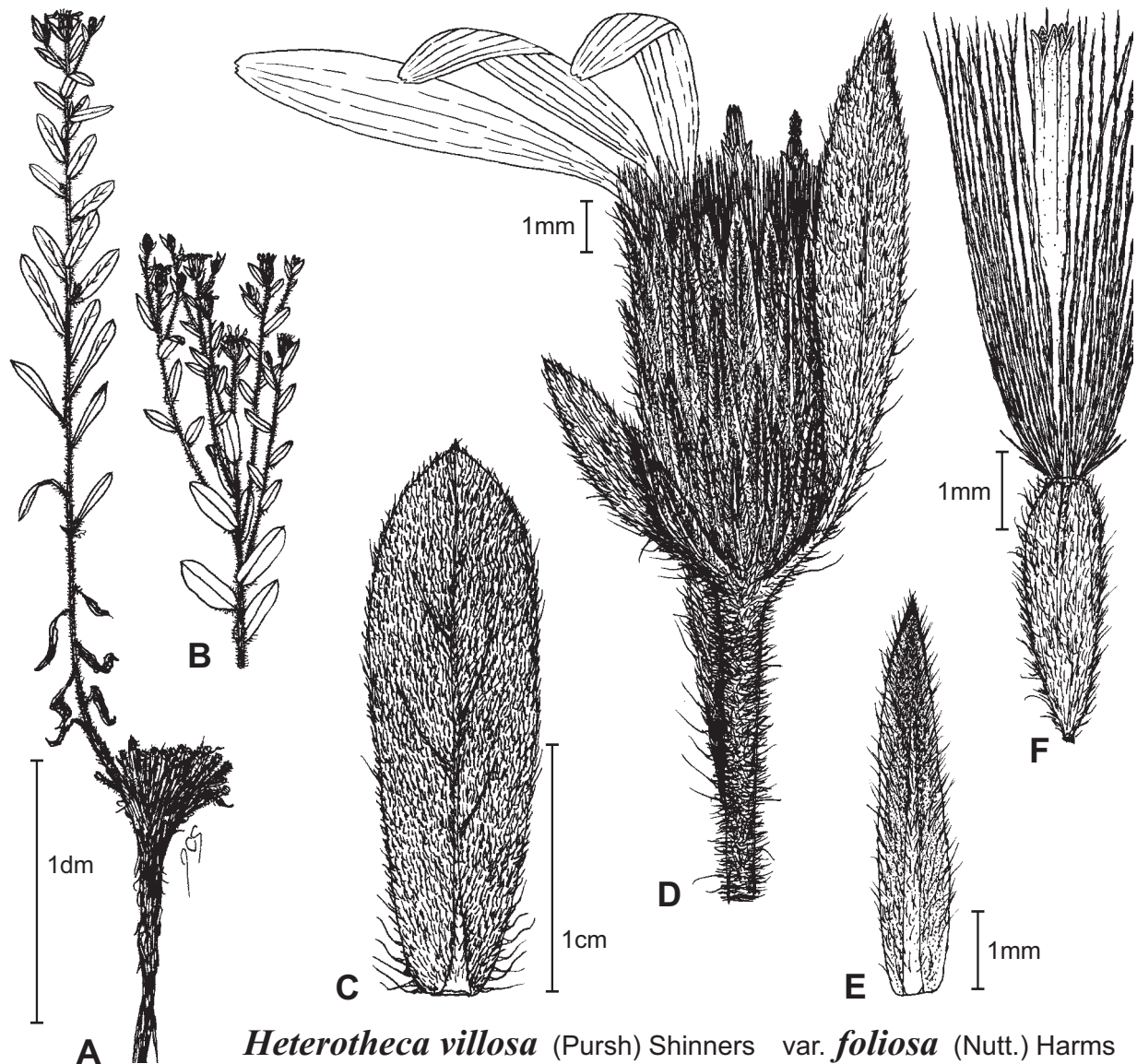
30-90 hairs/mm², its heads that are often subtended by narrow oblanceolate bracts, its phyllaries that are pubescent, glandless and apically anthocyanotic (Fig. 43). The variety is most common near the base of the Front Range of the Rocky Mts. in Colorado and Wyoming, but occurs scattered across the northern part of the range of the species in the mountains and western prairies. Plants that are glandular but otherwise like var. *foliosa* are presumed here to be hybrids with either var. *minor* (Fig. 46) or var. *nana* (Fig. 48). Variety *foliosa* is most similar to var. *ballardii* (Fig. 42), which could be treated merely as an eastern variant of the high plains *foliosa*. Both typically have oblong leaves, no glands, heads usually subtended by narrow bracts, but var. *ballardii* has somewhat larger heads with longer rays and more florets.

For some time the unique set of traits of the holotype and isotype (GH!) led me to believe that the name “*foliosa*” did not apply to plants from the plains near the Rocky Mts. (Semple 1990). However, the data accumulated since then for multivariate analyses have clarified the situation. My initial concern was that the type supposedly came from some place west of where Nuttall (1841) stated it did in the protologue because the collection data were not compatible with historical records on Nuttall's collecting route during 1834. The holotype has small, densely pubescent leaves (90 hairs/mm²) congested on an apparently short stem (fragmentary). Another fragmentary specimen (Nuttall s.n. GH!) clearly from a separate plant has similar shaped leaves with fewer hairs and longer internodes; this is annotated in Nuttall's hand as “*C. foliosa* / Rocky Mts.” The latter specimen is more like most collections treated here as var. *foliosa* and is a link between the aberrant holotype and average *foliosa* as treated here. The holotype may represent nothing more than a very early season plant that had flowered before expanding its leaves and elongating its internodes. Hair density correlates moderately negatively with leaf length ($r = -0.624$; $N = 18$); if the types of *Chrysopsis butleri* and *C. villosa* var. *discoides* are excluded from the sample and the log values are used, then the correlation is stronger ($r = -0.723$; $N = 16$; ANOVA regression F-ratio 15.305, $p = 0.002$; $\hat{\alpha} = 0.05$). The type of var. *foliosa* falls close to but above the 95% confidence curve for the regression line and thus is an extreme form of the variety for the pubescence trait.

In the southwest corner of its range, var. *foliosa* comes close to the northern portion of the range of *H. zionensis*, which also has numerous hairs/mm² on its sometimes broadly linear-oblong leaves, but it is also usually quite glandular. If Nuttall's type of var. *foliosa* is conspecific with *H. zionensis*, then either Nuttall ventured into the Great Salt Lake area in 1834 or some unknown trapper brought a few dried shoots from Utah to him at the Trapper's Rendezvous in southwestern Wyoming in 1834. This is too speculative a basis on which to make a completely aberrant specimen of uncertain provenance the type of the distinctive Utah taxon. Nonetheless, the similarity of the type of var. *foliosa* might be indicative of a relationship of the Utah taxon with the *foliosa* branch of the *villosa* complex. The morphological data base is not adequate to demonstrate conclusively possible relationships of var. *foliosa* to other species.

Specimens examined: CANADA. ALBERTA. SW Alta, *Shaw 1956* (BRY), *Shaw 2559* (BRY). Banff, *Brunton & Coneybear* et al. 1496 (CAN, DAO). NW of Hilda, *Wheeler 459* (CAN, DAO). Calgary, *McCalla 8956* (GH, UBC), *McCalla 10611* (UBC). East Calgary, *McCalla 11311* (UBC). E of Cardston, *Shaw 1137* (BRY). N of Calgary, *Howell 7842* (CAS). SW of Cardston, *Shaw 2176* (BRY). Edmonton, *Frankton 901* (DAO). W of Ft. MacLeod, *Harms 20225* (KANU, SASK). NW of Hilda, *Wheeler 459* (CAN, DAO). Kananaskis F.E.S., *Kendrick & Cooper s.n.* (WAT). Lethbridge, *Thompson s.n.* (CAN). W of Magrath, *Shaw 1652* (BRY). NE of Manyberries, *Shaw 2535* (BRY). Medicine Hat, *Ledingham s.n.* (WIS). W of Mt. View, *Shaw 1850* (BRY). Orions, *Moss 7174* (WIS). Near Red Deer, *Nelson & Nelson 4765* (DS). Rosedale, *Moodie 1171* (TEX). near Rosedale, *Moodie 1180* (CAS, DS, GH, NY). Standoff, *Shaw 816* (BRY). Waterdon Lakes N.P., *Breitung 17095* (NY, UC), E gate, *Blais & Nagy 2250* (CAN), Interpretive Bldg. Hill, *Blais & Nagy 2512* (CAN), Oil Basin end of Mt Galway, *Nagy & Blais 2358* (CAN). NE of Waterdon, *Douglas & Douglas 7600* (BRY, DAO). BRITISH COLUMBIA. Marysville, *Fodor 263* (CAN). Radium Hot Sprs, *Porsild & Breitung 15046* (CAN). Radium Hot Springs, *Rose 41379* (CAS, UC). Lake Wapta, *anon. Q-15* (WTU). SASKATCHEWAN. Near Caronport, *Morton NA 3441* (WAT). Cypress Hills Pk, *Breitung 4976* (DAO). E of Maple Creek, *Harms 19202* (KANU, SASK). Prince Albert N.P.: Waskesiu L., *Cooper 87* (MIN). Webb C.P., *Best 621* (WIS). U.S.A. COLORADO. “Mountains”, *Canby s.n.* (NY). Plum Cr Preserve, *Zobel s.n.* (CAS, NMC, NY). Boulder Co.: Boulder, *Ramaley 9762* (WTU). S of Boulder, *Robbins 4507* (NMC, RM). S Gregory Cyn, *Ewan 11085* (CAS). Lyons, *Harms 2102* (KANU, SASK). Costilla Co.: S of Monument L., *Wagenknecht 2884* (KANU). Denver Co.: Denver, *Kraus s.n.* (WIS), *Semple & K. Shea 2223* (CAN, WAT), *Semple & K. Shea 2228* (WAT). Douglas Co.: S Castle Rock, *Wasmer s.n.* (RSA). N of Deckers, *Freeman 26* (ASU). NE of Larkspur, *Semple et al. 5427* (WAT). S of Parker, *Semple 2225* (WAT). El Paso Co.: SW of Colorado Springs, *Semple et al. 5461* (WAT). N of Manitou Springs, *Harms 2017* (KANU, SASK). Trail Glen, *Clements & Clements 39* (MIN). Jefferson Co.: N of Golden,

Wagenknecht 3054 (KANU). Huerfano Co.: Cucharo Camps, *Wagenknecht* 2879 (KANU, SASK). Larimer Co.: E of Drake, *Harms* 2112 (KANU, WAT). ESE of Estes Park, *Harms* 2104 (KANU, SASK). SE of Estes Park, *Wagenknecht* 3051 (KANU, SASK). N of Ft. Collins, *Sundberg* 2566 (NMC, TEX), *Wheeler* 324 (POM). Horsetooth Reservoir, *Hagan* 80 (ASU), *Irving s.n.* (TEX). NW of La Port, *Harms* 2113 (KANU, SASK). Laramie Mts., Dale Fk. of Platte R, *Benson* 5031 (POM). E of Livermore, *Osterhout* 5679 (RM). S of Masonville, *Stephens & Brooks* 43349 (KANU). Rocky Mt. N.P., Indian Fort, *Wagenknecht* 3008 (KANU). N of Ted's Place, *Stephens & Brooks* 43415 (KANU). Thompson Cyn., *Osterhout* 5545 (RM(2)). Las Animas Co.: SE of Toba, *McGregor* 13429 (KANU). SW of Toba, *McGregor* 13428 (KANU). Park Co.: between Arkansas R. and S. Platte R., *Woodward s.n.* (GH). Pueblo Co.: N of Pinon, *Harms* 2004 (KANU, SASK). Teller Co.: SW of Colorado Springs, *Harms* 2029 (KANU, SASK, WAT), *Schmoll* 1550 (RM). North Cheyenne Cyn., *Harms* 2024 (KANU). Weld Co.: *Muir* 137 (RM). N of Keota, *Richardson & Robertson* 1381 (KANU). New Windsor, *Osterhout s.n.* (NY, RM), *Osterhout* 1326 (RM). Windsor, *Osterhout* 5572 (RM(2)), *Osterhout* 5572a (RM). IDAHO. *Allen s.n.* (NY). Adams Co.: Pinehurst, *Baker* 11944 (NY, WTU). Fremont Co.: S of Ashton, *Christ & Ward* 14971 (NY). Kootenai Co.: near Lakeview, *Heller* 752 (PH).



Heterotheca villosa (Pursh) Shinnery var. *foliosa* (Nutt.) Harms

Figure 43. Morphology of *Heterotheca villosa* var. *foliosa*. **A.** Habit of early season shoot. **B.** Capitulescence of mid season shoot with elongated branches. **C.** Small mid-upper stem leaf; larger leaves can be less densely pubescent. **D.** Head with only some florets drawn; subtending foliar bracts may be much smaller. **E.** Mid series phyllary with chlorophyllous zone dark and apical margins anthocyanotic. **G.** Mature achene with disc corolla attached.

KANSAS. Decatur Co.: S of Oberlin, *Harms 18496* (KANU, SASK). **MONTANA.** Great Spring, *Anderson 42* (UC). Beaverhead Co.: Canyon Cr., *Leithhead 67* (UC). Big Horn Co.: Yellowtail Reservoir, *Lichvar 6190* (RM). Carbon Co.: Beartooth N.F., Black Fork of Rock Cr., *Simms & Zeh 710* (USFS). Big Horn Cyn N.R.A., N of Devil's Cyn overlook., *Jones, Ditolla & Myers s.n.* (RM). Above Wyoming Cr, *Cotner s.n.* (DAO). Carter Co.: Needmore Ranger Stn., *Thompson 472* (USFS). Chouteau Co.: NW of Big Sandy, *Marks s.n.* (WIS). Custer Co.: Custer Flat, *Woolfolk W-178* (DAO, USFS). US Range Livestock Exp. Stn., *Kennedy K-67* (USFS). Dawson Co.: NW of Lindsay, *Stephens 67403* (KANU). Deerlodge Co.: Deerlodge N.F., *Wullstein & Follett LHW-3* (USFS). Fallon Co.: W of Plevna, *Stephens 66941* (KANU). NE of Kalispell, *Dunn 11568* (MIN, RSA). Gallatin Co.: S of Bozeman, *Bell s.n.* (GH). Hill Co.: E of Havre, *Shantz 782* (LL). Garfield Co.: S of Jordan, Big Dry Cr., *Woodland 1171* (DS). Jefferson Co.: Jefferson N.F., *Sutton 16* (USFS), *Greathouse 11* (RM). Judith Basin Co.: S of Raynesford, *Olmstead & Wendt G-41* (TEX). W of Stanford, *Stephens 68671* (KANU). Lewis and Clark Co.: Helena, *Butler 655* (NY), *Butler 656* (NY), *Kelsey s.n.* (DS), *Kelsey s.n.* (NY), *Kelsey s.n.* (POM). Lewis & Clark N.F., Sun R., *Saunders 228* (USFS), *Saunders 230* (USFS). Livingston Co.: *Scheuber 104* (NY). Madison Co.: Beaverhead N.F., mouth of Barton Gulch, *Schmautz JES-156* (USFS); Swamp Cr Ranger Stn, *Clack D8-10* (USFS). Near Pony, *Rydberg & Bessey 5068* (NY). McCone Co.: S of Brockway, *Stephens 67292* (KANU). Missoula Co.: *Osterhout 8081* (RM). Park Co.: Livingston, *Mason 3515* (UC). Pondera Co.: W of Dupuyer, *Brenckle & Shinners s.n.* (WIS). Prairie Co.: N of Terry, *Stephens 67147* (KANU). Richland Co.: W of Sidney, *Thomson s.n.*, (WIS). Rosebud Co.: S of Birney, *Bennett s.n.* (DS, MIN, UC). SW of Birney, *Bennett s.n.* (DS, NY, UC). W of Forsyth, *Brenckle & Shinners 41* (WIS). W of Hathaway, *Stephens 78675* (KANU). Sheridan Co.: Sandhills Wilderness Area, *Mooers 1218* (NY). Silver Bow Co.: Butte, *Keller s.n.* (PH). Stillwater Co.: Absarokee, *Hawkins s.n.* (WIS). Midnight Cyn., *Brown B448* (ASU). Valley Co.: Ft. Peck Rec. Area, *Bowers & Bowers 69-214* (CAN). Wheatland Co.: NW of Oka, *Hitchcock 2461* (CAS, POM). Wibaux Co.: N of Wibaux, *Stephens 67495* (KANU). Yellowstone Co.: Billings, *Lane MAL1652* (ASU). Hogan Hill, *Elliott 53* (WIS). Near Worden, *Hiller s.n.* (MIN). **NEBRASKA.** Oleson 129 (RM). Cherry Co.: Niobrara Reserve, *Krautter s.n.* (PH). Grant Co.: Whitman, *Rydberg s.n.* (WS). **NEW MEXICO.** Colfax Co.: E of Abbott, *Harms 1952* (KANU(2)). W of Farley, *Harms 1954* (KANU, SASK). Colfax Co.: NW of Springer, *Harms 19113* (KANU, SASK). S of Springer, *Harms 1945* (KANU). W of Springer, *Harms 1949* (KANU, SASK). Mora Co.: NW of Wagon Mound, *Stephens & Brooks 26180* (KANU). NE of Watrous, *Harms 1935* (KANU, SASK, WAT). Rio Arriba Co.: San Juan Pueblo, *Harms 19116* (KANU, SASK). Santa Fe Co.: S of Santa Fe, *Harms 1921* (KANU), *Harms 1922-B* (KANU), *Harms 1923-B(1)* (KANU), *Stephens & Brooks 26059* (KANU) **NORTH DAKOTA.** Ramsey Co.: Maza, *Kildahl s.n.* (MIN). **OREGON.** "Eastern Oregon," *Leach s.n.* (WTU). Gilliam Co.: Quinton, *Rose 41416* (CAS). Hood River Co.: *Henderson 702* (GH). Hood River, *Peck 18198* (NY). W of the Sherman, *Sundberg 2032* (ASU, TEX, WTU). Marion Co.: S of Talbot, *Nelson 4536* (WS). Multnomah Co.: Portland, *Demaree 13411* (DS, NY). Sherman Co.: near Biggs, *Peirson 3892* (RSA). Des Chutes R., *Sherwood 418* (LL). Above Miller, *Applegate 6527* (DS). Between Miller and Biggs, *Bartlett & Grayson 833* (NY). E of Rufus, *Call & Call 780* (MIN), *Call & Call 984* (WTU). Umatilla Co.: Hermiston, *Zivney s.n.* (UC). Wasco Co.: Creek Camp, *Lloyd s.n.* (NY). E of The Dalles, *Milburge 1257* (WTU). NE of The Dalles, *Brenckle & Shinners 41-230* (MIN, PH, WIS). **SOUTH DAKOTA.** Custer Co.: N of Hot Springs, *Harms 2139* (KANU). S of Pringle, *Stephens 89782* (KANU). Wind Cave N.P., *Franklin 5043* (NY). Harding Co.: E of Buffalo, *Stephens 7929* (KANU). Custer N.F., Eagles Nest Ranger Stn., *York 505* (USFS). Lawrence Co.: Spearfish, *Thatcher 114* (MIN). Whitewood, *Moore 378* (MIN). Meade Co.: Faith, *Moyer 153* (MIN). Todd Co.: near state line, *Semple & Brammall 2697* (WAT). Mellete Co.: Little White R., *Wallace 95* (NY). **WASHINGTON.** Yakima R., *Nelson 1508* (RM). Asotin Co.: S of Asotin, *Baker 15234* (NY, WTU). Garfield Co.: Lower Granite Dam, *Jenkins & Sirotta SD-1* (WS). Klickitat Co.: Bingen, *Suksdorf s.n.* (NY). Goldendale, *Gorman 7717* (DS, UC). W of Roosevelt, *Jenkins & Sirotta ST-14* (WS). Spedis, *Gorman s.n.* (DS). W of Wishram, *Semple & Brouillet 7082* (WAT). Whitman Co.: Illia, *Lake & Hull 752* (MIN, WS, WTU). Yakima Co.: E of Naches, *Hoover 6001* (CAS, OBI). **WYOMING.** Beaver Cr., *Nelson 8457* (RM, UC). Platte R., *Fremont s.n.* (GH). Shoshone N.F., *Thompson 108* (USFS). Albany Co.: Buford, *Keil K10911* (ASU, JCS). N of Ft. Laramie Buffum *s.n.* (RM). S of Hay Cyn., *Clarke 40* (RM). N of Tie Siding (City), *Osterhout 5685* (RM, UC). S of Tie Siding, *Harms 2116* (KANU, SASK(2)). Laramie, *Rowland s.n.* (RM). S of Laramie, *Cantelow s.n.* (CAS). E of Laramie, *Feddema 3192* (USFS). Laramie Hills, *Nelson & Nelson 6851* (GH, MIN, NY, RM). Lookout, *Macbride 2594* (RM). Middle Crow Cr., Laramie Hills, *Ownbey 303* (WS). Rogers Cyn., *Asplund 73-27* (RM). Campbell Co.: *Sanguinetti & Dueholm 449* (RM). N of Gillette, *Harner 17* (RM). SSE of Gillette, *Dueholm 5134* (RM). W of Gillette, *Dueholm 5793* (RM). N of Moorcraft, *Welsh & Moore 9249* (BRY). NE of N Pumpkin Butte, *Dueholm 5193* (RM). W of Rozet, *Porter & Porter 7567* (DS, RM, RSA, UC, WTU). N of Savageton, *Dueholm & Sanguinetti 3914* (NY, RM). NE of Soda Wells, *Dueholm 5451* (RM(2)). S of Spotted Horse, *Dueholm & Sanguinetti 4045* (MIN, RM). N of Weston, *Stephens 69771* (KANU). Carbon Co.: Elk Mt., *Gartner 92* (RM). Medicine Bow N.F., *Conley P-16* (USFS), *Douglas 111* (USFS). Converse Co.: Betty Reservoir, *Sanguinetti & Dueholm 8* (BRY). Douglas, *Barrow 49* (RM), *Pfadt 175* (RM). E of Glenrock, *Tresler 362* (ASU, RM). SE of Glenrock, *Brooks 21198* (KANU). Crook Co.: ENE of Aladin, *Nelson 11685* (RM). NE of Alva, *Hartman 16120* (RM). NW of Alva, *Nelson 11898* (RM). Between Alva and Aladdin, *Lichvar 3184* (NY). Beulah, *Hayward 206* (MIN). SSE of Beulah, Boundary Gulch, *Nelson 11957* (RM). Black Hills, *Lichvar 2195* (NY), Rocky Mt. Exp. Stn., *Pase 723* (USFS). W of Devils Tower, *Nelson 12010* (NY). Ewing, *Seig 21* (RM). NW of Sundance, *Stephens & Brooks 43836* (KANU). Fremont Co.: SE of Thermopolis, *Fisser 256* (RM). Goshen Co.: SW of Torrington, *Nelson 2367* (RM). Hot Springs Co.: SE of Washakie Needles, *Nelson, Kirkpatrick & Kirkpatrick 10531* (NY). Johnson Co.: Big Horn Mts., Caribou Cr., *Miller 323* (USFS), SE of Hazelton Pyramid, *Nelson 6736* (RM), NW of Hunter Ranger Stn., *Dueholm 9053* (RM). SW of Buffalo, *Nelson 6803* (RM). WSW of Buffalo, *Nelson 6721* (RM). Laramie Co.: NE of Buford, *Edwards 143* (RM). Cheyenne, *Nelson & Nelson 343a* (RM). NW of Cheyenne, *Current 200* (RM). W of Cheyenne, *Abrams 13562* (DS). Natrona Co.: NE of Casper, *Tresler 422* (RM). Noibrara Co.: N of Lusk, *Harms 2130* (KANU, SASK), *Stephens 70172* (KANU). S of Mule Creek Junction, *Harms 2134* (KANU, SASK(2), WAT). Newcastle, *Degener & Peiler 16230* (NY). Park Co.: NW of Cody, *Nelson 12992* (NY). Platte Co.: E of Guernsey, *Harms 2124* (KANU, SASK). Sheridan Co.: *Dueholm 7651* (UC). Dayton, *Tweedy 2039* (NY). E of Leiter,

Stephens 69853 (KANU). Teton Co.: E of Granite Cyn., *Heller* 14318 (DS, WTU). Washakie Co.: NE of Tensleep, *Nelson & Fonken* 7101 (RM). Weston Co.: W of Clareton, *Dorn* 5266 (NY). Newcastle, *Degener & Peiler* 16168 (RM), *Nelson* 8441 (RM).

aff. var. foliosa

CANADA. ALBERTA. Buffalo Jump area, *Campbell, Snelling & Chambers* 1282 (CAN). Calgary, *Johnson s.n.* (NY). S of Calgary, *Hitchcock & Martin* 7825 (WTU). Cardston, *Shaw* 1681 (BRY). W of Gatine, *Pinel & Harris V-439* (DAO). W of Elkwater, *Mosquin & Mosquin* 4722 (DAO). Sarcee Res., *Goddard* 465 (UC). **BRITISH COLUMBIA.** Cranbrook, *Fodor* 273 (UBC). Radium-Invermere District, *Brink* 50-33 (UBC). Wasa, *McCabe* 5032 (UC). **SASKATCHEWAN.** Cypress Hills, *Senn & Tisdale* 2341 (DAO). W of Elkwater, *Mosquin & Mosquin* 4722 (DAO). Product, *Russell* 3814 (DAO). N of Tompkins, *Frankton & Bibbey* 314 (DAO). **U.S.A. IDAHO.** Nez Perce Co.: E of Lewiston, *Semple & K. Shea* 2001 (CAN, WAT). **MONTANA.** *Corres s.n.* (NY ex Chickering). Jefferson Co.: Jefferson N.F., Mine Gulch, *Clark* 49 (USFS). **NEW MEXICO.** Rio Arriba Co.: S of Velarde, *Semple & Heard* 8050 (WAT, NMC, MT). San Miguel Co.: Las Vegas, *Arsène* 21082 (UC). S of Las Vegas, *Semple & Heard* 8089 (WAT, NMC, MT, KANU). N of Sapella, *Semple & Heard* 8086 (WAT, NMC, DAO, ASU). Santa Fe Co.: SE part of Santa Fe, *Bennett* 8296 (NY, TEX, WIS). **SOUTH DAKOTA.** Custer Co.: Custer, *Carter s.n.* (RM). Fall River Co.: NW of Hot Springs, *Goodman* 3301 (GH, NY, WTU). Perkins Co.: North Cave Hills, *Dodge* 26 (USFS). **WASHINGTON.** Klickitat Co.: Lyle Bridge, *Fye* 148 (ws). Rockland, *Suksdorf* 4080 (ws). **WYOMING.** Johnson Co.: SE of Buffalo, *Duelholm* 7451 (RM). Niobrara Co.: Mexican Mines, *Nelson* 585 (GH, MIN, NY, RM).

aff. var. foliosa (approaching var. *nana*)

U.S.A. COLORADO. El Paso Co.: N of Fountain, *Harms* 2005 (KANU, SASK(2), WAT). Larimer Co.: *Warnock* 850 (TEX). **NEW MEXICO.** Guadalupe Co.: NW of Santa Rosa, *Higgins* 8988 (ASU, BRY, NMC, NY). McKinley Co.: N of Gallup, *Harms* 1899-B (KANU, SASK). Santa Fe Co.: Santa Fe, *Boyle s.n.* (NMC).

aff. var. foliosa (approaching var. *minor* in indument)

U.S.A. COLORADO. El Paso Co.: Cascade, *Semple & Heard* 7721 (WAT). Weld Co.: E of Berthoud, *Semple & K. Shea* 2258 (CAN, WAT). **MONTANA.** Beaverhead Co.: Armstead, *Payson & Payson* 1905 (CAS, GH, NY, RM). Glacier Co.: SE of Browning, *Brenckle & Shinners* 41 (WIS). **NEW MEXICO.** San Miguel Co.: NE of Las Vegas, *Harms* 1931 (KANU, SASK, WAT). Santa Fe Co.: NE from Los Cerillos, *Bennett* 8298 (NY, TEX, WIS). **OREGON.** Dry Ground Summit, Columbia R., *Henderson s.n.* (DS). Wallowa Co.: mouth of Innaha R., *Kruckeberg* 2304 (CAN, DAO, NY, RM, RSA, UC, WS, WTU). **WASHINGTON.** Klickitat Co.: North Dalles, *Thompson* 11111 (LL, NY, WTU). **WYOMING.** Albany Co.: Laramie R *Nelson* 3411 (BRY, RM). Carbon Co.: Rock Cr. Cyn, *Williams & Williams* 3722 (GH, LL, NY). Seminoe Mts., *Porter* 4403 (DS, GH, NY, PH, RM, RSA, TEX, WTU). Johnson Co.: L. De Smet, *Dueholm* 8114 (RM). Natrona Co.: Casper, *Evermann s.n.* (DS). Casper Mt., *Hermann* 4614 (LL). Platte Co.: SE of Wheatland, *Harms* 2120 (KANU, SASK, WAT). Sheridan Co.: between Sheridan & Buffalo, *Tweedy* 3149 (NY, RM, WS).

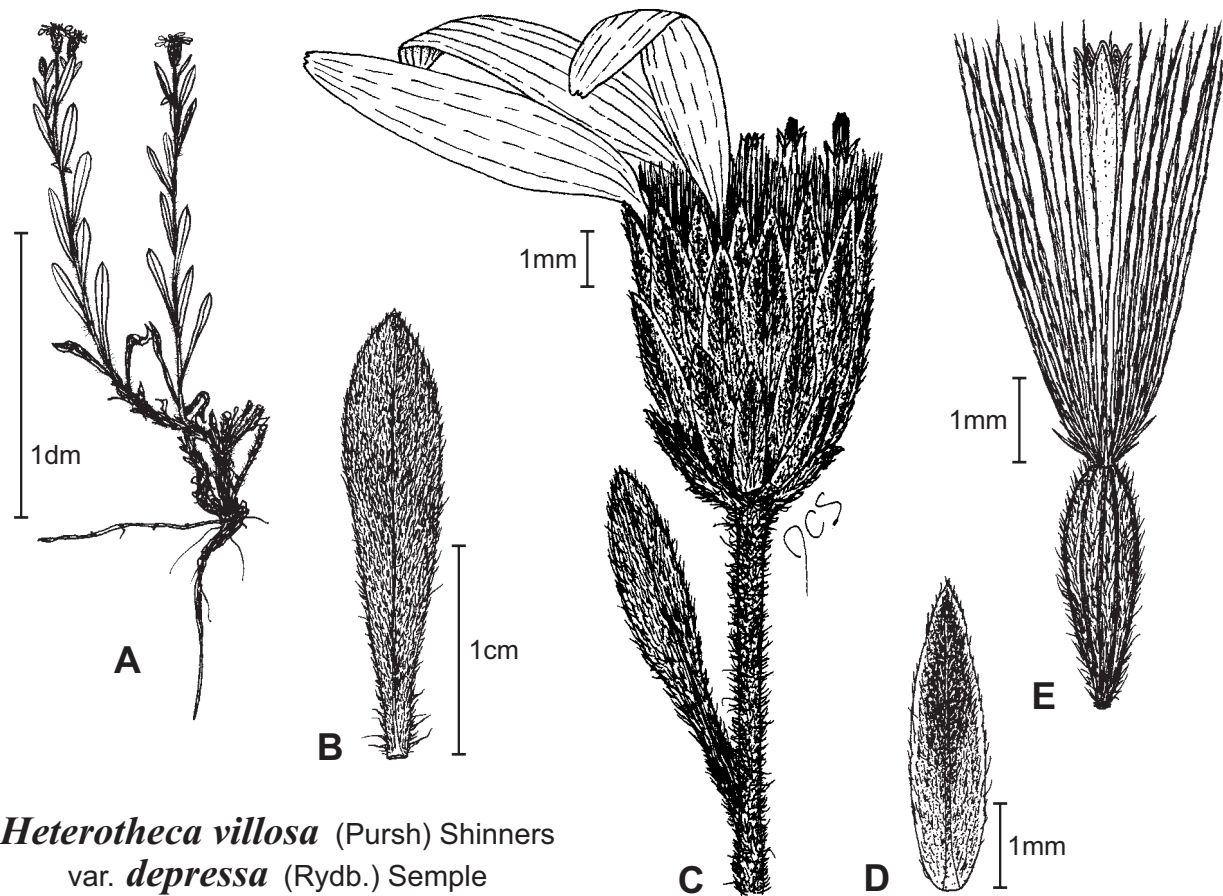
aff. var. foliosa (approaching var. *villosa* in leaf shape and mixed collections)

U.S.A. COLORADO. "Colorado Territory", *Coulter s.n.* (PH). Denver Co.: Denver, *Clokey* 3884 (CAN, CAS, DS, GH, LL, MIN, NY, PH, POM, RM, UC, WS, WTU). Weld Co.: Greeley, *Neil s.n.* (WIS). **IDAHO.** Idaho Co.: E of Slate Cr., *Jones* 125 (DS, GH, MIN, NY, RSA, WS, WTU). **MONTANA.** Custer Co.: Intermtn. For. & Range Exp. Stn., *Woolfolk W-180* (USFS). Roosevelt Co.: E of Wolf Point, *Stephens* 78414 (KANU). **NEBRASKA.** Sioux Co.: W of Harrison, *Stephens & Brooks* 16243 (KANU). **SOUTH DAKOTA.** Custer Co.: Pringle, *Murdoch* 3053 (NY). Fall River Co.: Rockford, *Rydberg* 758 (NY). Perkins Co.: Bixby, *Visher* 517 (RM). **WASHINGTON.** Benton Co.: W of Midway, *Baird* 204 (BRY, NY). Chelan Co.: Entiat, *Thompson* 10809 (CAS, DS, LL, NY, POM, WTU). Whitman Co.: Smoke R., *St. John & Warren* 3396 (NY, UC). **WYOMING.** Albany Co.: Laramie Hills, Morton Pass, *Harms* 2118 (KANU, SASK); Happy Jack Camp, *Yuncker & Yuncker* 12297 (NY, TEX). Goshen Co.: N of Lingle, *Harms* 2125 (KANU, SASK(2), WAT). Laramie Co.: NW of Cheyenne, *Williams* 2454 (GH, LL, UC, WS). Platte Co.: W of Guernsey, *Harms* 2122 (KANU, SASK(2)). Teton (?) Co.: Camp Crawford, *Clemens s.n.* (DS).

17.4 *Heterotheca villosa* (Pursh) Shinners var. *depressa* (Rydb.) Semple, Novon 4: 53. 1994.

Chrysopsis depressa Rydb., Mem. N.Y. Bot. Gard. 1: 381. 1900. *Heterotheca depressa* (Rydb.) Dorn, Vasc. Pl. Wyoming. 295. 1988. TYPE: U.S.A. MONTANA. Teton Co.: Yellowstone N.P., Lower Geyser Basin, 4 Aug 1897, *Rydberg & Bessey* 5067 (Holotype: NY!; isotypes: CAN!, US!)

STEMS several to many, ascending-erect, (5.4)-6.7-11.8-17-(22) cm tall, moderately to densely hispid-strigose, long spreading hairs numerous; (9)-10-14-18-(22) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (9)-12-18.3-25-(31) mm long, (2.4)-3.1-4-5-(5.7) mm wide, petiolate, cuneate, densely canescent and eglandular to moderately glandular on both surfaces; margins entire, strigose, longer hispid hairs along margins basally. UPPER STEM LEAVES linear-oblanceolate, (5.2)-9.2-13.9-18.7-(23) mm long, (2.3)-2.7-3.4-4.2-(4.7) mm wide, sessile, sometimes little reduced upward, acute, indument similar to lower, 0-6-13-(28) glands/mm², 84-102-118-(140) hairs/mm², margins flat, a few longer spreading hairs along margins basally. CAPITULESCENCE congested to open cymose-corymbiform, heads (1)-3-5-8-(10); peduncles moderately to densely hispid-strigose, eglandular to sparsely glandular, (7)-12-20-28-(37) mm long; bracts



Heterotheca villosa (Pursh) Shinners
var. *depressa* (Rydb.) Semple

Figure 44. Morphology of *Heterotheca villosa* var. *depressa*. A. Habit. B. Upper stem leaf, adaxial surface. C. Head with only some florets drawn. D. Mid series phyllary with chlorophyllous zone dark. E. Mature achene with disc corolla attached.

few, linear-oblong, reduced, indument like leaves. INVOLUCRES cylindrical to narrowly campanulate when fresh, campanulate upon drying, 5.5-6.1-6.8-(7.5) mm high; phyllaries in 4-5 imbricate series, 1/5-1/4 the length of the inner ones, narrowly triangular-lanceolate, moderately to densely strigose, eglandular to sparsely glandular, margins hyaline narrow, fimbriate-ciliate and often anthocyanotic apically; inner ones similar. RAY FLORETS (5)-8-10-13-(15), strap yellow, (5)-5.7-7.6-9.5-(11) mm long, 1-1.3-1.5-(1.8) mm wide, tube glabrate. DISC FLORETS (11)-14-19-24-(31), yellow, glabrous or a few minute hairs, corolla barely ampliate, (4)-4.4-5-5.6-(6.2) mm long, lobes 0.5-0.6-0.7-(0.9) mm long, hairs absent or few, 0.1-0.2-0.3 mm long. ACHENES (1.3)-1.9-2.3-2.8-(3) mm long, sparsely to moderately strigose; pappus off-white, double, outer whorl of linear scales 0.25-1mm long, inner whorl of 35-45 barbellate bristle 4.9-5.5-6.2-(6.9) mm long. Chromosome number: $2n = 36$; several reports.

Flowering Period: (June)-JULY-SEPTEMBER-(November).

Distribution and habitat: Hot springs and geyser basins in Yellowstone National Park and rare in rocky soils in Teton National Park, Wyoming and very rare in adjacent areas (Fig. 39B); hot springs formations, dry rocky hillsides, open slopes, gravelly river banks; dry sandy soil, broken travertine on old terraces, dry

geyserite; 1800-2350 m (6000-7700 ft.) elevation.

Discussion: Variety *depressa* is distinguished by its small stature, small heads, and oblanceolate leaves with many hairs and some glands (Fig. 44). It is similar to some morphs of var. *minor* (Fig. 46) which occur throughout the range of var. *depressa*. It is also similar to more hairy morphs of var. *villosa* (Fig. 41). Variety *depressa* hybridizes with var. *minor* in Yellowstone Park and adjacent locations. It is possibly a race of the species that evolved in isolation within Yellowstone Park at a time when surrounding habitats were less favorable to var. *minor* and var. *villosa*. The warm geyser basins may have provided suitable habitats in late glacial times for colonization, and by chance populations adapted to growing near the thermal sources lost the ability to grow in the ancestral habitats. Now typical individuals of the variety are tied to the hot springs and geyser basins and nearby river flood banks, while var. *minor* occupies other nearby habitats. Putative interspecific hybrids between var. *depressa* and var. *minor* and aff. var. *depressa* have been collected throughout the range of var. *depressa* except in the immediate vicinity of the geysers.

Specimens examined: U.S.A. IDAHO. Bingham Co.: "National Park, Hell's Half Acre," *Mulford s.n.* (MIN, NY). WYOMING. Lincoln Co.: Fossil, *Letterman s.n.* (PH). Snake Cyn., *Wehmeyer & Martin 5397* (DS). Park Co.: "Hot Springs," *Hayden Survey s.n.* (NY ex TC Porter). Yellowstone N.P., Fire Hole R., Nez Perce Cr., *Nelson, Nelson & Nelson 3198* (RM); Lower Geyser Basin, *Cooper s.n.* (MIN), *Cooper 54y* (RM), *Piper s.n.* (WS), *Thompson 14164* (GH, LL, NY, WTU), Surprise Pool, *Lichvar 1921* (RM); Mammoth Hot Springs, *Blake 10416* (LL), *Blake 10427* (LL), *Mearns 2723* (NY), *Oleson 127* (RM), *Van Dyke s.n.* (CAS); Norris, *Oleson 128* (RM); Norris, *Conard 1071* (RM); Norris Geyser Basin, *Mearns 3193* (NY); Old Faithful, *Davis 4861* (WS, WTU); near Old Faithful, *Means 4089* (MIN); E of Old Faithful Museum, *Harrison 240* (LL); Punchbowl Hot Springs, *Lichvar 1915* (RM); The Thumb, Yellowstone L., *Nelson & Nelson 6349* (RM, WTU); S of Tower Falls, *Lassetter 1427* (BRY); Upper Geyser Basin, *Blake 10458* (LL), *Jepson 2537* (CAN, JEPS); West Thumb, *Payson & Payson 3098* (RM). Teton Co.: Grand Teton N.P., Colter Bay, *anon. 4241* (WTU). N of Jackson Hole, *Semple & Brouillet 7217* (NY, WAT). Moran, *Reed & Reed 2526* (RM). Pilgrim Cr., *Shaw 1236* (BRY, RSA). Snake R., *Dorn 5096* (NY). Spread Cr., *Tweedy 510* (NY). Tetons Mts., *Nelson 1063* (GH, RM).

aff. var. *depressa* (approaching var. *minor* in indument)

U.S.A. MONTANA. Park Co.: N of Gardiner, Miner Basin, *Hitchcock & Muhlick 13577* (CAS, NY, PH, RM, WS, WTU; mixed collection of var. *depressa*, var. *minor*, and intermediates). WYOMING. "NW Wyoming," *Parry 147* (NY(2)). Jackson Co.: Kelly, Gros Ventre R., *Peirson 11957* (RSA), *Semple & Zhang 10434* (CAN, DAO, MO, RM, WAT). E of Kelly, Gros Ventre R., *Semple & Zhang 10438* (MT, RM, UC, WAT). Grand Cyn. of Snake R., *Williams 815* (CAS, NY, RM(2), WAT). Wilson, Snake R., *Fosberg 38862* (POM). Park Co.: Yellowstone N.P., *McDonald s.n.* (CAS), *Treakle 255* (POM). Mammoth Hot Springs, *Burglehaus s.n.* (MIN, RM, WTU), *Burglehaus 1510* (WIS), *Davis 5242* (RSA, UC), *Nelson & Nelson 6035* (RM). Teton Co.: Gros Ventre slide, *Munz 17005* (RSA). Teton Co.: Yellowstone N.P., Yellowstone L., *Nelson 6604* (BRY, DS, GH, MIN, NY, POM, RM; mixed population).

17.5 *Heterotheca villosa* (Pursh) Shinnery var. *pedunculata* (Greene) Harms ex Semple,

Brittonia 39: 383. 1987. *Chrysopsis pedunculata* Greene, Pittonia 4: 154. 1900. TYPE: U.S.A. COLORADO. Archuleta Co.: near Pagosa Springs, 20 Jul 1899, *Baker 651* (Lectotype (Semple 1986): NDG-053927!; isolectotypes: GH!, ND-G!(2), NMC!, NY!, POM!, RM!(2), UC!, US!).

STEMS several to many, decumbent to ascending-erect, (12)-17-**34.6**-52-(71) cm tall, moderately to densely hispid-strigose, few long hispid hairs; (13)-17-**31**-45-(61) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (14)-22-**31.5**-41-(51) mm long, (2)-4.5-**6.8**-9.1-(11) mm wide, petiolate, cuneate, densely canescent, eglandular to densely glandular on both surfaces; margins entire, strigose, longer hispid hairs along margins basally. UPPER STEM LEAVES oblanceolate, (4)-14-**21.1**-28-(31) mm long, (1.5)-3.7-**5.3**-7.8-(8) mm wide, sessile, sometimes little reduced upward, acute, indument similar to lower, 0-**12**-28-(49) glands/mm², (42)-61-**129**-188-(270) hairs/mm², margins flat, a few longer hispid hairs along margins basally. CAPITULESCENCE congested to open cymose-corymbiform sometimes subumbelliform, heads 1-**9**-18-(39); peduncles moderately to densely hispid-strigose, eglandular to sparsely glandular, (7)-12-**26**-39-(58) mm long; bracts few, linear-oblong, reduced, indument like leaves. INVOLUCRES cylindrical to narrowly campanulate when fresh, campanulate upon drying, (4.6)-6.6-**8.5**-10.4-(11) mm high; phyllaries in 4-5 imbricate series, narrowly triangular-lanceolate, densely strigose, eglandular to sparsely glandular, margins hyaline narrow, fimbriate-ciliate and often anthocyanotic apically; inner ones lanceolate. RAY FLORETS (9)-10-**14**-17-(26), strap yellow, (5.5)-6.6-**8.6**-10.5-(12) mm long, 0.7-**1.4**-2.1-(3.1) mm wide, tube glabrate. DISC

FLORETS (17)-18-32-47-(81), yellow, glabrous or a few minute hairs, corolla barely ampliate, (4.5)-4.9-5.6-6.2-(6.6) mm long, lobes 0.5-0.6-0.7-(0.85) mm long, hairs absent or few, 0-0.1-0.25 mm long. ACHENES (1.3)-1.7-2.3-2.8-(3.2) mm long, sparsely to moderately strigose; pappus off-white, double, outer whorl of linear scales 0.25-1 mm long, inner whorl of 35-45 barbellate bristle (4.5)-5.2-5.9-6.6-(7.1) mm long. Chromosome numbers: $2n = 18, 36$; several reports.

Flowering Period: (May-) JUNE-OCTOBER-(November in south).

Distribution and habitat: Colorado Plateau from Four Corners region to southeastern Arizona and adjacent New Mexico (Fig. 39E); ponderosa and fir-spruce forests, Upper Sonoran Zone (pinon-juniper), mixed grasslands, disturbed areas, rocky outcrops, pastures, riparian habitats; sandy soil; 1200-2900 m (4000-9500 ft.) elevation.

Discussion: Variety *pedunculata* is distinguished by its usually pale green to white, densely to very densely pubescent oblanceolate leaves that are also sparsely to moderately glandular and to a lesser degree by its often long pedunculate heads that are not subtended by large bracts and its anthocyanotic phyllary tips and margins (Fig. 45). Semple (1990) included it among tentative synonyms of var. *villosa*, but the results of multivariate analyses conducted since then indicate that it is sufficiently distinct from var. *villosa* to warrant recognition even when only non-diagnostic traits are used in the discriminant analysis. It is the only usually tetraploid taxon in sect. *Phyllothea* that has very densely pubescent leaves. All other tetraploids have fewer hairs/mm². In southeastern Utah, southwestern Colorado and northwestern New Mexico, var. *pedunculata* often becomes difficult to separate from more pubescent forms of var. *minor* and var. *scabra*. Both are tetraploid in this area. For example, the type material of *Chrysopsis hirsutissima* includes plants that can be assigned to var. *pedunculata* with high probability and plants that can be assigned to var. *minor* with moderately high probability. My own field work in the area resulted in a number of collections that were not readily assignable to either variety, as well as collections from populations that included only typical members of var. *pedunculata*.

Populations sampled on the Mogollon Plateau in eastern Arizona and hills in southwestern New Mexico included plants that were very tall (50-70 cm) for var. *pedunculata* and were glandless. Including these in var. *pedunculata* makes the taxon highly varied in stem height. Differences in soil conditions, moisture content and long growing seasons may account for the great range in stem height. A similar situation appears to be occurring in var. *scabra* further to the northwest in Nevada and Utah where soil moisture content varies greatly from year to year. These tall aberrant members of var. *pedunculata* might represent another regional morphotype that could be given nomenclatural recognition. Southeastern Arizona is most decidedly the region that caused Asa Gray his greatest difficulties; the same can be said for my studies.

Var. *pedunculata* can be similar to the Mexican species *H. gypsophila* (Fig. 25), *H. mexicana* (Fig. 22) and *H. mucronata* var. *mucronata* (Fig. 23) in habit and capitulescence features, but differs in indument traits. If the more pubescent forms of the *Mexicana* complex are primitive in the section, then var. *pedunculata* is likely to be similar to the ancestral form of *H. villosa* from which other taxa in the species evolved as the species migrated northward in the mountains and then out onto the Great Plains. The var. *minor* form resulted from loss of hairs to varying degrees. It is hypothesized here that var. *villosa* resulted from loss of glands in more hairy forms of proto-var. *minor* on the northern Great Plains area relatively recently rather than evolving directly from a less hairy, less glandular form of var. *pedunculata*.

Specimens examined: U.S.A. ARIZONA. *Rothrock s.n.* (MIN), *Rothrock s.n.* (CAN38842). Apache Co.: *Rothrock s.n.* (CAN). Black R., *Rothrock 791* (GH), *Rothrock 792* (GH(2)). E of Tsaile Cr., *Francke & Cazier 1155* (ASU). Lukachukia Mts., *Goodman & Payson 3183* (GH, NY); N of Buffalo Pass, *Anderson & Heil 87-140* (ASU); Red Rock, *Gould, Phillips 4840* (NY, UC). Navajo Ind. Res., E of Cross Cyn. Trading Post, *Harms 1895* (KANU, SASK); S of Mexican Water, *Hall s.n.* (NMC.); Navajo Comm. Coll., *Reeves 7798* (ASU); W of St. Michaels, *Harms 1896* (KANU, SASK). Coconino Co.: Coconino N.F., *Bruff & Bodley s.n.* (USFS); Big Fill Enclosure, *Merrick M-8* (USFS). Flagstaff, *Adams s.n.* (WIS), *Hanson A 12* (CAS, NY, PH, TEX), *Jones 359* (POM), *Jones 4099* (POM). W of Flagstaff, *Genelle & Fleming 1480* (CAS). Grand Canyon N.P., NW of Colcord Lookout, *Johnson 61-56* (KANU). Between Heber & Christopher Cr., *Engard 118* (NY). S of Happy Jack, *Hess 960* (MIN). Near Jacob L., *Korstian, Baker 133A* (USFS). Kaibab NF, Bright Angel Res. Stn.,

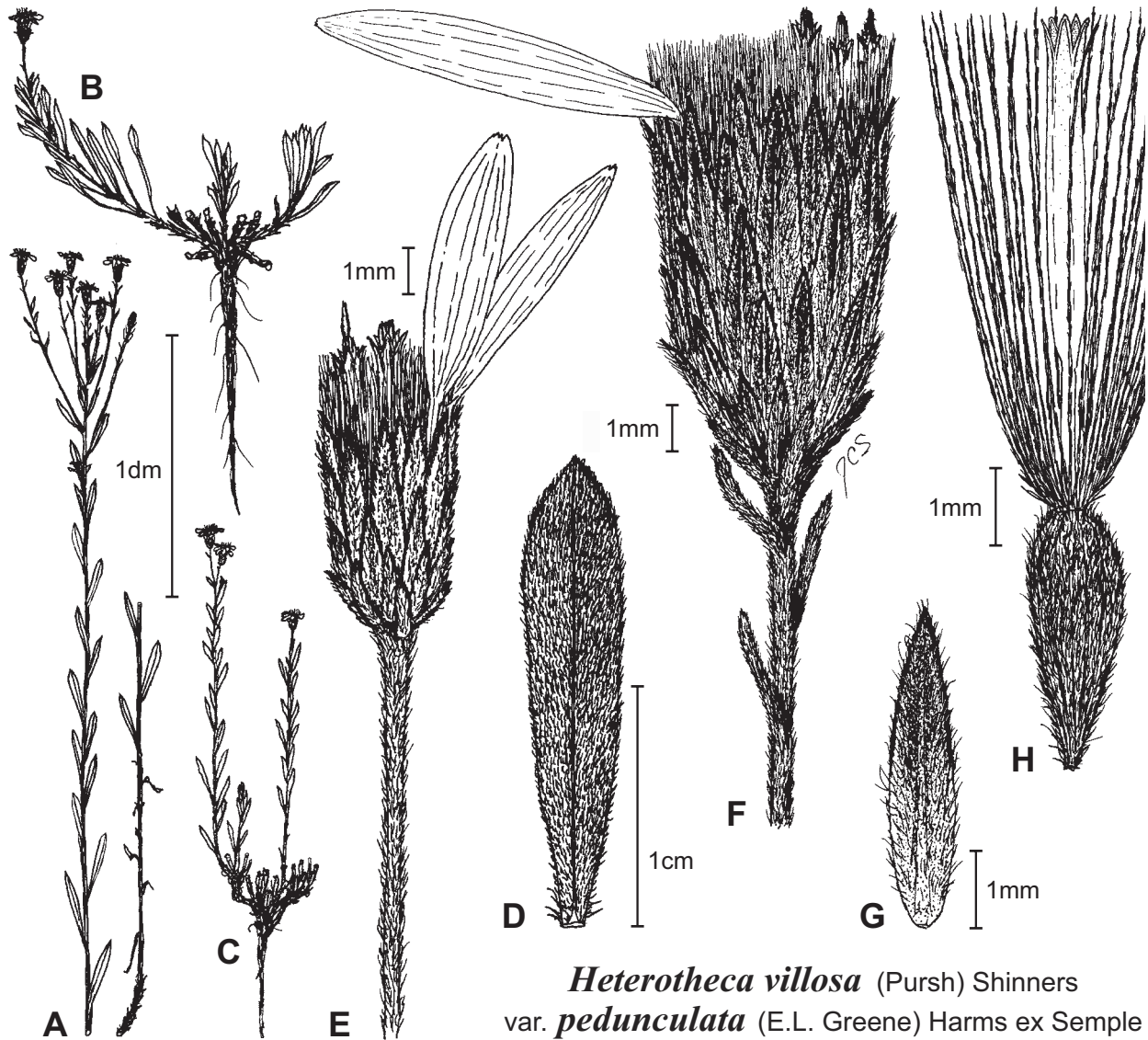


Figure 45. Morphology of *Heterotheca villosa* var. *pedunculata*. A. Shoot of taller plant. B-C. Habits of decumbent and dwarf plants, only some stems shown. D. Mid stem leaf. E-F. Heads of a small diploid and robust tetraploid with only some florets drawn. G. Mid series phyllary with chlorophyllous zone dark and apical margins anthocyanotic. H. Mature achene with disc corolla attached.

Korstian & Baker 74 (USFS). SE of Loom Rock, *Windham & Windham 91-322* (NY, UT). Mogollon Rim, *Semple & Chmielewski 9016* (WAT); W of Black Cyn., *Parfitt & Gallagher 2983* (ASU), *Pinkava, Keil & Lehto 14407* (ASU). Mormon Lake, *Toumey 615?* (DS, GH). N of Payson, *Johnson 1702* (KANU). NW of Promontory Lookout, *Johnson 1667* (KANU). S of Winslow, *Spellenberg 3508* (ASU, NY). Gila Co.: Carrizo Cr., *Pinkava, Keil & Lehto 14167* (ASU). Christopher Cr., *Lehto 7331* (ASU). E of Payson, *Semple & Chmielewski 9018* (WAT). SW of Show Low, *Semple & Chmielewski 9027* (WAT). Greenlee Co.: Clifton, Blue R., *Davidson 725* (DS, GH, UC). Navajo Co.: Chuska Mts., Whiskey L., *Carter 8232 2983* (NMC), *Klinger s.n.* (NMC), *Shirley 99* (NMC). Defiance Plateau, *Shirley 67* (NMC). N of Forestdale, *Lehto 7258* (ASU). NE of Forestdale, *Pinkava, Keil & Lehto 14091* (ASU). NE of Forestdale Trading Post, *Lehto, Pinkava & Keil L19002* (ASU), *Lehto, Pinkava & Keil L19002a* (ASU). E of Forest Lakes, *Semple & Chmielewski 9022* (WAT). E of Heber, *Semple & Chmielewski 9023* (WAT). W of Heber, *Lehto 1980* (OBI). Hopi Ind. Res., Second Mesa Villages, *Harms 19133* (KANU, SASK). Rim Rd., *Pinkava, Keil & Lehto 14422* (ASU). S of McNary Jct., *Moldenke & Moldenke 27902* (LL). Show Low,

Lambson s.n. (ASU), *Sutherland 19* (ASU). SW of Show Low, *Semple & Chmielewski 9024* (WAT), *Semple & Chmielewski 9026* (WAT), *Semple & Semple 10492* (ASU, WAT). *Semple & Semple 10493* (ASU, WAT). Snow Lake, *Lehto 2035* (ASU). N Fork White crossing, *Lehr 1986* (BRY). COLORADO. Lower Black Cyn., *Baker 123* (NDG!; holotype of "C. incana" Greene, unpublished). Archlueta Co.: NE of Chimney Rock, *Harms 2053* (KANU, SASK, WAT). Pagosa Springs, *Bethel, Willey & Clokey 4327* (CAN, CAS, DS, MIN, POM, RM, UC, WIS, WS, WTU), *Semple 8806* (WAT). NE of Pagosa Springs, *Harms 2050* (KANU, SASK), *Harms 2051* (KANU, SASK), *Semple 8804* (WAT). S of Pagosa Springs, *Hess 474* (UC, WTU). Piedra, *Schmoll 1335* (RM), *Schmoll 1335a* (RSA). W of Piedra, *Harms 2055-B* (KANU, SASK). Gunnison Co.: Rogers, *Baker 794* (DS, MIN, NY, POM, RM, UC). Hinsdale Co.: San Juan N.F., Bridge Ranger Stn., *Anderson A-54* (USFS). Montezuma Co.: Mesa Verde N.P., *Schmoll & Nusbaum 1755* (RM). Montezuma N.F., *Copple 62* (USFS), *Kauffman 367* (USFS), Glade Ranger Stn, *Wilson 655* (USFS). NW of Pleasant View, *Semple 8813* (WAT). Ouray Co.: E of Dallas Divide, *Wetter 633* (NY, WIS). S of Quray, *Watson 523* (TEX). Rio Blanco Co.: No Name Ridge, *Walker & Riefler 82-315* (ASU). San Juan Co.: W of Silverton, *Harms 2066* (KANU, SASK). NEW MEXICO. *Wooton s.n.* (NMC). Dona Ana Co.: Mesilla Valley, *Mead s.n.* (NMC). NW of San Miguel, *Fosberg S3850* (LL, UC). Grant Co.: near Silver City, *Greene s.n.* (NY, POM). McKinley Co.: Navajo Expt Stn, *Eastwood & Howell 6853* (CAS), *Eastwood & Howell 6870* (CAS). Zuni Mts., *Spellenberg 3527* (ASU, NMC, NY); McGaffey Camp, *Baad 1075* (WTU). Rio Arriba Co.: *Peabody & Sears 1959* (BRY). San Juan Co.: NE of Crystal, *Francke & Cazier 1099* (ASU). Above Toadlena, *Anderson 87-145* (ASU). W of Toadlena, Chuska Mt., Dead Man L., *McKnight 5808190106* (MIN), *Wright s.n.* (MIN). Union Co.: W of Gladstone, *Harms 19111* (KANU, SASK). UTAH. Grand Co.: LaSal N.F., Sallies Hollow, *DeSpain D-16* (RM). N of Thompson, *Foster & Foster 5031* (BRY). San Juan Co.: Colorado R, above Gretchen Bar, *Holmgren & Goddard 9982* (NY, UC). W of Eastland, *Semple 8814* (WAT). Elk Mts, Bears Ears, *Higgins & Welsh 14248* (BRY); Gooseberry Stn., *Cottam 9672* (RSA), *Flowers s.n.* (BRY), *Olsen O-5* (USFS).

aff. var. *pedunculata* (aff. var. *minor*)

U.S.A. ARIZONA. Mogollon Mts., Rim Rd., *Collom s.n.* (PH). Apache Co.: Lukachukai Mts., S of View Point, *Goodman & Payson 2875* (NY). Navajo Co.: Show Low L., *Sutherland 19* (ASU). COLORADO. Ouray Co.: S of Ouray, Red Mountain Rd., *Underwood & Selby 331* (NY). NEW MEXICO. Caton Co.: Mogollan Mts., high rocky summits, *Rusby 168* (MIN, NY(3), PH). UTAH. San Juan Co.: W of Monticello, *Ghiselin 632* (WIS).

aff. var. *pedunculata* (aff. var. *scabra* and mixed collections)

U.S.A. ARIZONA. Coconino Co.: Corral Valley, *Coombs & Bundy 2890* (ASU, BRY, NY). Grand Canyon N.P., Mather Point, *Harms 1884* (KANU(2), SASK(2), WAT). Navajo Co.: near Oraibi, *Carter 8148* (NMC). UTAH. Grand Co.: Courthouse Wash, *Allan 18* (BRY).

aff. var. *pedunculata* (possible hybrids with *H. fulcrata* var. *amplifolia*)

U.S.A. ARIZONA. Coconino Co.: Strawberry, *Semple & Chmielewski 9017* (WAT). NEW MEXICO. Catron Co.: near Luna, *Pinkava, Lehto & Reeves 12752* (ASU(2)).

aff. var. *pedunculata* (possible hybrid with *H. zionensis*)

U.S.A. ARIZONA. Navajo Co.: US-180 E of Holbrook, *Semple & Heard 7906* (WAT).

17.6 *Heterotheca villosa* (Pursh) Shinnery var. *minor* (Hook.) Semple, Novon 4: 54. 1994.

Chrysopsis villosa (Pursh) Nutt. [var.] â *minor* Hook., Pl. Geyer, Lond. J. Bot. 6: 244. 1847. TYPE: U.S.A. [WYOMING. Sweetwater Co.:] "Oregon [Territory]. On the granite masses of the Sweet Water River, only fringing the fissures," Jul 1843, *Geyer 7* (Holotype: K ex Hook.!; GH!, K ex Benth!)

Diplopappus hispidus Hook., Fl. Bor. Amer. 27: 22. 1834. *Chrysopsis hispida* (Hook.) DC., Prod. 7: 279. 1836.

Chrysopsis villosa (Pursh) Nutt. var. *hispida* (Hook.) A. Gray, Synop. Fl. N. Amer. 1, 2: 123. 1884.

Heterotheca villosa (Pursh) Shinnery var. *hispida* (Hook.) Harms, Brittonia 26: 61. 1974. TYPE: CANADA. SASKATCHEWAN. Carlton House [Fort], 1827, *Richardson s.n.* (Lectotype [Semple 1990]: BM!, shoot No.2).

Chrysopsis villosa (Pursh) Nutt. var. *discoidea* A. Gray, Synopt. Fl. N. Amer. 1,2: 123. 1884. *Diplogon villosum* (Pursh) Kuntze var. *discoidea* (Gray) Kuntze, Rev. Gen. Pl. 1: 334. 1891. TYPE: U.S.A. MONTANA. [Ravalli Co.:] cañon from Ravalli to Bitterroot Valley, 26 July 1880, *Watson 141* (Holotype: GH!, rays present on immature heads, eaten away on mature ones).

Chrysopsis columbiana Greene, Erythraea 2: 95. 1894. TYPE: CANADA. BRITISH COLUMBIA. Spence's Bridge, 30 May 1889, *Macoun s.n.* (Holotype: NDG!; isotype: CAN!)

Chrysopsis hirsuta Greene, Pittonia 3: 296. 1898. TYPE: U.S.A. WASHINGTON. near Spokane, banks of Hangman Creek, 3 Sept 1896, *Piper 2385* (Holotype: NDG!; isotype: GH!)

Chrysopsis floribunda Greene, Pittonia 3: 100. 1896. TYPE: U.S.A. COLORADO. Gunnison Canyon, 27 Aug 1896, *Greene s.n.* (Lectotype: NDG-053916!; isolectotype: NDG-053915)

Chrysopsis hirsutissima Greene, Pittonia 4: 154. 1900. TYPE: U.S.A. COLORADO. Arboles, 5 Jun 1899, *Baker 650* (Lectotype: NDG-053929!; isolectotypes: GH!, ?NDG-053921!, NMC!, NY!, RM!(2), UC!, US!). Harms annotated as type the second ND-G Baker collection which does not have a collection number. Some of the type material is close to or convarietal with var. *pedunculata*; thus the type population may have included hybrids

between var. *minor* and var. *pedunculata*.

Chrysopsis compacta Greene, Leafl. Bot. Obs. & Crit. 1: 150. 1905. TYPE: U.S.A. COLORADO. Jack's Cabin, 26 Jul 1901, 8280', *Baker 608* (Holotype: NDG!; isotypes: GH!, MIN!, NY!, RM!(2), US!)

Chrysopsis asprella Greene, Leafl. Bot. Obs. & Crit. 1: 150. 1905. TYPE: U.S.A. COLORADO. bottom of Black Canyon, 8 Jul 1901, *Baker 379* (Holotype: ND-G!; isotypes: GH!, MIN!, NY!, RM!(2), US!)

Chrysopsis arida A. Nels. ex Rydb., Fl. Colo., 340. 1906. nom. nud.

Chrysopsis arida A. Nels. in Coult. & Nels., New Man. Bot. Rocky Mts. 492. 1909. TYPE: U.S.A. WYOMING. Albany Co., Tie City, 20 Jul 1900, *Nelson 8224a* (Holotype: RM!; isotype: NY!)

Chrysopsis grandis Rydb., Bull. Torr. Bot. Club. 37: 129. 1910. TYPE: U.S.A. MONTANA. Jocko Creek, 16 Jun 1901, *MacDougal 275* (Holotype: NY!)

Chrysopsis bakeri Greene, Pittonia 4: 154. 1900. TYPE: U.S.A. COLORADO. near Pagosa Springs, 9000', 23 Aug 1899, *Baker 649* (Lectotype, Semple 1987: NDG!; isolectotypes: GH!, NDG(2)!, NMC!, NY!, POM!, RM!, UC!, US!)

Chrysopsis wisconsinensis Shinnars, Wrightia 1: 218-219. 1948. TYPE: U.S.A. WISCONSIN. Adams Co., 14 mi N of Wisconsin Dells, exposed sandy slope, 7 Jul 1947, *H. Greene s.n.* (Holotype: SMU!; isotypes: GH, IL, MIL, WIS)

STEMS several to many, ascending-erect, (9)-16-**25**-33-(48) cm tall, sparsely to densely hispid-strigose, long spreading hairs few to numerous; (9)-12-**18**-25-(39) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (16)-23-**33**-42.5-(60) mm long, (2.7)-4.1-**6**-7.8-(13) mm wide, petiolate, cuneate, sometimes slightly mucronate, sparsely to moderately densely hispid-strigose and sparsely to moderately densely glandular on both surfaces; margins entire, strigose, longer spreading hairs along margins basally. UPPER STEM LEAVES narrowly to broadly oblanceolate, (11)-16-**22**-28-(40) mm long, (2.3)-3.6-**5.1**-6.7-(12.5) mm wide, sessile, somewhat reduced upward, acute to sometimes obtuse, indument similar to lower, (1)-4-**11**-19-(32) glands/mm², (1)-12-**29**-47-(75) hairs/mm², margins flat, sometimes remotely undulate, a few longer hispid hairs along margins basally. CAPITULESCENCE congested to open cymose-corymbiform, heads 1-**6**-13-(42); peduncles moderately to densely hispid-canescens, glandular, (4.5)-16.9-**28.7**-40-(60) mm long; bracts few, linear-oblong, usually reduced, rarely foliar and linear-oblanceolate, indument like leaves. INVOLUCRES cylindrical to campanulate when fresh, campanulate-hemispheric upon drying, (5.5)-6.5-**7.5**-8.5-(9.3) mm high; phyllaries in 4-5 imbricate series, outer and mid series, narrowly triangular-lanceolate, sparsely to rarely densely strigose, sparsely to moderately glandular, rarely eglandular, margins hyaline narrow, fimbriate-ciliate and sometimes anthocyanotic apically; inner ones similar. RAY FLORETS (7)-10-**14**-18-(26), strap yellow, (4)-6.1-**8.1**-10.1-(12.6) mm long, (0.5)-0.9-**1.4**-1.8-(3) mm wide. DISC FLORETS (12)-24-**42**-60-(81), yellow, glabrous or a few minute hairs, corolla barely ampliate, (4.1)-5.1-**5.7**-6.3-(7.7) mm long, lobes (0.45)-0.52-**0.65**-0.78-(1) mm long, hairs usually absent or very few, 0.1-**0.15**-0.2-(2.8) mm long. ACHENES (1.2)-1.7-**2.2**-2.7-(3.4) mm long, sparsely to moderately strigose; pappus off-white, double, outer whorl of linear scales 0.25-1 mm long, inner whorl of 35-45 barbellate bristle (4.1)-5.2-**5.9**-6.5-(7.5) mm long. Chromosome numbers: $2n = 18, 36$; numerous reports.

Flowering Period: (May)-JUNE-AUGUST-(November).

Distribution and habitat: Scattered across the northern plains and throughout the western mountains from British Columbia and Alberta south to New Mexico and northern Arizona and down the Cascade Mts. to the central Sierra Nevadas in California (Fig. 40A); rocky slopes, stream banks, basaltic cliffs and lava flows, dry ledges, glacial outwashes, roadside and railroad embankments, in grasslands, ponderosa pine-oak woods, and open pinon-juniper associations; gravelly, sandy and loamy soils, crevices in granite, limestone rocks, and marble rocks, eroded granites and sandstones; (60)-300-2900-(3200) m ((200)-1000-9500-(10500 ft.)) elevation.

Discussion: Variety *minor* is distinguished by its upper stem leaf shape and indument (Fig. 46). The leaf bases are usually narrowly to broadly tapering (rarely more oblong than oblanceolate) and usually about 10-50 hairs/mm² and about 4-20 glands/mm² on the upper surfaces of the upper leaves. The stem indument

varies greatly with few to many long hairs extending outward beyond the sparse to dense lower layer of appressed to spreading hairs. The leaf indument density of the lectotype of *Chrysopsis hispida* is very low for any *Heterotheca*: 2 to 3 curved hairs/mm² and 8 to 9 glands/mm², while the isotype (GH) of var. *minor* is about average with 28 hairs/mm² but at the high end for gland density with about 25 glands/mm². The variety has often been treated as differing from typical *villosa* only in the number of glands and by having numerous long hispid stem hairs. While such plants are included here in var. *minor*, they comprise only a small portion of the range of variation in the variety. Both diploids and tetraploids are known in var. *minor* from much of the taxon's western range in the mountains; head size suggests the type is probably a diploid. East of the Rocky Mountains the variety appears to be predominantly tetraploid. Variety *minor* is the "matrix" that links all other varieties of the species together; thus it is analagous in concept to var. *echioides* of *H. sessiliflora* and var. *fulcrata* in *H. fulcrata*.

Variety *minor* converges with var. *villosa* (Fig. 41) across the Great Plains, where the former is rarer and the latter is more common, and throughout the Rocky Mts. in the northern United States and southern Canada where the former is more common and the latter is rarer. Like var. *fulcrata* and var. *amplifolia* in *H. fulcrata*, var. *minor* and var. *villosa* are not readily separated due to the many intermediates that occur. Pure populations occur throughout the range of var. *minor*. Many plants identified by others as var. *villosa* have some glands scattered among the many leaf hairs; these are treated here as members of var. *minor*.

Atypical forms occasionally occur throughout the range and may be the result of unusual growing conditions or local genetic divergence rather than the consequence of hybridization. For example in California, var. *minor* shows considerable variation in indument density and leaf shape; some of the extremes are similar in diagnostic features to other varieties in the species which occur nowhere near California. The occasional individual of var. *minor* can have oblong leaves like those of var. *nana* (Fig. 48), but these appear to represent convergence rather than being true var. *nana*. A few plants from near Lake Tahoe have large *fulcrata*-like bracts subtending the heads; again, these are considered to be the result of convergence rather than members of the taxon they resemble. Specimens from northwestern California include glandular, sparsely glandular and non-glandular individuals. The former are easily included in var. *minor*; the latter have been assigned to var. *villosa* (Semple 1993) although these may just be extreme variants in isolated populations of var. *minor*. The less glandular plants are also placed in var. *minor*.

The taxon reaches its eastern limits in a small group of disjunct populations in southcentral Wisconsin and northwestern Illinois (Fig. 40A). The Wisconsin plants were described as a separate species *H. wisconsinensis* Shinnars. They are less pubescent and relatively much more glandular than most plants of var. *minor* from adjacent Minnesota, but not very different from other forms of var. *minor* occurring further west. Some of the Wisconsin plants have leaf bases like those of var. *nana* (Semple 8845 WAT), and some have tapering upper leaf bases (the holotype). Either "wisconsinensis" originated as an eastern disjunct of var. *nana* rather than var. *minor*, or it is merely a marginal population of var. *minor* that has diverged from the typical form and converged to var. *nana* on this trait. Alternatively, both varieties may have reached the driftless area and now local plants contain genes of both taxa. Both diploids and tetraploids have been found in the area. Additional experimental work should be done to determine the origins of this Wisconsin form of *H. villosa*.

Specimens examined: CANADA. ALBERTA. *Sanson* 22179 (CAN). SE28 32 16 W4, *Brinkman* 148 (NY). Anthracite, *Macoun* 9877 (CAN). Banff, *Fletcher* 7885 (CAN), *Jenkins* 1362 (DAO), *Laing* 359 (CAN); near Banff, *Farr s.n.* (PH); Tunnel Mt., *Macoun s.n.* (CAN), *Scott s.n.* (DAO). Banff N.P., 3rd Lake Banff, *Thompson s.n.* (CAN), above Sheep Lick, *Mair* 106 (UBC); base of Mt. Cory, *Porsild & Breitung* 13145 (CAN); Vermilion L., *Malte & Watson* 916 (CAN). Bonnyville, *Groh* 1102 (DAO). E of Bow Island, *Semple & K.Shea* 1944 (WAT). Buffalo, *Smith s.n.* (CAN). Between Medicine Hat and Calgary, *Scott s.n.* (DAO). Cardston, *Macoun* 10819 (GH), *Scotter* 10088 (DAO). Castlemount, *Malte & Watson* 455 (CAN). Clearwater For. Res., *Porsild* 20654 (CAN). W of Coleman, *Semple & K.Shea* 1958 (WAT). Mile 24 on Coleman to Kananaskis road, *Morton* NA4684 (WAT). Craigmyle Dist., *Brinkman* 726 (GH), *Brinkman* 5342 (DAO, UBC). N of Craigmyle, *Brinkman* 4721 (PH, POM, UBC). Crows Nest For. Res., *Malke s.n.* (CAN). Crowsnest area, *Ogilvie s.n.* (UBC). NE of Edmonton, *Moss* 4133 (CAN, WIS). S Edmonton, *Muhlenbach s.n.* (DAO). E of Ft Macleod, *Semple & K.Shea* 1946 (CAN). Hardisty, *Moss* 9726 (CAN). back of Hillsdale, Mt. Cory, *Porsild & Breitung* 15504 (CAN). Lethbridge Dist., Milk R.,

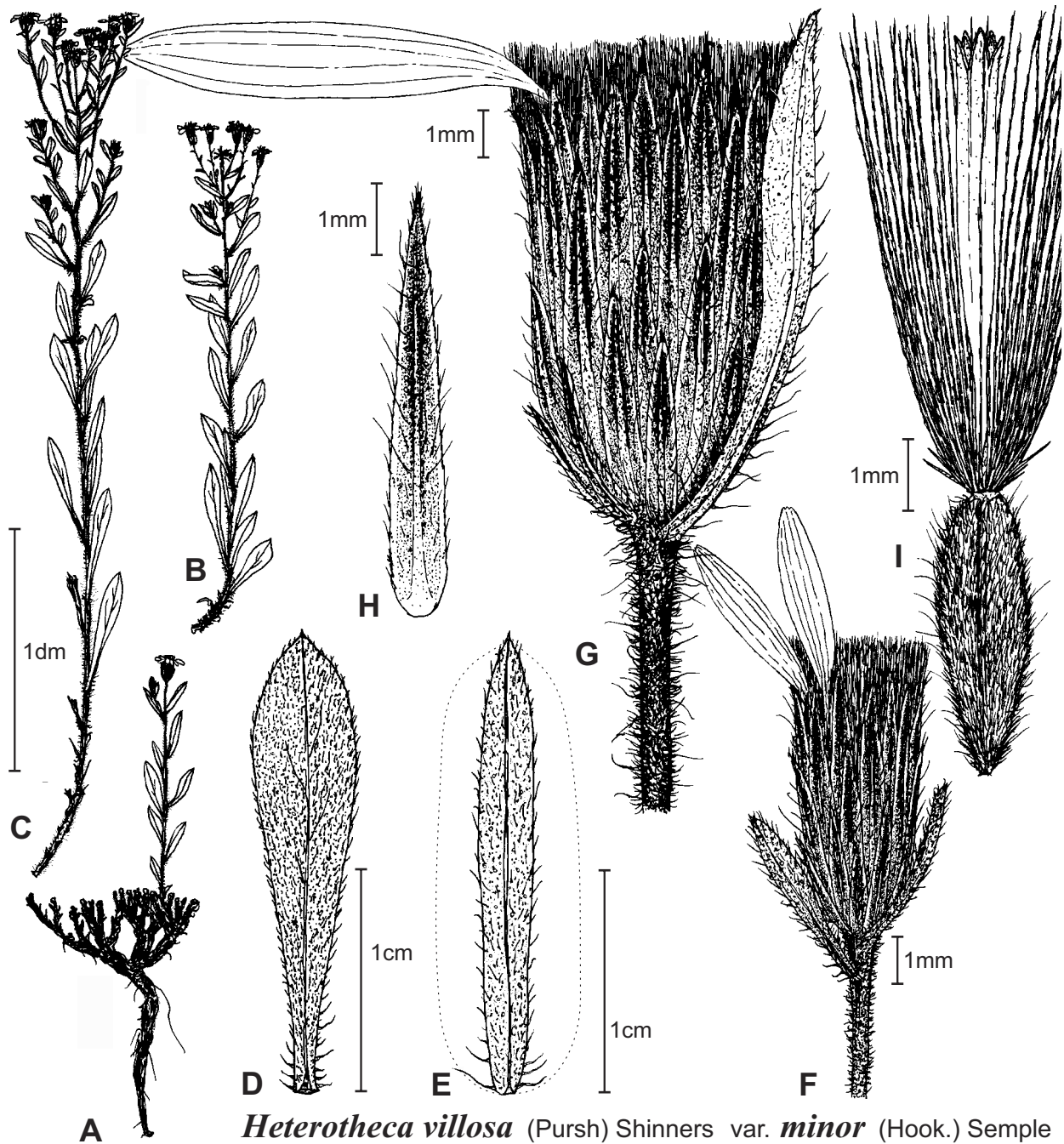


Figure 46. Morphology of *Heterotheca villosa* var. *minor*. A. Habit of dwarf plant, only one of many shoots drawn. B. Shoot of average size. C. Shoot of robust plant (holotype of *Chrysopsis grandis*). D. Lower-mid stem leaf of a moderately densely pubescent plant; leaves can be narrowly oblanceolate; basal leaves can be much longer. E. Mid-upper stem leaf, sparsely pubescent; leaves may be oblong (broken line) or more oblanceolate like lower stem leaves. F-G. Heads of dwarf diploid and robust tetraploid plants with only some florets drawn; foliar bracts often not present. H. Mid series phyllary with chlorophyllous zone dark; may be more pubescent and less glandular; the apical margins can be somewhat anthocyanotic. I. Mature achene of tetraploid plant, disc corolla attached.

Boivin & Perron 12261 (DAO, GH). Lethbridge, *Brink s.n.* (UBC). Medicine Hat, *Morton NA 3426* (WAT). Morley, *Wiehler 6991* (WIS). near Morley, *Packer s.n.* (DAO). W of Nordegg, *Porsild 20687* (CAN). Red Deer R by Hwy-585, *Hainault 7109* (DAO). N of Vermilion, *Bird 126* (DAO). SSE of Vermilion, *Bird 134* (DAO). vicinity of Banff, *Hunnewell 3858* (GH), *McCalla 2032* (NY). Waterton Lakes N.P., edge of Red Rock Cyn Nature Tr, *Sudol 52* (DAO), 1 mi W of Blakiston Falls, 5500', *Blais 2896* (CAN), Waterton River transition zone, *Breitung 16279* (NY), E park boundary, *Brietung 17142* (NY), *Brietung 17142a* (NY). **BRITISH COLUMBIA.** Ashnola Rd. (mp29), *Hainault 7937* (DAO, UBC). Ainsworth Bluffs, *Eastham s.n.* (UBC(2)). Baynes Lake near Fernie, *Pringle s.n.* (UBC). Beaverdell, *Eastham s.n.* (UBC). Bluebell Mt., Crawford Bay, *Murray s.n.* (UBC). Columbia Valley, *Murray s.n.* (UBC). Cranbrook, *Eastham s.n.* (UBC(2)). NE of Cranbrook, *Weber 2244* (CAN, GH, NY, UC, WS, WTU). S of Cranbrook, *Semple & K.Shea 1961* (CAN, WAT). N of Cranbrook, *Rogers s.n.* (UBC), *Goward 81-1583E* (UBC), *Eastham s.n.* (UBC). Crown L., *Beamish 630214* (UBC). W of Delmas, *Harms 17066* (KANU, SASK(2)). Flathead, *Davidson 602* (UBC). Fraser Canyon near Big Bar Creek, *Pojar s.n.* (UBC). Fraser R S of Sheep Cr, *Marchant s.n.* (DAO, UBC). W of Hedley, *Straley & Schofield 2129* (UBC). Hot Springs, Kootanie L., *Macoun 9878* (CAN, NY). Kamloops Lake, *Wilson s.n.* (UBC). near Kamloops, *Tice s.n.* (UBC), *Eudes 5062* (DAO); N of Paul L., *McCabe 2400* (UC). N of Kamloops *McCabe 2404* (UC), *McCabe 2439* (UC). Kelowna, *Taylor 1133* (UBC). East Kelowna, *Brink s.n.* (UBC). N of Killedeer, *Harms & Skoglund 19351* (KANU, SASK). Kimberley, *Fodor 102* (UBC), *Oseko 44* (UBC). N of Kimberley, *Rogers s.n.* (UBC). NE of Kimberley, *Douglas & Douglas 7489* (BRY). Knob Hill, Okanagan, *Wilson s.n.* (UBC(2)). Kootenay, *Ruhman s.n.* (UBC(2)). Kootenay L. area, Koocanusa L., *Goward 81-1730B* (UBC). Kootenay N.P., Sinclair Cyn., *Seel 123* (DAO). Lillooet, *Brink s.n.* (UBC), *Anderson 760* (WS(2)). E of Lillooet, *Straley 3640* (UBC). Limestone Pt, *Macoun 9876* (CAN). near international boundary between Kettle and Columbia Rivers, *Macoun 65027* (NY). WNW of Lower Nicola, *Goward 81-1239B* (UBC). W of Mabel Lake, *Bohm 1949* (UBC). Natal, *Taylor & Ferguson 2288* (DAO, DS). Nicola, *Tisdale s.n.* (GH). Okanagan L., *Dawson 9875* (CAN). S of Oliver, *McCabe 4585* (UC). Osoyoos, *Brayshaw 49294* (UBC). Osoyoos L., *Fisher s.n.* (UBC), *Calder & Savile 9622* (GH), N of lake, *Crins & Cannings 7377* (UBC). Palliser to Glenogle, *Brown 788* (GH, NY). Pavillion Lake, *Taylor & Lewis 12* (UBC), *Taylor & Lewis 194* (UBC); *Taylor, Krajina & Tusko 14* (UBC). Peachland, *Bowers 1062* (UBC). Pend'Oreille R, *Macoun 65024* (CAN). Pentiction, *Eastham s.n.* (UBC). Quesnel, *Taylor s.n.* (UBC). Richter Pass (Okanagan SW), *Tisdale 40-742* (GH). Sinclair Canyon, *McCalla 3803* (UBC). Lower Stein Valley, *Sharpe 24* (UBC). Summerland, *Bostock s.n.* (DAO); Trout Creek Ecological Res., *Larmour & Ng s.n.* (UBC). Surrey, *Lomer s.n.* (UBC). SW of Williams Lake., *Goward, Roberts & Schuen 81-2145B* (UBC). Tranquille Range, *Tisdale s.n.* (UBC(2)). Waldo, *Brayshaw s.n.* (CAN), *Edgar s.n.* (UBC). Waneta, *Jamieson 62352* (CAN). Wasa, *Adams RJA433* (WAT). Windermere, *MacKenzie s.n.* (UBC). **MANITOBA.** *Walker s.n.* (DAO). Aweme, *Criddle s.n.* (DAO). Broomhill, *Scoggan 11047* (CAN, GH). W of Deleau, *Bassett & Kemp 3618* (DAO). NW of Melita, *Scoggan 11045* (CAN, GH, MIN). E of Oak L., *Semple & Brouillet 4194* (WAT). Quesnel L (Caribou), *Keleher 74-278* (DAO). Rivers, *Krajina 20* (UBC), *Oldenburg 40-11B* (MIN). Stoney Mt., *Groh s.n.* (DAO). Turtle Mt., *TTWB 939* (DAO). **SASKATCHEWAN.** *Bourgeau s.n.* (NY). SE of Chamberlain on Hwy 6, *Harms 2529-B* (KANU). E of Coronach, *Harms 19363* (KANU). Cypress Hills, *Breitung 5466* (DAO); WSW of Maple Cr., *Semple & K.Shea 1940* (CAN, WAT). Girvin L., *Russell S52099* (DAO). Hoosier, *Jenkins s.n.* (DAO). NW of Hoosier, *Jenkins 853* (DAO). Indian Head, *Macoun 9882* (CAN). Kipling, *Taylor s.n.* (DAO). Lumsden, *Calvert s.n.* (WAT). W of Moose Jaw, *Semple & K.Shea 1935* (WAT). Near Prince Albert, *Macoun 12215* (CAN, NY). Pilot Butte, *Shevkenek 2* (DAO). Near Prince Albert, *Macoun 12215* (CAN, NY). E of Prince Albert, *Boivin & Breitung 6107* (DAO, NY). Near Prince Albert, *Macoun 12215* (CAN, NY). NW of Prince Albert, *Anastasiou & Gilliland 51-A-62* (UBC). Regina, *Carmichael 2* (DAO). Saskatoon, *Fraser 7* (WIS). E of Saskatoon, *Argus 9097* (CAN). Scott, *Russell s.n.* (DAO). E of Shaunavon, *Taylor s.n.* (DAO). Sturgis, *Allen 41* (WAT). E of Success, *Looman 13453* (DAO). Swift Current, *Hammond 9984-4* (NY). Totnes, *Perret 123* (DAO). W of Waldeck, *Semple & K.Shea 1936* (CAN, WAT). **U.S.A.** "Willamette to California," *Wilkes Expedition s.n.* (NY). **ARIZONA.** Deer Spring, *Rothrock 182* (GH). Apache Co.: Carrizo Mts., *Nash N211* (ASU). Cyn. de Chelly N.Mon., Battle Cove Ruins, *Halse 157* (LL); above White House, *Bailey 310* (UC), *Bailey 335* (UC). E of Lukachukai, *Francke & Cazier 1065* (ASU). Navajo Ind. Res., Bihiline Cyn., *Reeves 8069* (ASU), *Reeves 8074* (ASU). St. Johns, *Hope 9334* (UC). Window Rock, *Bohrer 626a* (UC). Coconino Co.: Echo Cliffs, *Hevly & Mead s.n.* (NY). Grand Cyn., *Moldenke 7027* (NY). Long Valley, *Hutchinson 4096* (ASU). Navajo Ind. Res., Navajo Mt., *Clute 38* (RM). NE of Pine, *Partch 410* (ASU). San Francisco Pk., *Lepper s.n.* (WIS). Navajo Co.: Shonto, *Eastwood, Howell 6585* (CAS). **CALIFORNIA.** *Hanks 7* (RM). *Vasey s.n.* (KANU). "Northern California," *Wilkes Expedition s.n.* (NY). Chat, *Hillman s.n.* (POM), *Jones s.n.* (POM). Head of American R., *Greene s.n.* (GH). Lake Tahoe region, *Van Dyke s.n.* (CAS), *Abrams 4786* (DS, GH, MIN, NY, UC). Upper Fall River Valley, *Jepson 5783* (JEPS). Alpine Co.: Pigeon Flat, *Hoover 4154* (LL, UC). Between Raymond L. and Pleasant Valley, *Hardham 17711E* (TEX). Eldorado Co.: Heather L., *Abrams 12737* (DAO, LL, WS(2), WTU). Lassen Co.: Ft. Sage Mts., *Schoolcraft 735* (NY). Near Hellalujah Junction, *Williams 74-61-61* (TEX). Nevada Co.: *Brandagee sn.* (UC). Plumas Co.: Chilcoot, *Rose 34419* (CAS, WTU). N of Chilcoot, *Schoolcraft 814* (NY). Frenchman's Reservoir, *Williams, Howell & Folette 77-70-3* (NY). S of Johnsville, *Denton 3882* (WTU). N of Loyalton, *Howe 5080* (SD), *Semple, Suario & Ahmed 9314* (WAT). E of Portola, *Barclay, Barbee, Blum & Koch 1516* (LL), *Semple, Suario & Ahmed 9313* (WAT). Sierra Valley, *Lemmon 27* (PH). Taylorville, *Semple, Suario & Ahmed 9309* (WAT). S of Vinton, *Lavin 4419* (CAS, TEX). Shasta Co.: E of Old Station, *Semple et al. 5715* (ASU, CAN, JEPS, JCS, MT, NY, WAT, UAC). N of Old Station, *Semple, Suario & Ahmed 9302* (WAT). Sierra Co.: old shingle mill near state line, CPRR, *Sonne s.n.* (UC). Near Verdi, Nev. *Sonne s.n.* (MIN). Siskiyou Co.: *Howell 12405* (CAS, POM). Marble Mts, Marble Rim, *Howell 15049* (CAS, UC); Lookout, *Muth 311* (CAS, RSA). Marble Valley, *Butler 338* (JEPS, UC), *Muth s.n.* (CAS, RSA), *Muth 453* (CAS, JEPS). **COLORADO.** "Colorado Terr.," *Wolf & Rothrock 464* (PH). Arkansas Valley, *McCosh & Greene s.n.* (NY). Archlueta Co.: Arboles, *Baker 850* (POM). NE of Pagosa Springs, *Harms 2051-B* (KANU, SASK); W of town, *Harms 2052* (KANU, SASK). Chaffee Co.: Buena Vista, *Harper s.n.* (WIS). Conejos Co.: S of Bighorn Corral, *Rollins 1479* (DS, JEPS, LL, UC). Gunnison Co.: Almont, *Harmon 1120* (BRY, DS, WIS). Black Mesa, *Turner 115* (USFS, WIS). NE of Crested Butte, *Booth 49C315* (KANU, WTU). Roaring Judy Gulch, *Langenheim 464* (MIN). W of Sapinero, *Harms 2077* (KANU, SASK). S of county

airport, *Neese 15893* (BRY, RSA). West Elk Crk, Curenati Reservoir Proj., *Stock & Hall 423* (RSA). Huerfano Co.: N of Cuchara, *Harms 2034* (KANU, SASK). Lake Co.: Twin Lakes, *Clokey 3450* (CAS, GH, NY, UC), *Coulter s.n.* (PH). Larimer Co.: Chamber's L., *anon.* 2772 (NY). North Park, *Johnson 299* (RM). Mesa Co.: East Cr., *LeDoux & Dunn 667* (BRY), *Wilken & Kelley 13969* (BRY). NE of Gateway, *Maguire & Piranian 12919* (GH), *Neese 13669* (BRY, NY, RM). Grand Jct., *Crandall s.n.* (RM). Grand Mesa, *Ramaley 15424* (RM). Mack, *Jones s.n.* (POM). SW of Mack, *Neese & Abbott 13598* (BRY). S of Whitewater, *Harrington 2663* (ASU). Moffat Co.: W of Billiard Table, *Neely 4149* (NY). Between Craig and Maybell, *Stein 1901* (RM). W of Craig, *Grant & Grant s.n.* (BRY). Dinosaur N.Mon., *Holmgren, Jensen & Reveal 481* (NY), *Peterson, Emrich, Painter & Pease 1230* (ASU), *Rodeck 4439* (WTU); E of Gates of Lodore, *Neely 4267* (RM); S of Lodore Ranger Stn., *Neely 4245* (RM). N of Starvation Valley, E of Big Joe Draw, *O'Kane 3147* (RM). S of East Cactus Flat, *Neely 4049* (RM). E of Elk Springs, *Semple et al. 5764* (NY, WAT). SE of Greystone, Douglas Mt., *MacLeod 693* (TEX). Pool Cyn., *O'Kane 2996* (RM). Montezuma Co.: Cortez, *Semple et al. 5522* (WAT). S of Dolore, *Douglass 54-222* (NY). W of Durango, *Peirson 12501* (RM, UC). Mesa Verda N.P., *Bader 105* (RM), *Schmoll & Nusbaum 1638* (RM), *Selesnick s.n.* (ASU), *Wilson 363* (USFS). Montezuma N.F., *Emerson 658* (USFS). Paradox, *Walker 148* (DS, GH, MIN, RM). S of Purgatory Ski Resort, *Kass 2543* (BRY). Montrose Co.: LaSal Cr., *Cutler 2634* (DS, NY). LaSal Mts., *Franklin 2148* (BRY, CAN, NY), *Sharsmith 4442* (CAN, DAO, DS, GH, KANU, LL, NY, RM, SD, UC, WIS, WTU). Montrose, *Baker 15* (GH, NY, POM). Paradox Cr., *Walker 235* (GH, MIN, RM, WS). N of Ridgeway, *Harms 2073* (KANU, SASK). Uncompahgre N.F., *Lancaster 64* (USFS), *Maupin 18* (USFS), *Pool P-36* (USFS, WIS). Ute, *Payson & Payson 3894* (GH, LL, RM, UC). West Paradox, *Payson 2316* (CAS, GH, NY, RM). CO-145, *Mears & Mears 2803* (TEX). Ouray Co.: E of Colona, *Payson 2338* (RM). Ouray, *Osterhout 5276* (RM). N of Ouray *Beaman & Erbsich 1167* (RM). S of Ouray, *Mosquin & Mulligan 5069* (DS). W of Ouray, *Underwood & Selby 135a* (NY). Ridgway, *Payson & Payson 3835* (GH, RM). Pitkin Co.: Aspen, *Procajlo 74-47* (WAT). E of Aspen., *Semple & Zhang 10446* (RM, WAT), *Semple & Zhang 10452* (RM, WAT). NW of Aspen, *Greene 422* (PH). Basalt, *Nelson & Nelson 1411* (WS). Pueblo Co.: N of Pinon, *Harms 2004* (SASK). Rio Blanco Co.: Buford, *Duce 7288* (WTU), *Hermann 5682* (PH). Figure Four Spring, *Walker & Riefler 82-260* (NY). Stuart Gulch, *Walker & Waters 82-269* (BRY, RM). Rio Grande Co.: East Pinus Creek, *Gierisch 1062* (MIN, NY, USFS). South Fork, *Baker 15* (GH, NY, POM). Paradox Cr., *Walker 235* (GH, MIN, RM, WS). Routt Co.: Big Cr. Gulch, *Crandall s.n.* (NY). Columbine, *Tweedy 4025* (NY). Little Snake R, *Ewan 13949* (CAS). Routt N.F., *Lane 3132* (KANU), *Peck 98* (USFS), *Weber 6708* (WTU). Steamboat Springs, *Gooding 1655* (BRY, DS, GH, NY, PH, RM, UC). NNW of Steamboat Springs, *Nelson 4027* (RM). SE of Steamboat Springs, *Semple et al. 5773* (WAT). Walden, *Johnson & Hedgcock 299* (RM). Saguache Co.: San Juan Co.: L. Cutter Cyn., *Wynhoff KL-12* (ASU). Marshall Pass, *Turner 15999* (TEX). Ojo Rito Mesa, *Lister 47* (USFS). San Miguel Co.: Norwood Hill, *Walker 412* (GH, MIN, NY, POM, RM, WS). Summit Co.: Breckenridge, *Brandege 122* (NY). E of Frisco, *Harms 2091* (KANU). Gray's Peak, *Tidestrom 4080* (UC). Foot of Loveland Pass, *Harms 2092* (KANU, SASK), *Harms 2092-B* (KANU). IDAHO. Salmon N.F., Fenster Cr., *Romano 269* (USFS). Lake Pend d'Oreille, *McDougal s.n.* (MIN). Benewah Co.: S end of L. Pend d'Oreille, *Sandberg 752* (CAS, NY). Boundary Co.: N of Bonners Ferry, *Baker 13865* (NY, WTU). Moyie Springs, *Epling 10420* (MIN). S of Naples, *Keck 6541* (NY, RSA, UC). Clearwater Co.: Ahsahka, *Christ & Smith 15408* (NY). Franklin Co.: Franklin Basin, White Cyn, *Cottam & Allan 15304* (BRY, DS). Fremont Co.: county Burn Project, *Lingenfelter 557* (USFS), *Pechanec 34-45* (USFS). St. Anthony, *Cronquist 685* (UC). SW of St Anthony, *Lindsay 1984* (BRY). Snake R., Lower Falls, *Cronquist 1653* (RM). Idaho Co.: Pittsburgh Landing, *Laysen 3032* (NY). Selway Falls, *Christ 2601* (NY). Selway R., *Barkworth 242* (WS). S of Slate Creek, *Baker 8368* (NY, WTU(2)). Salmon R., *Abair s.n.* (MIN). Kootenai Co.: *Sandberg s.n.* (MIN, UC), *Sandberg s.n.* (MIN(3)), *Sandberg 265* (MIN), *Sandberg 5067* (POM), *Sandberg 6008* (NY). L. Pend d'Oreille, *Sandberg & MacDougal 752* (DS, GH, NY, POM, RM). Lakeview, *Heller 753* (UC), *McDougal 5067* (NY, POM). Lemhi Co.: Big Cr. Hot Springs, *Bradley 87* (USFS). Nez Perce Co.: Gifford, *Jones s.n.* (POM). Mouth of Potlatch R., *English 1179* (WS). Spalding, *Christ 4022* (NY). Mouth of Salmon R, *Eastwood 13292* (CAS). ILLINOIS. Jo Daviess Co.: Sand Prairie, *Pepono 10202* (F, WIS). KANSAS. Graham Co.: W of Bogue, *Imler 35* (NY). MINNESOTA. Anoka Co.: Bethel Twp., Cedar Creek Nat. Hist. Area, *Moore 25588* (MIN), *Moore 27399* (MIN). Cass Co.: near shore of Lake Cass, *Richards & Massey 1905* (MIN). Dakota Co.: Pine Bend, *Lange 4767* (MIN). Hennepin Co.: Minneapolis, *Sandberg 292* (MIN, WS). Pipestone Co.: Pipestone N.M., *Moore 22585* (MIN). Polk Co.: Dugdale, *McMillan & Skinner 83A* (MIN). SW of Fertile, Agassiz Dunes, *Ottoson 37* (MIN). N of Glenwood, *Tucker 3877* (MIN). Holmes Station, *Macmillan & Skinner 388* (MIN). Ramsey Co.: *Sister Lawrence Koehmstedt 73* (WIS). N of Savage, *McCartney 44* (MIN). Stearns Co.: N Sartell, *Westkaemper s.n.* (MIN). Swift Co.: Appleton, *Moyer 55-14* (MIN). MONTANA. "Western Mont.," *Whited s.n.* (LL). Glandin, *Aiton s.n.* (WIS). Long Prairie N of Bowman Cr., *Yuncker & Yuncker 6823* (NY). Mts. near Indian Cr, *Rydberg & Bessey 5069* (CAN, GH, MIN, NY, PH, RM). Stillwater Cyn., *Hawkins s.n.* (WIS). Blaine Co.: near Chinook, *Degener 1677* (NY). Broadwater Co.: S of Townsend, *Booth c82* (KANU, WTU). Carbon Co.: Beartooth N.F., Willow Cr., *McDonald 720* (USFS); Hell Roaring Cr., *Lackschewitz 7832* (NY). US-212, rest area, *Semple & Brouillet 4435* (WAT). Cascade Co.: S of Belt, *Harms 20227* (KANU, SASK). Cora Cr, *Anderson 129* (UC). Chouteau Co.: Geraldine, *Aiton s.n.* (UC). Deerlodge Co.: *Howard 253* (RM). W of Anaconda, *Pennell & Cotner 23556* (GH). Fergus Co.: E of Lewistown, *Stephens 68942* (KANU). Flathead Co.: *Dunn 9921* (MIN, RSA), *Dunn 10076* (RSA). Bigfork, *Butler 2372* (NY), *Jones 8515* (POM), *MacDougal 755* (NY). Columbia Falls, *Dunn 9842* (MIN), *Dunn 11789* (MIN). SE of Columbia Falls, *Rogers & Rogers 1063* (NY, WTU). SW of Columbia Falls, *Dunn 11295* (MIN), *Dunn 11293* (RSA). Kalispell, *Somes 118* (NY). Near Kalispell, *Cotter 1347* (MIN). NW of Kalispell, *Dunn 11536* (RSA). W side of Teakettle Mt., *Dunn 12163* (MIN). Gallatin Co.: Bozeman, *Blankinship 263* (PH). NE of Bozeman, *Dorn 868* (RM). Gallatin N.F., Wilson Cr, *Whitham 1801* (USFS). Logan, *Butler 4158* (NY). Sedan, *Jones s.n.* (GH). Glacier Co.: WSW of Babb, roadside, *Lynch 6100* (WS). Glacier N.P., *Somes 89* (NY), *Van Dyke s.n.* (CAS). Midvale *Umbach 456* (GH, MIN, NY, WIS, WTU). S of St. Mary, *Shaw 1073* (BRY). Granite Co.: N of Phillipsburg, *Cronquist 6751* (DAO, MIN, NY, RSA, WS, WTU). Jefferson Co.: Deerlodge N.F., Sunnyside RS, *Sparrow 8* (USFS). Lewis & Clark S.P., *Britton 1654* (DAO), *Lassetter 1404* (BRY). E of Pipestone, *Stuessy 1673* (UC). E of Whitehall, *Brenckle & Shinnors 41* (WIS). I-90 E of Continental Divide, *Semple & K.Shea 2018* (WAT). Lake Co.: SW of Flathead

Lake, W of Polson, *Cotter 1218* (MIN). Jocko Cr., *MacDougal 265* (NY(2)). Polson, *Crow 602* (PH), *Thomas 11665* (DS), *Umbach 235* (NY), *Umbach 18260* (WIS). S of Polson, *Hitchcock 17751* (RM, RSA, UC, WS, WTU). Ravalli, *Butler 121* (NY), *Butler 3015* (NY), *Elrod 200* (NY), *Jones s.n.* (POM). Wild Horse Is., *Butler 481* (NY), *Butler 491* (NY), *Elrod s.n.* (UC), *Jones 5414* (POM). Lewis and Clark Co.: Helena, *Butler 653* (NY), *Butler 4119* (NY), *Kelsey s.n.* (NY). S from Helena, *Scribner s.n.* (NY). Lincoln Co.: Kootenai N.F., Boulder Cr., *Whitham 208* (USFS); Horse Mt., *Whitham 198* (USFS); Warland RS Pasture, *Whitham 52* (USFS). Rexford, *Jones s.n.* (POM). Madison Co.: SW of Anceney Mt., *Booth 2894* (DAO, KANU, RM, WTU). Madison Co.: Beaverhead N.F., *Beeson 72* (USFS), *Clack D8-15* (USFS). E of Rochester, *Benson B-225* (USFS). Meagher Co.: W of White Sulphur Springs, *Hitchcock 16178* (CAN, DS, GH, NY, RSA, UC, WTU). Missoula Co.: Missoula, *Kirkwood s.n.* (DS, POM(2)), *Kirkwood 1337* (CAS, DS, GH, NY, RM, UC). E of Missoula *Brenckle & Shinnors 41* (MIN, WIS), *Hitchcock & Muhlick 9097* (CAS, TEX, UC, WS, WTU), *Rose 143* (WS), *Rose 234* (WS). N of Missoula, *Woodland 250* (DS). SW of Missoula, *Barkley 1683* (NY, PH, POM, UC, WS). Missoula Bridge, *Watson 180* (GH). Missoula N.F., *Richards R-23* (USFS). Park Co.: Bear Tooth N.F., Rock Cr., *Livingston s.n.* (WIS), *MacDougal 127* (CAN, NY). NE of Bozeman, *Teigen s.n.* (WTU). Powell Co.: W of Deer Lodge, *Semple & K.Shea 2015* (CAN). Ravalli Co.: Bitter Root N.F., *Leiberg s.n.* (CAN). Richland Co.: Lambert, *Rogers & Rogers 1397* (WS). NW of Sidney, *Stephens & Brooks 23581* (KANU). Roosevelt Co.: Wolf Pt., *Degener 1669* (NY). Sanders Co.: Clarkplace, *Hudson 159* (WTU). Silver Bow Co.: Butte, *Kellar s.n.* (PH). S of Butte, *Rose 32494* (GH). SW of Butte, *Harms 19143* (KANU, SASK). S of Opheim, *Stephens 78312* (KANU). Yellowstone Co.: SE of Custer, *Stephens 69365* (KANU). **NORTH DAKOTA.** Benson Co.: Leeds, *Lunell s.n.* (MIN). Divide Co.: SE of Fortuna, *Harms 18511* (KANU, SASK). SW of Fortune, *Stephens & Brooks 13163* (KANU). Mountrail Co.: S of New Town, *Stephens & Brooks 12790* (KANU). E of Palmera, *Stephens & Brooks 40141* (KANU). Pembina Co.: Icelandic S.P., *Ward 566* (KANU). Stutsman Co.: Montpelier, *Bergman 1326* (MIN, NY). Ward Co.: Minot, *Lakela 214* (MIN). N of Minot, *Lautenschlager 462* (CAN, MIN). Williams Co.: Grenora *Larsen 64* (GH). W of Ray, *Stephens & Brooks 40184* (KANU). Williams Co.: Williston, *Bell s.n.* (WTU). **NEW MEXICO.** *Fendler s.n.* (NY ex Torrey). *Fendler s.n.* (UC). *Vasey s.n.* (NY). Carson N.F., Blair Cyn., *Parker s.n.* (ASU). Bernalillo Co.: Pajarito Park, *Bartlett s.n.* (NMC). Sandia Mts, Sandra Crest, *Bennett 8787* (BRY). Cibola Co.: SE of Grants, *Kass 2465* (BRY). Curry Co.: S of Melrose, *Wooton s.n.* (NMC). Harding Co.: W of Mills, *Ward 81-265* (NMC). McKinley Co.: E of Continental Divide, *Jackson & Jackson 2672-2* (KANU). Gallup, *Eastwood 5604* (CAS). Mexican Springs, *Carter s.n.* (NMC). Zuni Mts., S of Sixmile Spring, *Reeves 7878* (ASU). Mora Co.: Watrous, *Arsène 17982* (DS). Rio Arriba Co.: S of Abiqui, *Sundberg & Hardison 1995* (TEX, WAT). N of Counselor, *Peabody & Sears 1869* (BRY). Rito de los Frijoles, *Robbins 8192* (CAS, RM, RSA, TEX). Santa Fe N.F., Tank Cyn., *Springfield 416* (TEX, USFS). Sandoval Co.: N of Cuba, *Jackson 2464* (KANU). N of Jemez Spring, *Harms 1914* (KANU, SASK). San Juan Co.: SE of Blanco, *Peabody & Sears 1769* (BRY). NW of Cedar Hill, *Faulkner & Martin 153* (BRY). Chaco Cyn N. Mon., *Sears & Peabody 224* (BRY). Cutter Cyn., *Wynhoff KL-9* (ASU). S of Farmington, *Faulkner & Martin 136* (BRY). Knowlton, *Porter 84-314* (BRY). SE of Nageezi, *Peabody & Sears 1637* (BRY). Navajo Reservoir, *Peabody & Martin 1302* (BRY). Santa Fe (Pecos) N.F., Holy Ghost Cr, *Renner 148* (RM), Indian Cr, *Stewart 133* (RM). San Miguel Co.: *Arsène 22112* (UC). Las Vegas, *Arsène 17559* (GH, LL), *Cockerell s.n.* (CAS). Pecos, *Bartlett 266* (NMC). Pecos Cyn, *Eastwood 15505* (CAS). Upper Pecos River, *Maltby & Coghill s.n.* (NMC). Sandoval Co.: SE of Cuba, Silver L. Fish Hatchery, *Weber 65* (GH). Santa Fe Co.: near Glorieta, *Ripley & Barneby 2626* (NY). Sangre de Cristo Mts., Big Tesuque Ski Area, *Lepper s.n.* (WIS). N of Santa Fe, *Harms 19127* (KANU, SASK). Santa Fe Cyn., *Rose 17738* (NY). Taos Co.: Ojo Caliente, *Earle s.n.* (NY). Ojo Caliente-Taos Rd., *Brown s.n.* (TEX). Palo Flechado Pass, *Lepper 182a* (WIS), *Lepper 388* (WIS). Taos, *Hein s.n.* (WIS). E of Taos, *Harms 19114* (KANU). SW of Taos, *Harms 19115* (KANU, SASK). **NEVADA.** Washoe Co.: S of Granite Pk., *Tiehm 10816* (BRY, NY, TEX). Seven Lakes Mt., *Tiehm 10228* (BRY, LL, NY, RM). N of Reno, near Verdi at Shingle Mill, *Sonne s.n.* (UC). **OREGON.** *Howell s.n.* (PH). Baker Co.: near Cornucopia, *Thompson 13325* (CAS, GH, NY, WS, WTU). Douglas Co.: Dillard, *Peck 23728* (POM). Hood River Co.: Hood R., *Drake & Dickson s.n.* (GH, WTU), *Henderson 703* (GH), *Suksdorf 1948* (WS). Wasco Co.: Bybees Bridge E of Central Pt., *Heller 13080* (CAS, DS, GH, NY, WIS, WTU). City of Rogue River, *Roberts & Roberts s.n.* (UBC). Winner, *Hammond 233* (NY(2)); Evans Cr., *Hammond L33* (PH). Josephine Co.: Grant's Pass, *Brandegees s.n.* (GH). N of Grants Pass, *Abrams 11239* (DS). Siskiyou N.F., Illinois R, *Ingram 1234* (USFS). Multnomah Co.: *Howell 201* (GH). Polk Co.: N of West Salem, *Nelson 4902* (GH, PH). Sherman Co.: mouth of Des Chutes R., *Peck 9927* (DS(2), NY). Wallowa Co.: Imnaha, *Cusick 979* (NY), *Sherwood 433* (PH), *Sherwood 434* (LL). E of Imnaha, *Maguire & Holmgren 27034* (CAN, DS, GH, NY, UC, WS, WTU). W of Imnaha, *Howell 28552* (CAS), *Mason 1173* (ASU). Snake R. Cyn., Johnson's Bar, *Murley 1716* (NY). Wallowa Mts, *Cusick 2074* (DS, GH, MIN, RM(2), UC, WS); Hurricane Cr, *Cusick 2186* (GH, MIN, UC), *Mason 7070* (ASU); Slickrock Cr., *Maguire & Holmgren 27045* (GH, NY, UC). Wasco Co.: Dalles City, *Suksdorf 440* (WS). The Dalles, *Howell 7199* (CAS), *Shantz & Piemeisel 6178* (LL), *Thompson 2820* (DS, PH). S of Dufur, *Peck 26289* (DAO). Mosier, *Bacigalupi, Heckard & Weiler 7892* (JEPS). Between Mosier and Rowena, *Abrams 9467* (DS, POM, RM). Wheeler Co.: E of Mitchell, *Kruckeberg 2194* (CAN, DAO, GH, NY, RM, RSA, UC, WS, WTU), *Peck 18634* (DS, NY). **SOUTH DAKOTA.** Custer Co.: S. Black Hills, Bear Butte, *Kemp s.n.* (NY). **UTAH.** Bridge Cyn, *Darrow 2813* (CAS). Cache Co.: Bear R. Range, *Neely 589* (BRY); Tony Grove L., *Snell 1049* (GH, UC, WTU(2)). N of Tony Grove L., *Cronquist 1088* (UC). S. Tony Grove L., *Price 62* (USFS). Mt Naomi, *Snell s.n.* (BRY). Carbon Co.: Scofield Reservoir, *Welsh & Taylor 15983* (BRY, NY). Daggett Co.: Ashley N.F., *Saling WMS-52* (USFS); Cart Cr, *Hutchings 117* (BRY, USFS). Browns Pk., *Ostler 256* (BRY). Carter Cr., *Jensen s.n.* (NY, TEX, UC, WTU). Flaming Gorge N. Rec. Area Dowd Mt., *Ostler 951* (BRY); Fire Fighter Mem., *Shaw 3843* (NY). Green River, *Flowers, Hall & Groves 216* (RSA). Taylors Flat, *Neese 5659* (BRY). N of Vernal, *Neese 14687* (BRY, NY). Uinta Mts, E. Green L., *Hermann 4801* (CAS, GH, LL, NY, PH, RM, WS). Davis Co.: Antelope Is., *Jones s.n.* (POM), *Jones 763* (BRY). Duchesne Co.: N of Altamont, *Goodrich 20987* (BRY). N of Neola, *Goodrich 2184* (BRY). Rock Cr., *Brotherson 1599* (BRY). Uinta, *Weight W-68* (BRY, USFS). Uinta River Cyn, *Hermann 5263* (RM). Uinta R., Pole Cyn., *Ostler 425* (BRY). Emery Co.: Calf Springs Wash, *Maguire 18330* (NY). Manti-LaSal NF, near Ferron Cyn., *Lewis 4205* (BRY). San Rafael Reef, Iron Wash, *Harris 776* (BRY); Lower Black Box, *Despain 230* (BRY). Garfield Co.: N of Escalante R., *Wilson*

et al. 5621 (ASU). Hubbards Cave, *Thomson RT-77* (RM). Grand Co.: Grand River Crossing, *Rydberg & Garrett 8355* (NY). LaSal Mts., *Franklin 1177* (BRY, NY); Miners Basin, *Lewis 6345* (BRY). Moab, *Trotter R-333357* (NY). E of Moab, *Franklin 3430* (BRY, NY). N of Moab, *Franklin 2930* (BRY). NE of Moab, *Franklin 3146* (BRY, NY, RM). Between Post and Florence Cyns., *Graham 9914* (GH). Pritchett Cyn., *Rydberg & Garrett 8517* (NY). Seven Mile Mesa, *Franklin 1629* (BRY, NY, RM). E Tavaputs Plateau, *Vickery & Wiens 1704* (GH, RSA, UC, WTU). N of Thompson, *Clark & Thorne 3095* (BRY). NE of Thompson, *Foster & Foster 4972* (BRY), *Welsh & White 15845* (BRY). Hurricane, *Foster & Foster 5335* (BRY). Kane Co.: Powell N.F., Clay Cr., *Taylor T-11* (USFS); Lost Cr., *Korstian & Baker 20* (USFS). Salt Lake Co.: Big Cottonwood Cyn., *Kildale 6684* (DS(2)). San Juan Co.: Abajo Mts., *Howell & True 44959* (CAS), *Rydberg & Garrett 9233* (NY), *Rydberg & Garrett 9749* (CAN, NY, RM, UC, WIS), *Shultz, Shultz & Prigge 9016* (NY). Blanding, *Eastwood & Howell 6746* (CAS). NNE of Blandings, *Semple 8815* (WAT). Between Blanding and Kigolia R.S., *Holmgren & Hansen 3485* (CAN, GH, NY, TEX, WS, WTU). W of Blanding, *Magurie, Richards, Maguire & Hammond 5681* (GH, UC). Cataract Cyn., *Welsh & Welsh 21987* (BRY). Devils Cyn., *Cottam 9527* (BRY, RSA). Elk Mts., *Rydberg & Garrett 9365* (NY), *Rydberg & Garrett 9544* (NY), *Rydberg & Garrett 9584* (NY), *Rydberg & Garrett 9585* (NY), *Rydberg & Garrett 9586* (NY). NE of LaSal, *Taye 1808* (BRY, RM). LaSal Mts, *Cottam C2216* (POM), *Franklin 1216* (BRY, NY), *Purpus 6652* (POM, UC); Bayles Rch N.F., *Jensen RJ-74* (USFS); LaSal Mt. Loop Rd., *Franklin 688* (BRY); LaSal Guard Stn., *Lewis 6272* (BRY), *Maguire & Redd 2142* (GH); Little Springs, *Rydberg & Garrett 8562* (NY). Manti N.F., *Willey 313* (USFS); near Williams R.S., *Palmer 471* (USFS). SE of Moab, *Franklin 647* (BRY). Monticello, *Twiss s.n.* (RSA). S of Monticello, *Howell 24734* (CAS). Roan Bailey Mesa, *Grimes & Meurer 2950* (TEX). Sanpete Co.: Upper Gooseberry, *Lewis 6954* (BRY). Sevier Co.: W of Emery, *Neese & White 9202* (BRY, NY). Summit Co.: Kamas, *Brown 325* (RM). E of Kamas, *Mosquin & Gillett 5319* (DS). Summit Co.: East Cyn near Gogorza, *Garrett 8631* (UC). E of Kamas, *Ostler 824* (BRY). W of Kamas, *Semple, Suropto & Ahmed 9236* (WAT). Peterson, Weber R., Devil's Gate, *Pammel & Blackwood 3914* (CAS, GH). Uintah Co.: *Harrison 7773* (UC). Ashley N.F., Elk Horn Ranger Stn., *Christensen C-4* (RM). Bear R. Range, *Smith 2275* (DS, NY, RM). Blue Mt, *Smith & Trent 1751* (BRY). Brush Cr. Gorge, *Graham 10008* (UC). Diamond Mt., *Neese 6254* (BRY), *Solbrig 3137* (GH, NY), *Williams & Atwood 80-141-1* (BRY, CAS, RSA). Ft. Duchesne, *Carter 48* (RM). N of Maeser, *Neese, Welsh & Moore 7815* (BRY, RM). Red Cloud Loop, *Welsh & Moore 6747* (BRY, NY, UC). Red Wash NW of mouth of Split Mt Cyn above Island Pk., *Graham 9174* (GH). NW of Vernal, *Neese 14378* (BRY, NY). UT-44 S of Ashley N.F., *Peterson 1527* (BRY). Utah Co.: Aspen Grove, *Garrett 3405* (NY), *Larsen 7143* (USFS); Mt Timpanogos, *Allred 980* (BRY). Provo, *Garrett 3311* (RM). Wasatch Co.: E of Heber City, Low Pass Cr, *Goodrich 16104* (BRY). Provo R., *McDonald 340* (USFS). Washington Co.: Canaan Mt., *Shultz & Anderson 5358* (NY). Wayne Co.: Capitol Reef N.M., *Vickery 571* (UC). WASHINGTON. "Cascade Mts. to Ft Colville," *Lyall s.n.* (GH). Ferry Co.: Haag Cove, *Saufferer 294* (DS, NY, TEX). Klickitat Co.: *Milburge 526* (WTU). Bingen (cult. from Mont.), *Suksdorf 10886* (WS), *Suksdorf 11435* (WS). E of Bingen, *Hitchcock & Muhlick 13775* (WTU). N of The Dalles, *Cotton 1550* (WS). Fallbridge, *Whited 1148* (WS), *Munz 24228* (GH, RSA, UC). White Salmon, *Halse 2708* (CAS, NY, UBC, WTU). Okanogan Co.: Columbia R., Nespelem Rd., *Fiker 1551* (WS). Riverside, *St. John 7714* (NY, WS). Tonasket, *Thompson 8697* (DS, GH, LL, MIN, NY, WTU). Pend Oreille Co.: Boundary Dam, *Layser 1113* (WS, WTU). Spokane Co.: Spokane, *Johnson 1312* (MIN). near Spokane, *Turesson 60* (RM). S Spokane, *Weber 2234* (CAN, GH, NY, UBC, UC, WS, WTU). Stevens Co.: Loon L, *Winston s.n.* (GH). Meyers Falls, *Beattie & Chapman 2198* (UC, WS). Whitman Co.: Wawawai, *Elmer 1017* (MIN, WS). Yakima Co.: Yakima Region, *Brandege s.n.* (UC). WYOMING. Big Horn Mts., *Williams s.n.* (NY). Fish Hatchery, *Buffum s.n.* (RM). Albany Co.: Bacon's Ranch, Nelson 8921 (GH, NY(2), RM, UC). Centennial, *Ownbey 203* (WS). N of Centennial, *Stephens & Brooks 43562* (KANU). NE of Centennial, *Russell 10639* (ASU, UC). NW of Centennial, *Hartman 3046* (RM, SASK). SE of Centennial, *Rollins 950* (NY). Laramie, *Buffum s.n.* (MIN), *Macbride 2478* (RM), *Nelson 127* (NY). E of Laramie, *Stephens & Brooks 35994* (KANU). Laramie Range, *Finzel 129* (RM). Rock R., *Macbride 2781* (RM, WS). Sheep Mt., *Jones 34* (USFS), *Myers 244* (RM). Sybille Cyn, *Asplund 71-12* (RM). Big Horn Co.: headwaters of Crazy Woman R., *Tweedy 3148* (NY, RM). NE of Hyattville, *Hoffman 709* (RM). Hyattville Logging Rd, *Despain 394* (RM). SW of Snowshoe Pass, *Nelson 6645* (NY, RM, TEX). W of Tyrell R.S., *Hartman & Odasz 9227* (RM). Carbon Co.: Battle L., *Davis s.n.* (NY), *Ownbey 414* (WS). N of Battle L., *Williams 443* (RM). Bridger Pk., *Gooding 2010* (GH, NY, RM, UC). Deep Cr. Rd., *Holmes 298* (RM). Elk Range N.F., Douglas Cr., *Ward 40* (RM). Encampment, *Tweedy 4024* (NY). Ferris Mts., Cherry Cr., *Lichvar 4604* (NY). Medicine Bow N.F., *Douglas 131* (USFS). N of Rambler, *Rose 114* (USFS); Sandstone Expt Plot, *Rose 160* (USFS). Rawlins, *Degener & Peiler 16125* (NY), *Dorn 2911* (RM). S of Riverside, *anon. 4335* (WTU). Sage Cr., *Holmes 394* (RM). FR-801 N of WY-70, *Semple & Zhang 10416* (RM, WAT). Converse Co.: Douglas, *Pfadt 200* (RM). Fremont Co.: ENE of Dubois, *Day & Berner 91* (RM). ESE of Jeffrey City, *Haines 6313* (NY). NE of Jeffrey City, *Haines 5579* (NY). NE of Linch, *Dueholm 5589* (NY). N of Lost Cabin, NE of Riverton, *Nelson 5773* (NY, RM). WSW of Muddy Gap Junction, *Haines, Haines & Little 4736* (RM). Split Rock Hist. Marker site, *Semple & Zhang 10417* (RM, WAT). Hot Springs Co.: Gaging Stn at N Fork Owl Cr., *Hardy 484* (BRY). Johnson Co.: E of Buffalo, *Duelholm 5872* (RM). SE of Buffalo, *Dueholm 7451* (BRY). W of Buffalo, *Fonken 1050* (RM). WSW of Buffalo, *Fonken & Nelson 456* (RM). NE of Linch, *Dueholm 5589* (NY, RM). Soldier's Park, *Williams s.n.* (NY). Laramie Co.: E of Pine Bluffs, *Lepper s.n.* (WIS). Natrona Co.: NNE of Arminto, *Hartman 10437* (RM, TEX). Casper Mt., *Bissell s.n.* (BRY), *Tresler 2* (RM). SE of Powder River, *Duelholm 7853* (RM). W of Midwest, *Duelholm 8737* (RM). Park Co.: Beartooth Pass, *Porsild & Johnson 22829* (CAN). Clark, *Pearson 241* (RM). Clarks Fork valley, Yellowstone R., *Witt 1283* (CAS, MIN, RSA, WS, WTU). Cody, *Nelson 9552* (GH, NY, RM, UC). E of Cooke City, *Stolze 1109* (GH, WIS). Shoshone N.F., Crandall Cr, *Pearson 96* (RM). Yellowstone N.P., *Kraus s.n.* (WIS), *Miller 1892* (PH), *Tweedy s.n.* (KANU); Loaf Cr., *Knoweson s.n.* (CAN); Gardiner River, S of Hot Springs, *Nelson & Nelson 5967* (BRY, MIN, NY, POM, RM); Mammoth Hot Springs, *Harms 20228* (KANU), *Mearns 1561* (NY); Old Faithful, *Jones 5300* (DS), *Rose 32388* (CAS, WIS); Yellowstone L., *Peirson 8151* (DS, RSA). E of Wapiti, *Evert 2838* (BRY, RM). Platte Co.: N of Wheatland, *Bennett, Dunn & Dziekanowski 590* (NY). Sheridan Co.: Dayton, *Tweedy 2038* (NY). W of Parkman, *Duelholm 8916* (RM). Sweetwater Co.: Leucite Hills, *Merrill & Wilcox 508* (NY, RM). Minnies Gap, *Lichvar 1785* (RM). Point of

Rocks, *Nelson 7157* (GH, NY, POM). Rock Springs, *Degener & Peiler 16096* (NY). SSW of Rock Springs, *Aldrich 676* (RM). US-191 NE of state line, *Semple & Zhang 10440* (RM, WAT). Teton Co.: Death Cyn., *Wehmeyer, Martin and Loveland 5507* (NY). Jackson L. Dam, *Shaw 4832* (TEX). Gros Ventre R., *Nelson 1084* (GH, MIN, RM). Kelley, *Payson & Payson 3083* (RM). Three Rivers Jct., *Thorne 5033* (BRY). Yellowstone N.P., Bunsen Pk., *Harrison 163* (LL); Yellowstone R., *Mearns 4209* (NY). Washakie Co.: E of Meadowlark, *Semple & Brouillet 4448* (NY, WAT). Ten Sleep Cyn., *Nelson & Nelson 1088* (RM).

aff. var. minor (aberrant forms or damaged specimens)

U.S.A. COLORADO. Archuleta Co.: S of Pagosa Springs, *Wolf 3081* (CAS, DS, RSA). Boulder Co.: Boulder, *Meebold 19583* (NY). Jackson Co.: Ute Pass Camp, Mt. Zinkel, *Warren 26* (RM). **ILLINOIS.** Jo Daviess Co.: *Pepoon s.n.* (PH). **MONTANA.** Glacier Co.: Glacier Pk., *Kelley s.n.* (CAS). **NEW MEXICO.** Dona Ana Co.: Bishop Cap, *Worthington 16489* (TEX). Sandoval Co.: N of San Ysidro, *Keil K10882* pro parte (ASU). Santa Fe Co.: Camino de Cruz Blanca, *Bennett 8786* (BRY). Taos Co.: N of Pilar, *Semple & Heard 8055* (WAT). **OREGON.** Jackson Co.: S of Ruch, *Wolf 944* (DS, RSA). **UTAH.** Summit Co.: ESE of Kamas, *Bennett 8418* (CAS). **WYOMING.** Centennial, *Nelson 8814* (RM, UC).

aff. var. minor (approaching var. *ballardii*)

CANADA. MANITOBA. Bede, *Dore & Lindsay 11106* (DAO, DS, GH). **SASKATCHEWAN.** St. Laurent, *Russell s.n.* (DAO). **U.S.A. NORTH DAKOTA.** McKenzie Co.: N of Grassy Butte, *Stephens 28674* (KANU). Ward Co.: NW of Harvey, *Harms 2527* (KANU). Williams Co.: W of Grenore, *Stephens & Brooks 13249* (KANU). **MINNESOTA.** Chisago Co.: Amador, *Taylor s.n.* (DS, UC, WS). Hennepin Co.: Robbindale, *Moore & Moore 10252* (CAN, KANU, MIN).

aff. var. minor (approaching var. *depressa* and mixed collections)

U.S.A. MONTANA. Gallatin Co.: Spanish Basin, *Rydberg & Bessey 5070* (CAN, GH, NY). **WYOMING.** "Northwestern Wyoming", *Parry 147* (NY(2)). Park Co.: Yellowstone N.P., *Nelson 10141* (RM, UC), *Treacle 53* (POM). Teton Co.: Grand Teton N.P., below Jackson Lake Dam spillway, *Shaw 4979* (TEX). Gros Ventre River, *Nelson 1084* (GH, MIN, RM). Pacific Creek, *Dorn 4727* (NY). Snake R bottom, *Williams 982* (CAS, GH, NY, RM, WIS).

aff. var. minor (approaching var. *foliosa* in leaf shape and mixed collections)

CANADA. ALBERTA. Bow R F Res Red Deer R crossing, *Porsild 20420* (CAN). NW of Calgary *McCalla 12058* (GH, UBC). Cardston, *Macoun 10819* (CAN). Crows Nest L., *Macoun 22730* (CAN). Lacombe, *Dixon 585* (NY). W of Nordegg, *Dumais 4750* (CAN). Red Deer, *Macoun 10820* (CAN). Waterdon Lakes N.P.; Bellevue Hill', *Nagy 2878* (CAN); Lakeview Ridge, *Nagy 2604* (CAN); Pincher Cr. Gate, *Nagy & Armstrong 4300* (CAN). **BRITISH COLUMBIA.** N of Crows Nest Pass, *McCabe 4878* (UC). Fort Steele, *Anderson 750* (WS). Grand Forks, *Eastham s.n.* (UBC). E of Grand Forks *McCabe 4640* (UC). N of Windermere, *McCabe 5178* (UC). **SASKATCHEWAN.** Cypress Hills, *Breitung 5676* (DAO). S of Indian Head, *Sallens & Ledingham s.n.* (DAO). WNW of Payton, *Harms 2533* (KANU, SASK, WAT). NW of Saskatoon, *Harms 2530* (KANU, WAT). **U.S.A. COLORADO.** Boulder Co.: SE of Lyons, *Stephens & Brooks 43274* (KANU). N of Nederland, *Wagenknecht 2973* (KANU, SASK). Costilla Co.: W of La Veta Pass, *McGregor 13348* (KANU). **IDAHO.** Bear Lake Co.: Bloomington L., *Davis 1651* (LL). Fremont Co.: St. Anthony, *Merrill, Wilcox 794* (NY, RM). Idaho Co.: SW of Riggins, *Davis 2365* (LL, WS). Nez Perce Co.: near Sewista, *Henderson 2805* (GH, RM). **MONTANA.** Belt Cr., *Anderson s.n.* (UC). Beaverhead Co.: Cyn. Creek, *Leithhead 87* (WTU). S of Dillon, *Hitchcock 15797* (DS, GH, NY, RSA, UC, WS, WTU). S of Wise R, *Hitchcock & Muhlick 14983* (NY, RSA, WS). Big Horn Co.: N of Hardin, *Stephens 69426* (KANU). Yellowtail Reservoir, *Lichvar 6885* (BRY, RM). Blaine Co.: W of Ft. Belknap, *Stephens 68271* (KANU). Broadwater Co.: NW of Townsend, *Mosquin & Mulligan 5170* (DAO, DS). Carbon Co.: Beartooth For, Pryor Dist, Sage Cr., *Ferguson & Lockhart 754* (USFS). Big Horn Cyn N.R.A., E side above Deadman Cr., *Jones, Ditolla & Myers s.n.* (RM). Morgan, *Strack 88* (RM). S of Red Lodge, *Sundberg 2045* (TEX, WTU). SE of Roscoe, *Hitchcock 16554* (CAN, DS, GH, NY, RSA, UC, WTU). Carter Co.: Needmore R.S., *Thompson 465* (USFS). Cascade Co.: Great Falls, *Anderson 120* (UC). Chouteau Co.: N of Big Sandy, *Stephens 68507* (KANU). Custer Co.: NE of Miles City, *Stephens & Brooks 23717* (KANU), *Stephens 78636* (KANU). W fork of Sun R., *Kirkwood 2356* (GH, RM). Dawson Co.: 10 mi E of Glendive, *Seiler 572* (KANU). Deerlodge Co.: Deerlodge N.F., *Ketridge 211* (USFS). Racetrack, *Howard & Christianson PFS-253* (DS, USFS). Flathead Co.: *Dunn 9992* (MIN, RSA). Flathead L., *Zwickel 83* (WS). Mt. Holbrook, *Kirkwood 2234* (GH, RM). SSW of Columbia Falls, *Dunn 10779* (MIN, RSA). Gallatin Co.: Bozeman, *Moore s.n.* (RM, UC). N of Bozeman, *Chase 14209* (WIS). Ft. Ellis, *Applegate 6392* (DS, LL). Glacier Co.: Browning, *Harms 20226* (KANU, SASK). Glacier N.P., Park Cr, *Piranian 15683* (GH, UC). Glacier Pk, *Osterhout 8088* (RM). Midvale, *Umbach 564* (NY). Granite Co.: E of Drummond, *Booth 56595* (GH). W of Drummond, *Cronquist 6746* (DS, NY, RSA, WS). Jefferson Co.: Jefferson N.F., *Donaldson D-16* (USFS). Lake Co.: NW of Polson, *Thomas 10772* (DAO, DS). Ravalli, *Clemens s.n.* (GH). Wild Horse Is., *Butler 480* (NY), *Butler 485* (NY). Lewis and Clark Co.: W of Augusta, *Bartlett & Grayson 1145* (NY). Lewis and Clark Co.: Ford Cr., *Storm 42* (RM). Helena, *Kelsey s.n.* (NY). S of Helena, *Howell 7904* (CAS). McDonald Pass, *Hitchcock & Muhlick 11754* (NY, WS, WTU). Sun R., *Kirkwood 2356* (UC). Madison Co.: N of Glendale, *Long D1-27* (USFS). N of Norris, *Hitchcock 15853* (CAN, DS, GH, NY, POM, RSA, UC, WS, WTU). Mineral Co.: NW of Superior, *Cronquist 6740* (DAO, GH, MIN, NY, RSA, WS, WTU). Missoula Co.: above Bonner, *Hitchcock & Muhlick 11448* (CAS, NY, PH, RM, WTU). Missoula, *Adder 190* (DAO). Phillips Co.: NE of Malta, *Stephens 68171* (KANU). Powder River Co.: W of Broadus, *Stephens 69656* (KANU). Powell Co.: Garrison, *Jones s.n.* (POM). Ravalli Co.: W of Skalkaho Rd. Summit, *Hitchcock & Muhlick 14522* (NY, RSA, WTU). Rosebud Co.: SE of Rosebud, *Stephens 69176* (KANU). Sanders Co.: *Thomas 11866* (DAO). Sheridan Co.: 4 mi W of Westby, *Stephens & Brooks 13194* (KANU). Silver Bow Co.: Butte, *Booth s.n.* (WTU). E of Columbus, *Semple & K.Shea 2025* (WAT). S of Columbus, *Hitchcock 16560* (NY, RSA, WS, WTU). Treasure Co.: E of Sanders, *Stephens 69290* (KANU). **NEW MEXICO.** Santa Fe Co.: NE of Santa Fe, *Mosquin & Gillett 5414* (DAO). **OREGON.** Woodville, *Howell s.n.* (PH). Polk Co.: Independence, *Nelson 1838* (GH). Sherman Co.: mouth of John Day R, *Henderson 5265* (CAS, DS). Wasco Co.: The Dalles, *Harford & Dunn s.n.* (NY, UC), *Jones s.n.* (POM), *Kellogg & Harford 408* (GH), *Munz 9906* (POM). E of the Dalles,

Milburge 1471 (WTU). Dalles Dam, *Semple & K.Shea 1974* (CAN, WAT). UTAH. Oneida Co.: Bear R. Range, Franklin Basin, *Smith 2275* (DS, NY, RM). WASHINGTON. Entiat, *Thompson 6368* (PH, WTU). Chelan Co.: Icicle Cr., *Denton 4251* (NY, WTU). Okanogan Co.: near Tonasket, *Thompson 11701* (CAS, DS, GH, LL, NY, POM, WTU). Kittitas Co.: Columbia R Valley, Rock Is., *Sandberg & Leiberg 454* (CAS, GH, NY, UC). Klickitat Co.: NE of the Dalles, *Cotton 1551* (WS). Okanogan Co.: Omak, *Jones s.n.* (POM). W of Omak, *Fiker 466* (LL, WS, WTU). Spokane Co.: Spokane, *Milburge 788* (WTU). Stevens Co.: NW of Northport, *Hedgcock s.n.* (RSA, WS). Wallawalla Co.: Walla Walla, *Savage, Cameron, & Lenocker s.n.* (PH). WYOMING. Big Horn Mts., *Patsky s.n.* (PH). Near summit of Rocky Mts. on UP RR, *Dudley s.n.* (DS). Albany Co.: Bacons Ranch, *Nelson 8919* (DS, GH, NY, RM(2), UC). NW of Centennial, *Crawford 176* (SASK). Laramie Range, Sybille Cyn., *Porter & Porter 9958* (UC). Big Horn Co.: Dayle Cr., *Goodding 358* (RM). Red Bank, *Goodding 331* (DS(2), GH, NY, POM, RM, WIS, UC(2)). Carbon Co.: Seminole Mts., *Nelson 4938* (NDG, RM). Converse Co.: Deer Cr., *Nelson 8374* (GH, NY, POM, RM, UC). N of Douglas, *Stephens & Brooks 43730* (KANU). E of Shawnee, *Stephens 70238* (KANU). Fremont Co.: Birds Eye, *Nelson 9342* (GH, NY, RM, UC, WIS). E of Shoshone, *Osterhout 8297* (RM). Goshen Co.: W of Ft. Laramie, *Stephens 70866* (KANU). Johnson Co.: Rocky Mt. Range Ex.S., *Kissinger K-34* (RM, USFS). Natrona Co.: *Dueholm 8737* (NY). W of Casper, *Stephens 70329* (KANU). N of Egerton, *Stephens 70025* (KANU). Platte Co.: W of Guernsey, *Harms 2122-B* (KANU, SASK, WAT). SE of Wheatland, *Harms 2120-B* (KANU, SASK, WAT). SW of Wheatland, *Harms 2121* (KANU, SASK), *Stephens & Brooks 43710* (KANU). Sheridan Co.: SW of Big Horn, *Hartman 10767* (RM). Washakie Co.: Big Horn Mts., ESE of Big Trails, *Nelson 4294* (RM), *Nelson 8144* (NY, RM).

aff. var. minor (approaching var. *nana*)

U.S.A. ARIZONA. Apache Co.: Ft. Defiance, *Demaree 44621* (NY), *Demaree 44623* (CAS, NY). COLORADO. Chaffee Co.: W of Buena Vista, *Haber & Given 2029* (CAN). S of Granite, *Harms 2087* (KANU, SASK, WAT). W of Nathrop, *Stephens & Brooks 36106* (ASU, KANU). El Paso Co.: Trail Glen, *Clements & Clements 39* (DS). Larimer Co.: Rist Cyn., *Marshall 2771* (NY). Montrose Co.: Black Cyn. of the Gunnison N. Mon., *Harms 2074* (KANU, SASK(2), WAT). E of Cimarron, *Harms 2076* (KANU, SASK, WAT). Rio Blanco Co.: Meeker, *Robbins 7156* (GH, RM, WTU). Rio Grande Co.: SW of South Fork, *Harms 2049* (KANU, WAT). Saguache Co.: W of Sargents, *Harms 2078* (KANU, SASK). Moffat Co.: near confl. of Green R. and Yampa R., *Porter 3635* (DS, GH, RM, TEX, UC, WTU). S of Hamilton, *Larson 18L* (USFS, WIS). Eagle Co.: Wolcott, *Osterhout* (RM(2)). Garfield Co.: Glenwood Springs, *Osterhout 5830* (RM, POM), *Osterhout 5837* (RM). New Castle Harrington *4313* (DAO). La Plata Co.: N of Durango, *Semple 8812* (WAT). Larimer Co.: Chamber's Lake, *Baker s.n.* (NY). Las Animas Co.: near Morley, *Ferris & Duncan 3551* (DS). ILLINOIS. Henry Co.: S of Green River, *Keil 2518* (ASU). MONTANA. Glacier Co.: Raes Cr. Campground, *Bailey & Bailey 409* (UC). Park Co.: Yellowstone N.P.: Gardiner, *Mearns 1561* (DS); NEW MEXICO. Cibola, *Parker s.n.* (ASU). Therma, *Whitehouse 7747* (TEX). Colfax Co.: Philmont Scout Rch, NE of Clarks Fork, *Hartman 2332* (RM, TEX). McKinley Co.: N of Gallup, *Harms 1899-A* (KANU(2)). N of Prewitt, *Barrie 1416* (TEX, WS). E of Pueblo Pintado School, *Reitzel & McKinney 4157* (NMC, NY). Rio Arriba Co.: Ghost Ranch, *Ubelaker 2548* (TEX). Sandoval Co.: S of Cuba, *Preece & Turner 2750* (WS). Santa Fe Co.: N of Glorieta, *Standley 5236* (NMC). Socorro Co.: Socorro, *Plank s.n.* (NY). Taos Co.: Rio Grande Cyn. Bottom, N of Red R., *Baker 1052* (NMC). Torrance Co.: Mosca Saddle, *Baad 909* (WTU). Valencia Co.: Bluewater, *Degener 4871* (NY). Duchesne Co.: Uintah Mts., Hells Cyn., *Goodrich 22968* (NY). WISCONSIN. Adams Co.: *Shinners 4314* (PH, UC). Easton Twp., *Hartley 8927* (GH, RSA). NE of Wisconsin Dells, *Davis & Fassett 16938* (GH). WYOMING. Lions Den Valley, *Willits 450* (RM). Albany Co.: Chugwater, *Nelson s.n.* (RM). Laramie, *Nelson 9310* (RM(2), UC). Laramie Mts., *Kemp 9* (NY). NE of Sheep Mt., *Nelson 736* (RM). Campbell Co.: S. Pumpkin Butte, *Duelholm 5057* (RM). N of Wyodak, *Duelholm 4889* (RM). Carbon Co.: W of Cooper Cove, *Goodwin s.n.* (RM). Converse Co.: Douglas, *Pfadt 81* (RM). Park Co.: E of Cooke City, *Mosquin 4809* (DS). Yellowstone N.P.: Crescent Hill, *Mason 3464* (UC); Pebble Crk, *Nelson & Nelson 3178* (GH, RM, UC).

aff. var. minor (approaching var. *pedunculata*)

U.S.A. ARIZONA. Coconino Co.: Mogollon Mts., Rim Road, *Collom 640* (ASU, RSA). Navajo Co.: Hopi Ind. Res., S of Keames Cyn. Village, *Harms 1894* (KANU, SASK). COLORADO. Archuleta Co.: W of Pagosa Springs, *Weber 3643* (CAS, TEX). Gunnison Co.: Rogers, *Baker 794* (DS, MIN, NY, POM, RM, UC). La Plata Co.: W of Bayfield, *Harms 2056* (KANU, SASK(2), WAT). Mesa Co.: Unaweap and Cold Springs R.S., *Siplivinski & Beck 4214* (NY). NEW MEXICO. McKinley Co.: E of Gallup, *Peabody & Sears 1719* (BRY). Rio Arriba Co.: N of Espanola, *Jackson 3116* (KANU). San Juan Co.: S of LaBaca, *Peabody & Martin 1262* (BRY). Taos Co.: N of Vadito, *Semple & Heard 8062* (WAT). UTAH. Grand Co.: Arches N.P., *Allan 116* (BRY); Devil's Garden, *Keil 10854* (ASU, JCS). Roan Cliffs, *Holmgren & Reveal & La France 2297* (KANU, MIN, NY, TEX, UBC, WIS, WTU). San Juan Co.: S of Monticello, *Rydberg & Garrett 9144* (GH, NY, RM). Navajo Mts., *Gentry & Davidse 1787* (ASU, KANU, NY, PH, RM, RSA, TEX, UC, WTU).

aff. var. minor (approaching var. *scabra*)

U.S.A. ARIZONA. *Neally 210* (NY). Apache Co.: Hwy-180 & 666, 20 mi S of St. Johns, *Lehto, McGill, Nash & Pinkava 11574* (ASU). COLORADO. Montezuma Co.: Mesa Verde N.P., *Erdman 13* (CAN, DAO, MIN, NY, TEX, WTU). NEVADA. Washoe Co.: Granite Range, S of Granite Peak, *Tiehm 10816* (BRY, NY, RM, TEX). OREGON. Josephine Co.: Rogue R. below Galice, *Ripley & Barneby 9625* (CAS). UTAH. Sevier Desert, Harris s.n. (MIN). Box Elder Co.: Corrine Hot Springs, *Thorne 3209* (BRY). Daggett Co.: SE of Manila, *Welsh & Moore 18697* (BRY, NY, RM). Grand Co.: *Mikus 543* (BRY), *Mikus 597* (BRY). Arches N.P., E of Devils Garden, *Allan 63* (BRY). NE of Mt. Waas, *Franklin 2384* (BRY, NY). Iron Co.: Pine Valley Mts., *Atwood 5432* (BRY). Piute Co.: Bullion Cyn., *Rydberg & Carlton 7288* (CAN, MIN, NY, RM). Uintah Co.: Jones Hole N.Fish Hatch., *Welsh & Welsh 115* (BRY, NY). Wayne Co.: San Rafael Desert, *Stanton 1067* (LL).

aff. var. minor (approaching var. *villosa* and mixed collections)

CANADA. ALBERTA. Billy R, *Dawson 26442* (CAN). Clive, *Bickle s.n.* (CAS). Fraser R Cyn. near Cisco, *Howell 7795* (CAS, NY).

Handhills, *Brinkman* 5247 (LL). Medicine Hat, *Fowler s.n.* (DAO). Merritt-Coyle, *Krajina s.n.* (GH, UBC). **BRITISH COLUMBIA.** Ashnola Rd. (MP16), *Hainault* 8005 (DAO, UBC). Columbia Valley S of Canal Flats, *Eastham s.n.* (DAO). W of Lytton, *McCabe* 2664 (UC). S of Merritt, *McCabe* 4511 (UC). S of Radium, *Semple & Brouillet* 4359 (WAT). Skagit R., *Macoun* 76937 (CAN, NY). Stemwinder campsite Hwy-3, *Beamish & Gilmartin* 7470 (UBC). Tete Jaune Cache, Fraser R., *Spreadborough* 19671 (CAN). **MANITOBA.** Hartney, *Kemp* 3565 (DAO, UBC). Virden, *Groh s.n.* (DAO). E of Woodside, *Löve & Löve* 5688 (DAO). **SASKATCHEWAN.** Ravenscrag, *Ledingham* 48-559 (DAO). Saskatoon, *Fraser* 8A (WIS). Yorkton, *Priestly s.n.* (DAO). **U.S.A. CALIFORNIA.** Parry & Lemmon 200 (NY). Siskiyou Co.: Black Mt., *Tucker, Mann, & Holloway* 3753 (RSA). NE of Weed, *Bacigalupi, Heckard, & Weiler* 7982 (JEPS). **COLORADO.** Garfield Co.: Middle Fork of Stuart Cr., *Graham* 9752. (GH). Moffat Co.: Blue Mt., *Neese & Snyder* 11890 (BRY, NY). **IDAHO.** Cassia Co.: City of Rock, *Watson* 585 (GH). Idaho Co.: Middle Fork of Clearwater R., *Jones* 363 (DS, MIN, NY, RSA, WTU), *Constance* 1978 (LL, UC, WTU). Whitebird, *Davis* 959 (LL, RM, UC). **MINNESOTA.** Hennepin Co.: St. Anthony, *Schuette s.n.* (NY). Nez Perce Co.: Clearwater R. above Lewiston, *Sandberg, MacDougal & Heller* 280 (DS, NY(2)). **MONTANA.** Gallatin Co.: NE of Bozeman, *Hitchcock & Muhlick* 12471 (CAS, DS, NY, RM, UC, WS, WTU). Park Co.: Absaroka N.F., Dome Mt. R.S., *Cooney* 22 (USFS). Livingston, *Scheuber s.n.* (MIN, NY, UC). Silver Bow Co.: Desert Butte, *Rose* 32482 (CAS). **NORTH DAKOTA.** McHenry Co.: Towner, *Wright s.n.* (NY). **NEW MEXICO.** Catron Co.: SW of Horse Springs, *Smith* 87 (PH). **OREGON.** Douglas Co.: Riddle, *Peck* 3712 (GH). Hood River Co.: Hood R., *Suksdorf* 3399 (CAN, DS, GH, MIN, NY, RM, RSA, UBC, WTU(2)). Klamath Co.: Klamath Falls, *Peck* 3707 (GH). Wallowa Co.: Innaha, Innaha Cyn., *Baker* 9033 (NY, WTU(2)). Snake R Cyn., Christmas Cr., *Packard* 236 (UC, WS). Wasco Co.: Rowena, *Chambers* 4899 (CAS). **SOUTH DAKOTA.** Minnehaha Co.: Palisades Rec. Area, *Harms* 2646 (KANU(2), NY). **UTAH.** Duchesne Co.: N of Neola, *Goodrich* 21284 (BRY, NY). **WASHINGTON.** Franklin Co.: N of Kahlotus, *Constance & McMurray* 1138 (LL, MIN, WS). Spokane Co.: Spokane, Spokane R., *Johnson* 1160J (WTU). Stevens Co.: Meyers Falls, *Kreager* 516 (GH, MIN, NY, UC, WTC, WS). Whitman Co.: Snake R., *Barkworth* 381 (WS). Yakima Co.: Yakima, *Brandegee* 838 (NY, UC). **WYOMING.** Albany Co.: S of Laramie, *Crawford* 187 (SASK). Sherman Hill, *Williams* 1062 (CAS, GH, NY, RM(2), WIS). Campbell Co.: NE of Hilight, *Dueholm & Sanguinetti* 4167 (MIN, RM).

17.7 *Heterotheca villosa* (Pursh) Shinnery var. *scabra* (A. Eastwood) Semple, *Phytologia* 73: 453.

1992. *Chrysopsis villosa* (Pursh) Nutt. var. *scabra* A. Eastwood, *Proc. Calif. Acad. Sci.* 2.6: 294. 1896. TYPE: U.S.A. UTAH. San Juan Co., Willow Creek, *Eastwood* 38 (Holotype: CAS!)

Chrysopsis viscida A. Gray ssp. *cinerascens* S.F. Blake, *Proc. Biol. Soc. Wash.* 35: 173. 1922. *Heterotheca horrida* (Rydb.) Harms ssp. *cinerascens* (S.F. Blake) Semple, *Brittonia* 39: 381. 1987. TYPE: U.S.A. UTAH. Beaver Canyon, among rocks in the oak region, 2 Sept 1909, *Tidestrom* 2873 (Holotype: US!; isotype: WIS!)

Perennial from stout woody taproots, STEMS several to many, ascending-erect, (20)-23-33.7-44-(52) cm tall, moderately to densely hispid-strigose, long spreading hairs numerous; (8)-14-23-31-(40) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, 19-28-36-(45) mm long, 3-5.3-7.7-(12) mm wide, subpetiolate, cuneate, sometimes somewhat mucronate, moderately hispid-strigose and moderately to densely glandular on both surfaces; margins entire, strigose, longer spreading hairs along margins basally. UPPER STEM LEAVES lanceolate to triangular-lanceolate, (12)-14.5-21-26-(34) mm long, 3-4.3-5.7-(8) mm wide, sessile, somewhat to much reduced upward, usually sharply acute, often at right angles to stem, indument similar to lower or more glandular, (8)-10-25-39-(49) glands/mm², 5-30-57-(90) hairs/mm², margins flat, a few longer hispid hairs along margins basally. CAPITULESCENCE congested to very open cymose-corymbiform, heads (1)-2-10-19-(35); peduncles moderately to densely hispid-strigose, sparsely to densely glandular, (14)-24-35.5-47-(58) mm long; bracts few, linear-lanceolate, reduced, rarely foliar, indument like leaves. INVOLUCRES narrowly campanulate when fresh, campanulate-hemispheric upon drying, (6)-6.8-8.2-9.7-(11) mm high; phyllaries in 4-5 imbricate series, outer and mid series narrowly triangular-lanceolate, very sparsely to moderately strigose, moderately to densely glandular (rarely sparsely), margins hyaline narrow, fimbriate-ciliate, rarely anthocyanotic apically; inner ones similar. RAY FLORETS (7)-9-12-15-(18), strap yellow, (5)-5.8-8.2-10.6-(12.4) mm long, 1-1.5-1.9-(2.5) mm wide, tube glabrate. DISC FLORETS (10)-14-30-47-(65), yellow, glabrous or a few minute hairs, corolla barely ampliate, (4.4)-4.6-5-5.4-(5.7) mm long, lobes (0.4)-0.5-0.6-0.7-(0.8) mm long, hairs usually absent, 0-0.1-0.35 mm long. ACHENES (1.3)-1.5-2.1-2.7-(3.2) mm long, moderately strigose; pappus off-white, double, outer whorl of linear scales 0.25-1.3 mm long, inner whorl of 35-45 barbellate bristle (4.3)-4.5-5-5.6-(6.1) mm long. Chromosome numbers: $2n = 18, 36$; many reports.

Flowering Period: (January, May-) JUNE-OCTOBER-(November in south).

Distribution and habitat: Utah, northern and central Arizona and isolated plateaus and mountains in eastern and southern Nevada (Fig. 40B), rare in southern Idaho; rocky embankments and outcrops in oak woods and juniper-pinyon scrub, cracks and crevices in rocks, ledges, lava crevices, limestone cliffs, rocky slopes, sand flats near rivers and streams, dry rocky washes red sandstone soil, sand flats near rivers and streams, rocky sandstone loams, red sandstone soils; 420-3200 m (1400-10500 ft.) elevation.

Discussion: *Heterotheca villosa* var. *scabra* is distinguished by its moderately to densely glandular and sparsely to moderately hispid-strigose narrowly deltoid-lanceolate leaves and heads with very sparsely hispid-strigose phyllaries which are moderately to densely glandular (Fig. 47). Lower to lower mid stem leaves are typically narrowly oblanceolate (Fig. 47D), while there is considerable variation in mid to upper stem leaf size and width (Figs. 47E-G). The variation is thought to be due to differences in growing conditions and time of the year shoots are produced. Even when many leaves are more *nana*-like and oblong (Fig. 48D), some leaves are deltoid-lanceolate. In southwestern Utah and north central Arizona var. *scabra* and var. *nana* can be difficult to distinguish. In much of Utah, northern Nevada and adjacent Idaho, var. *scabra* and var. *minor* can be difficult to distinguish. The upper stem leaves often arise at right angles to the stem (patent).

Semple (1987) discussed this taxon under the synonym *Heterotheca horrida* ssp. *cinerascens*. Additional work on the genus and the *villosa* complex (Semple 1990) resulted in treatment of *H. horrida* ssp. *horrida* and *H. horrida* ssp. *cinerascens* as tentative synonyms of *H. villosa* var. *minor*. Subsequently, Semple (1992) determined that at the varietal level Alice Eastwood's epithet had priority over a combination based on Blake's epithet and a combination was proposed and is used here.

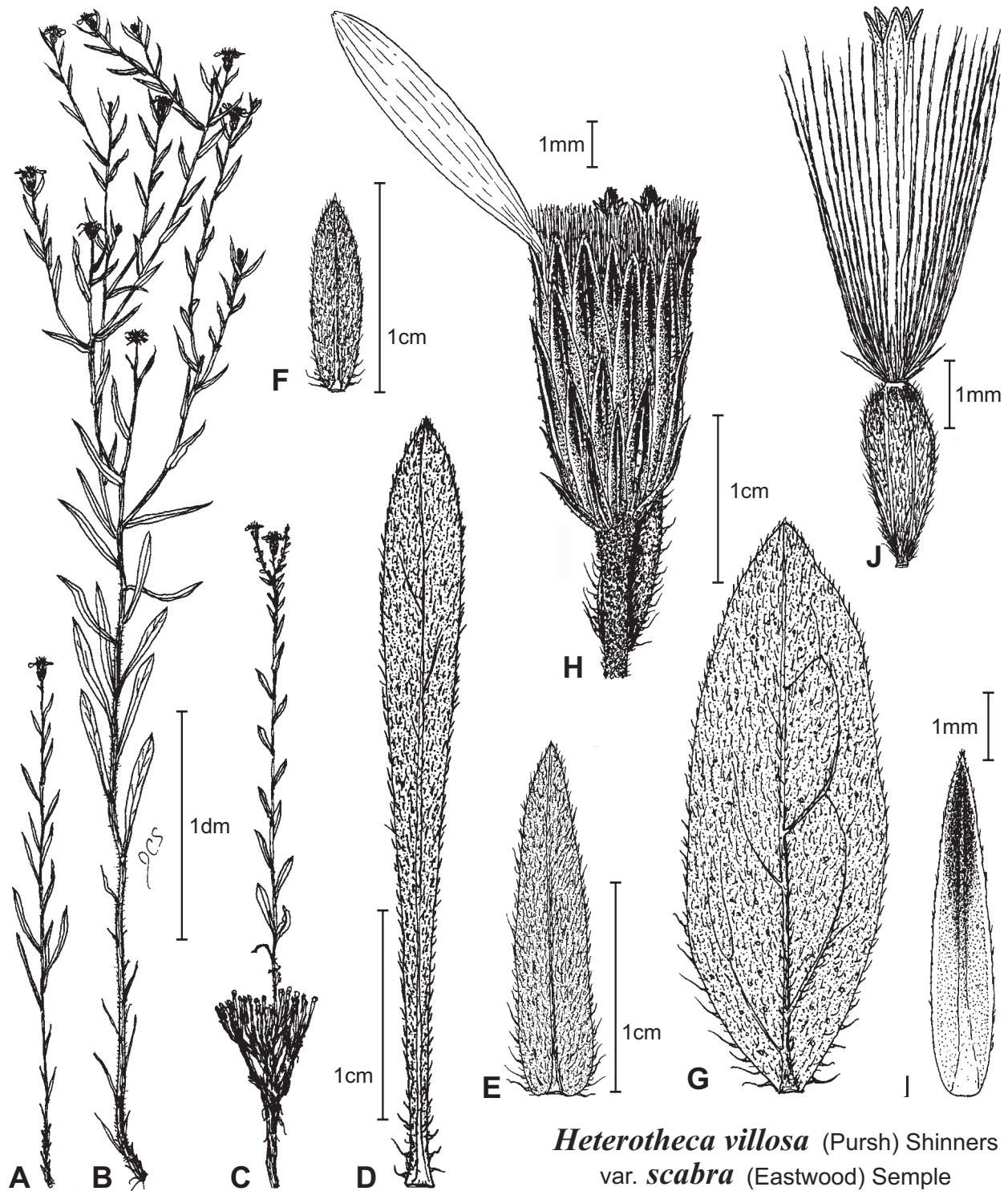
The species may bloom early in the year and again in the late summer or fall. Early blooming plants can be quite different in capitulescence form and leaf indument traits. Usually the upper stem leaves are reduced compared to the lower stem leaves which are usually less glandular and more densely hispid-strigose. The capitulescence may consist of solitary heads on long peduncles with small foliar bracts (Fig. 47H). Later in the season, the same individual may produce short shoots with smaller lanceolate leaves that are much more glandular and less hispid-strigose below a compact capitulescence.

Specimens examined: U.S.A. ARIZONA. Havasu Cyn., *Whiting s.n.* (NMC). Navajo Reservation, *Vorhies 115* (GH, UC). Apache Co.: Cyn. de Chelly N.M., *Knobloch 1774* (MIN). Chinle P.O., *Demaree 42680* (CAS). Banks of Chinle Wash, *Demaree 42903* (NY, RSA). Cyn. del Muerto, Massacre Cave, *Cutler, Goodman & Payson 2911* (DS, NDG). Morrison, Lukachukai Cyn., *Cazier & Cazier 1035* (ASU). Kin Li Chee Tribal Park, *Lowenstein s.n.* (ASU). Coconino Co.: Halfway between Cameron and Desert View, *Ramsey & Ramsey 2857* (POM). N of Cedar Ridge, *Ripley & Barneby 4909* (CAS). W side of Cockscomb, *Atwood 03063A* (BRY). Near Flagstaff, *Leiberg 5874* (DS). S of The Gap, *Turner 4899* (TEX). S of Glen Cyn.-Page, *Moore, Pinkava & Lehto 7024* (ASU). Grand Cyn of the Colorado R., *Eastwood 3578* (CAS, GH). Grand Cyn. N.P., *MacDougal 177* (GH, NY, RM, UC), *Rattan s.n.* (UC); Bright Angel Camp, *Condit s.n.* (UC); Cyn. Village, *Harms 1885* (KANU, SASK); Cape Royal, *Peirson 7420* (DS, RSA), *Ramsey & Ramsey 2851* (POM); Grand View Trail, *Eastwood 5700* (CAS), *Ferris & Duncan 2251* (CAS, DS, NY); Hotel to Hopi Point, *Blake 9823* (LL); Hualpai Cyn., *Howell 26368* (CAS); Hualapai switchbacks, *Theroux 1697* (ASU); Mather Point, *Harms 1884* (KANU(2), SASK(2), WAT); Kaibab trail to Roaring Springs, *Howell & Eastwood 1082* (CAS); S of Montezuma Point, *Degener 4477* (NY); North Rim, *Howell & Eastwood 932* (CAS); Red Cyn. Trail, *Ward s.n.* (NY); S entrance, *Munz 13079* (DS, POM); Toroweap, Saddly Horse Cyn., *Cottam 13535B* (CAS); Toroweap Point, *Jaeger s.n.* (DS), *Merkle & Merkle 870* (CAS). S of Grand Cyn., *Degener & Park 4418* (NY). E of Jacobs L., *Ferris 10242* (DS, GH, RSA, UC), *Semple & Heard 7886* (WAT), *Semple & Heard 7895* (WAT), *Semple & Heard 7897* (WAT). E of Jacob Lake Inn, *Holmgren & Holmgren 4703* (KANU, NY, WTU). Kaibab Plateau, Big Saddle-Pine Flat Rd, *Gooding 358-48* (UC). Lees Ferry, *Hevly s.n.* (NY), *Keil K11751* (ASU). N of Lees Ferry, *Jaeger s.n.* (POM). S of Lee's Ferry, *Jones s.n.* (RSA). Mogollon Rim, E of Kehl Springs Campground, *Daniel & Hensold* (ASU). Navajo N.M., Inscription House, *Fairchild & Brotherson 127* (BRY). Paria Plateau, *Atwood, Moore 4277* (BRY), *Atwood, Moore 4286* (BRY). Paria Cyn, Paria Primitive Area, *Woodruff 1124* (BRY). SE of Tonalea, *Harms 1890* (KANU, SASK(2)), SW of Tonalea, *Harms 19139* (KANU, SASK). Near Tuba City, *Clute 59* (GH, NY, RM), *Kearney & Peebles 12873* (CAS). Walnut Cyn., *Ramsey & Ramsey 2844* (POM). Gila Co.: Tonto NF, Parker Cr Cyn, *Johnson J-30* (USFS). Mohave Co.: Cottonwood Spr., *Gierisch 4548* (ASU, BRY, NY). Holbrook, *Luck s.n.* (NY). Near Horse Mesa Dam, *Peebles 11670* (GH, LL). SW of Kayenta, *Semple et al. 5531* (WAT), *Taylor & Taylor 29536* (NY). Robinson Reservoir, *Coombs, Bundy 2826* (ASU, BRY). SW of Second Mesa, *Baker 4747* (ASU(3)). Short Cr., *Cottam 8578* (RSA). Toroweap Valley, *McClintock 52-563* (CAS, NY, WS). Yavapai Co.: between Prescott and Ash Fork, *Eastwood 16765a* (CAS, LL). CALIFORNIA. Riverside Co.: Little San Bernardino Mts, Morongo Pass, *Jaeger s.n.* (RSA), *Munz 4536* (RSA); Joshua Tree N.M., Hidden Valley, *Thorne, Dahlgren & Dahlgren 53593* (RSA); Wonderland of Rocks, *Roos 2571* (RSA), *Roos & Roos 5011* (DS, NY, RSA). COLORADO. Rio Blanco Co.: E of Dinosaur, *Welsh & Moore 312* (BRY), *Welsh & Moore 320* (BRY).

IDAHO. Blaine Co.: 12 mi E of Carey, W edge of the, *Christ 16088* (NY). Butte Co.: Craters of the Moon, *Eggler 175* (MIN(2)). 12 mi E of Carey, W edge of the Craters of the Moon, *Christ 16085* (NY). Cassia Co.: City of Rocks, *Goodrich, Wellner, & Webster 17878* (BRY, NY), *Watson 545* (NY). **NEW MEXICO.** Rio Arriba Co.: NE of Chama, *Harms 19121* (KANU, SASK). San Juan Co.: SE of Shiprock, *Spellenberg & Ward 6096* (NMC, NY). NM. San Miguel Co.: Las Vegas, Collinas W, *Arsène 18794* (DS, LL, POM). E of Las Vegas, *Hill & Levandoski 12077* (TEX). **NEVADA.** Juniper Range, *Purpus 6247* (UC), *Purpus 6248* (UC). Clark Co.: Charleston Mts, Excelsior Cyn., *Clokey 8759* (CAN, CAS, DS, GH(3), LL, MIN, NY, PH, RM(2), RSA, TEX, UC UNCC, WS, WTU(2)); near La Madre Spring, *Jaeger s.n.* (UC). N of Hoover Dam, *Nickerson s.n.* (ASU). Muddy Mts, valley into Colorado Quarry, *Swearingen 1438* (RSA); W of Logandale, *Swearingen 1206* (RSA). Spring Mts., *Niles & Bostick 855* (NY); Calico Hills, Red Spring, *Pinzl & Barkley 9868* (NY). Elko Co.: W of Collar Elbow Basin, *Foster 8378* (BRY, NY, RM). SE of Elko, Brown Rk Cyn, *Holmgren, Holmgren & Keller 10265* (CAS, NY, RM, RSA, WTU). SSE of Elko, *Holmgren & Holmgren 10265* (BRY). Humboldt NF, head of Cottonwood drainage, *Lewis & Walters 4538* (BRY). Jarbridge Mts, Copper Crk Basin, *Train 662* (DS, GH, NY, WIS). Jarbridge R. Cyn, 1-3 mi from Jarbridge, *Train 783* (UC). Little Humboldt Ranch, *Holmgren 756* (RM, WTU). Ruby Mts., Lamoille Cyn., *Holmgren 1763* (UC), *Munz 16176* (CAS, POM, UC, WTU), *Williams & Tiehm 84-105-1* (BRY, NY); Soldier Cr. Cyn., *Price 216* (USFS), *Train 4650* (NY, UC); Soldier Creek Trail, *Semple, Suario & Ahmed 9270* (WAT). N end of Spruce Mt., *Pinzl 10152* (TEX). Esmeralda Co.: W of Tonopah, Lone Mt., *Tiehm & Wharff 8250* (DAO, KANU, LL, NY, RSA). Eureka Co.: Diamond Mts., Davis Cyn., *Tiehm & Williams 8187* (BRY, DAO, KANU, MIN, NY, RSA, TEX, WTU). *Tiehm 11844* (KANU, NY, TEX, WTU). New York Cyn, *Train 1248* (DS, UC). Roberts Cr Mts, Roberts Cr, *Tiehm & Williams 8179* (ASU, NY, RSA, WS). S of Eureka, Fish Creek Range, Goodwin Cyn, *Tiehm 8414* (ASU, MIN, NY, RSA, TEX, WS). Monitor Range, Allison Cr., *Goodrich 13172* (BRY, NY). Windfall Cyn., Eureka, *Train s.n.* (NY). Lander Co.: 17 mi from Austin, Birch Crk Cyn, *Henning 41* (GH, NY, WIS). Lincoln Co.: E of Alamo, *Tiehm 6890* (CAS), *Tiehm 7231* (CAS, NY, RSA). N of Caliente, *Train 2473* (GH, UC). Mahogany Mts, *Tiehm 8375* (ASU, KANU, NY, RSA, TEX, WS). Pahrangat Range, Mt. Irish, *Tiehm & Crisafulli 11408* (NY); W of Crystal Springs, *Train 2395* (DS, NY, WIS). Panacea, *Jones s.n.* (POM(2)). Panaca Hills, above Condor Cyn., *Williams & Tiehm 83-68-2* (NY). Nye Co.: Grant Range, Troy Cyn, *Tiehm & Nachlinger 8300* (BRY, KANU, MIN, NY, RSA, WTU). Gold Flat Basin, *Beatley 2916* (DS), *Beatley & Carl 3122* (DS), *Beatley 3930* (DS, NY). Pahute Mesa, N of Area 19 Camp, *Beatley 9915* (NY, RSA); Columbine Cyn, *Beatley 3132* (RSA); Deadhorse Flat Rd., *Reveal 2029* (DS, NY); E of Deadhorse Flat, *Reveal 1646* (BRY, DS, NY); Plateau Rd., *Reveal 1738* (DS, NY); N of Twin Pks., *Beatley 9693* (NY), *Beatley 13226* (DS, NY, RSA, TEX). Monitor Range, Miniature Grand Cyn, *Goodrich 10775* (BRY). Nellis Airforce Base, Thirty Cyn, *Reveal & Beatley 1694* (DS, NY). Toiyabe Range, SW of Austin, *Goodrich 12236* (BRY, NY); crest of range between San Juan Tierney Cr. and McLeod Cr., *Goodrich & Schlatterer 12150* (RM). S end of Toquima Range, NNW of Baxter Spr, *Genz 8895* (BRY). White Pine Co.: Cherry Cr., *Jones s.n.* (POM). Egan Range, Huesser Mt., Rattlesnake Cyn., *Tiehm 9750* (NY). Mt. Sherman, *Hitchcock & Martin 5679* (DS, GH, NY, RSA, UC, WS, WTU). Schell Creek Range, McCoy Creek, *Tiehm 10127* (BRY, NY, RM). Shell Crk Range, Steptoe Crk, *Train 999* (GH, NY, WIS). Snake Range, Murphy's Wash, *Tiehm 10104* (BRY, LL, NY, RM). **TEXAS.** Brewster Co.: Del Norte Mts. S of Alpine, *Warnock & Hinckley 7543* (SRSC). **UTAH.** Deer Creek, *Jones 1271A* (RSA). Fillmore For., N of Dry Fork, *Miller 59* (USFS). Mt. Irish, *Purpus 6352* (UC). Beaver Co.: E of Beaver, Fishlake N.F., *Semple & Heard 7818* (WAT). W of Beaver, *Watson 255* (TEX). Pine Grove Cyn., *Welsh & Chatterley 20186* (BRY, NY). Spring area, *Mutz 82-1012* (BRY). Tushar Mts., Beaver Cyn, *Taye 2442* (BRY), *Taye 3132* (BRY). Wah Wah Mts., Pine Grove Cyn., *Welsh & Christansen 2705* (NY). S of Wah Wah Pass, *Holmgren & Bethers 3830* (KANU, NY, MIN, RSA, UBC, WTU). Box Elder Co.: Sulphur Springs, *Garrett 5408a* (BRY, LL, RM, WIS). Cache Co.: Wasatch Range, Tony Grove L., *Thorne & Thorne 2187* (BRY). Davis Co.: Antelope Is., *Clark 4468* (BRY). Emery Co.: W of Greenriver, *Atwood, Thompson & Anderson 12432* (BRY, NY). NW of Hanksville, *Tuhy 2398* (BRY). SE of Huntington, *Welsh & Clark 16168* (BRY, NY). SSE of Price, Cedar Mt., *Allen 692* (BRY), *Welsh & Atwood 10784* (BRY). San Rafael Reef, Cottonwood Wash, *Harris 240* (BRY). S of San Rafael R., *Welsh, Atwood & Moore 10818* (BRY). San Rafael Swell, *Jones s.n.* (DS); Black Dragon Cyn., *Kass 2984* (NY); Mexican Bend, *Despain 210* (BRY); Old Smith Cabin area., *Despain 646* (BRY), *Harris 323* (BRY). Garfield Co.: S of Boulder, *Semple 8823* (WAT) N of Bullfrog Basin, *Neese 6903* (BRY, MIN). Calf Cr. and Escalante R., *Cottam 14687* (GH, WTU). Capitol Reef N.P., *Porter 3601* (BRY). Escalante, *Stanton 870* (LL), *Stanton 871* (LL). E of Escalante, *Cottam 4409* (LL, UC). N of Escalante, *Pennell & Schaeffer 21963* (NY); near Hells Backbone, *Lewis 6125* (BRY, RM); S of Hells Backbone Rd., *Tuhy 2373* (BRY); Hells Backbone Bridge Rd., *Semple & Chmielewski 8827* (WAT). SW of Escalante, *Franklin 6683* (ASU). Flint Tr. Overlook, *Tuhy 597* (BRY). N of Flint Flat, *Tuhy 588* (BRY). W of Glen Cyn. N.R.P., *Semple 8819* (WAT). E of Gulch on Burr Tr, *Foster & Foster 4048* (BRY, NY). Henry Mts., N of Gibbon Spr, *Neese & White 4102* (BRY); Penellen Pass, *Neese 2456* (BRY), *Neese 5988* (BRY, MIN); E of Mt Heller, *Neese 2420* (BRY). Hite Bridge, *Welsh & Welsh 21955* (BRY). S of the Post, *Woodruff 1178* (BRY). UT-95 S of UT-276, *Neese & White 2809* (BRY, RM). Under the Ledges, *Neese & White 2796* (BRY). Grand Co.: Arches N.P., near Double Arches, *Moran 1408* (DS); Hanging Garden, *Allan 274* (BRY). Moab, *Harrison 5947* (LL). W of Moab, *Howell & True 44747* (CAS, NY). Iron Co.: Cedar Cyn., *Garrett 6035* (LL). E of Cedar City, *Welsh & Christensen 2652* (NY, WIS), *Harms 19141* (KANU). Grants Ranch, *Warrick 2541* (BRY). Paradise Spring Tr., *Warrick 2182* (BRY). Juab Co.: E of Leamington, *Baird 293* (BRY), *Welsh & Moore x5146* (NY). Kane Co.: *Welsh & Welsh 22361* (BRY). Cockscomb, *Atwood*

Figure 47. Morphology of *Heterotheca villosa* var. *scabra*. A-C. Habit and shoots of small and robust plants; shoots A and B could be formed by the same plant at different times of the year; leaves often more patent than shown. **D.** Lower-mid stem leaf. **E-G.** Typical, dwarf and very robust mid to upper stem leaves, respectively. **H.** Diploid head with only some florets drawn; heads of tetraploids can be much larger. **I.** Mid series phyllary with chlorophyllous zone dark; phyllaries may be much more glandular. **J.** Mature achene with disc corolla attached. ➔

3615 (BRY). Collet Cyn., *Woodruff 1162* (BRY). Coral Pink Sand Dunes S.P., *Franklin & Franklin 887* (BRY, NY, RM). Pink Sand Dunes, *Foster & Foster 4143* (BRY, NY). Cottonwood Wash, *Atwood & Allen 02804* (BRY). S of Glen Cyn. City, *Atwood 3129A* (BRY), *Atwood & Welsh 02720* (BRY), *Foster 5791* (BRY). W of Glen Cyn City, *Atwood 2921* (BRY). Hole in the Rock area, *Higgins & Higgins 14085* (BRY). W of Kanab, *Tuhy 2363* (BRY, CAN). NW of Orderville, *Maquire 18858* (DAO). Paria, *Foster 5778* (BRY). Paria



Heterotheca villosa (Pursh) Shinnors
 var. *scabra* (Eastwood) Semple

R., *Atwood & Higgins 4013* (BRY). SE of Old Paria, *Cronquist & Thorne 12061* (NY). Vermillion Castle, *Levi & Levi s.n.* (WIS). Smoky Mt, *Atwood & Woffinden 03296* (BRY). E of Zion N.P., *Ertter & Strachan 2871* (CAS, NY, WTU), *Semple & Heard 7876* (WAT), *Semple & Chmielewski 8828* (WAT), *Semple & Semple 10490* (BRY, WAT). Millard Co.: House Range, Painter Spring, *Kass 554* (BRY), *Kass & Preston 624* (BRY). S of Leamington Pass, *Guidinger 1380* (BRY). SE of Oak City, *Goodrich 16084* (BRY, NY). Near Scipio, *Goodrich 14941* (BRY). Piute Co.: Bullion Falls, *Jones 5903* (NY, POM, RM, UC). Bullion Cyn, *Rydberg & Carlton 7288* (RM(2)). Rich Co.: Bear Lake, *Flowers F1683* (LL). Salt Lake Co.: Big Cottonwood Cyn., *Semple, Suropto & Ahmed 9247* (WAT). San Juan Co.: N of Blanding, *Cutler 2348* (CAS, GH). Bluff, *Holmgren 3785* (GH, NY, UC). N of Bluff, *Maguire et al. 5682* (UC). Bulter Wash, *Howell & Eastwood 6724* (CAS). Canyonlands N.P., Elephant Hill, *Howell & True 44794* (CAS). Gypsum Cyn., *Higgins & Welsh 14177* (BRY, NY). N of Hole-in-the-Rock, *Jeppsen 366* (BRY). LaSal Mts., *Purpus 7017* (POM, UC). Indian Hills S.P., *Howell & True 44782* (CAS). S of Moab, *Wright 97* (BRY). WSW of Monticello, *Tuhy 1531* (BRY). Muley Pt, GCNRA, *Welsh & Welsh 22236* (BRY). Natural Bridges, White Cyn, *Welsh & Moore 2468* (NY), *Rydberg & Garrett 9400* (NY, RM, UC). Navajo Mt., *Davey s.n.* (NY); E side, *Atwood & Allen 02978* (BRY); S side, *Atwood 4145* (BRY); road to Navajo Mt, *Atwood & Kaneko 03399* (BRY). W slope Navajo Mt., *Cutler 2806* (DS). N fork of Forgotten Cyn, *Welsh & Chatterley 1496* (BRY). NW of Goulding Trading Post, *Atwood, House, Anderson & Thompson 11053* (BRY, CAN, NY, RM). Rainbow Bridge Tr., *Howell 24626* (CAS). Rone Barely Mesa, *Higgins & Higgins 15813* (BRY, NY). San Juan R., Hanging gardens, *Atwood & Allen 3179* (BRY), *Toft & Welsh 164* (BRY), *Atwood & Allen 3185* (BRY). Three Garden, *Welsh & Atwood 11672* (BRY). Youngs Cyn., *Mikus 603* (BRY). San Pete Co.: Ephraim, Maple Cyn, *Olsen s.n.* (UC). Sevier Co.: W of Emery, *Welsh 23174* (BRY). Summit Co.: *Garrett 7816* (KANU). Slate Gorge, *Semple, Suropto & Ahmed 9234* (WAT). Tooele Co.: Stansbury Mts., *Taye & Herrick 1429* (BRY). Uintah Co.: S of Bonanza, *Holmgren, Reveal & LaFrance 2264* (UC, WTU). Between K Ranch and Jensen, *Osterhout 6409* (RM). Split Mt, near Dinosaur N. Mon., *Neese & Chatterley 9871* (BRY). Between Spring and Kane Hollows, *England 1071* (BRY). Near Vernal, *Andrews & Noble s.n.* (WTU). N of White R., Bonanza-Watson Rd, *Neese & Peterson 6091* (BRY, MIN). Utah Co.: Thistle, *Eastwood 7701a* (CAS). Washington Co.: Bitter Cr. Cyn., *Warrick 133* (BRY), *Warrick 415* (BRY), *Warrick 417* (BRY, NY), *Warrick 1605* (BRY, NY). SE of Cinder Hill, *Meyer 3193* (NY). N of Clear Cr. at county line, *Thorne & Franklin 5749* (NY). Near Enterprise Reservoir *Meyer 1198* (NY). SE of Fort Pearce, *Spencer 68* (NY). Kolob Terrace, *Welsh, Clarke & Thorne 24100* (NY). W of Leeds, *Semple & Heard 7857* (WAT). Lower Sand Cove Reservoir, *Barnum 1054* (BRY). W of Lytle Preserve, *Baird 2475* (NY). Mill Cyn., *Warrick & Romano 2669* (BRY). Paradise Spring Trail, *Warrick 2161* (BRY). Pine Valley Mts., *Atwood 5382* (BRY), *Gentry & Jensen 2239* (BRY, NY, WTU); L Fork of Santa Clara R, *Munz 16941* (DS, POM, WTU). Red Cliffs Rec Area, *Warrick 1824* (BRY), *Warrick 1827* (BRY), *Warrick 2052* (BRY). Snow Cyn., *Meyer 2083* (BRY). N of Springdale, *Semple & Heard 7875* (WAT). St. George, *Hardy 114* (BRY). N of St. George, *Gould 1357* (CAS, DS, GH, NY, POM, UC). St. George, *Degener & Peiler 16639* (NY), *Palmer s.n.* (GH, NY). Zion N.P., *Anderson 2143* (GH, SASK), *Ballou s.n.* (DS), *Eastham* (UBC), *Foster 5650* (BRY), *Garrett R2676* (NY), *Higgins* (NY), *McDonald 1161* (USFS), *Thackery 507* (LL, TEX), *Thorne & Chandler 5604* (NY); Clear Creek, *Howell & Eastwood 6325* (CAS), *Howell & Eastwood 6353* (CAS), *Howell & True 45326* (CAS). Emerald Pool Tr, *Ramsey & Ramsey 1267* (POM), *Ramsey & Ramsey 1268* (POM). N of Mt Carmel Hwy, *Boyle 158* (UC), *Boyle 169* (UC); Narrows Trail, *Howell & True 45301* (CAS). Zion Creek, Near Narrows, *Moore N 29286* (MIN). Wayne Co.: N of Caineville, *Kass & Neely 2295* (BRY). Capitol Reef N.M., Robber's Roost farm, *Vickery 571* (DS). Canyonlands N.P., E of Visitor Centre, *Harrison 1345* (BRY), *Harrison 1350* (BRY), *Harrison 1488* (BRY), *Welsh 22617* (BRY), *Welsh 22633* (BRY). SSE of Fruita, *McVaugh 14531* (CAS, NY, TEX). W of Hanksville, *Tuhy 2506* (BRY). Natural Bridge, *Harrison 7394* (KANU). San Raphael Desert, *Stanton 494* (LL).

aff. var. *scabra*

U.S.A. ARIZONA. Coconino Co.: E of Jacobs Lake, *Hitchcock, Rethke & van Raadshooven 4527* (CAS, DS, GH, UC, WS, WTU). Meteor Crater, *Sauleda & Sauleda 6448* (ASU, WAT). COLORADO. Moffat Co.: Dinosaur N. Mon., *Lane & Longstreth 2930* (TEX). Montezuma Co.: Mesa Verde N.P, *Mathias 639* (GH, POM). TEXAS. Val Verde Co.: W of Comstock, *Warnock 21379* (SRSC). Seminole Cyn State Historical Park, *Labus 036* (TEX). UTAH. Emery Co.: W of Castle Dale, Straight Cyn, *Keck 687* (DS). San Juan Co.: Armstrong and White Cyn.s, near the Natural Bridges, *Rydberg & Garrett 9399* (NY). S of Moab, overlooking Hook and Ladder Gulch, *Cronquist 12077* (NY, RM). Between Moab & Monticello, *Rydberg & Garrett 9120* (CAN, MIN, NY, RM, UC, WIS). Utah Co.: N of Provo, *Galway 2258-G* (UC). Washington Co.: Zion N.P., Narrows Trail, *Nelson 10134* (RM), Virgin River, *Thorne & Chandler 5586* (NY).

aff. var. *scabra* (approaching var. *nana*)

U.S.A. ARIZONA. Coconino Co.: Top of Walnut Cyn. on North Rim, *Mishler 1305* (ASU). UTAH. Grand Co.: Salt Wash, Arches N. Mon., *Welsh & Moore 2740* (NY).

aff. var. *scabra* (approaching var. *minor*)

U.S.A. ARIZONA. Navajo Co.: Beaver Dam, NW Ariz., *Palmer 200* (CAN, NY(3)). COLORADO. Montrose Co.: Bedrock, *Payson & Payson 3922* (RM). NEW MEXICO. San Juan Co.: E slope of Hogback, S of San Juan R., *Lehto, Barrett & Kramp L23208* (ASU, TEX). NEVADA. Elko Co.: Bull Run Mts, ridge E of Bull Run Reservoir, *Tiehm & Williams 9295* (BRY, NY, RSA, TEX, WTU). UTAH. Garfield Co.: Escalante Cyn., *Wilson et al. 5489* (ASU). Kane Co.: Coral Pink Sand Dunes, *Welsh & Clark 15551* (BRY, NY). Salt Lake Co.: Moss Falls Trail, Big Cottonwood Cyn, *Garrett 8353* (UC). Summit Co.: near Snyderville, *Garrett 6777* (LL). Uintah Co.: S of Bonanza, *Holmgren, Reveal & La France 2264* (DS, GH, KANU, MIN, NY(2), TEX, UBC, UNCC). Washington Co.: Zion N.P., Echo Cyn, *Higgins 18189* (NY).

aff. var. *scabra* (approaching var. *pedunculata* or mixed collection)

U.S.A. ARIZONA. Coconino Co.: Corral Valley, *Coombs & Bundy 2890* (ASU, BRY, NY). UTAH. San Juan Co.: Tuwa Cyn., Natural Bridges N. Mon., *Welsh & Moore 2390* (NY).

17.8 *Heterotheca villosa* (Pursh) Shinnery var. *nana* (A. Gray) Semple, *Novon* 4: 54. 1994.

Chrysopsis canescens (DC.) Torr. & Gray var. *nana* A. Gray, *Mem. Amer. Acad. Sci.* 4: 78. 1849. TYPE: U.S.A. NEW MEXICO. [possibly Mora Co.], "elevated rocky region 2 mi E of the Mora River," Aug 1847, *Fendler* [391c] (Holotype: GH!)

Chrysopsis horrida Rydb., *Bull. Torr. Bot. Club.* 31: 648. 1904. *Heterotheca horrida* (Rydb.) Harms, *Wrightia* 4: 17. 1968. *Heterotheca villosa* (Pursh) Shinnery var. *horrida* (Rydb.) Semple, *Novon* 4: 54. 1994. TYPE: U.S.A. COLORADO. New Windsor, 8 Aug, 1900, *Osterhout 2326* (Holotype: NY!, isotypes: RM!(2), WIS!)

STEMS several to many, ascending-erect, (9)-13-**26.8**-40-(63) cm tall, moderately to densely hispid-strigose, long spreading hairs often numerous; (12)-11-**28**-41-(79) nodes below capitulescence. LOWER STEM LEAVES oblanceolate to oblong, (8)-14-**24**-33-(40) mm long, (2)-3.6-**5.6**-7.6-(8.4) mm wide, petiolate, cuneate, rarely somewhat mucronate, sparsely to moderately hispid-strigose and moderately to densely glandular (rarely sparsely) on both surfaces; margins entire, sometimes weakly undulate, strigose, longer spreading hairs along margins basally. UPPER STEM LEAVES narrowly to broadly oblong, (6)-10-**17**-24-(32) mm long, (2)-3.4-**5.1**-6.7-(8) mm wide, sessile, somewhat reduced upward, acute to often obtuse, indument similar to lower or more glandular, (2)-9-**18**-27-(36) glands/mm², (9)-12-**28**-44-(56) hairs/mm², margins flat, a few longer spreading hairs along margins basally. CAPITULESCENCE congested cymose-corymbiform, heads (2)-3-**11**-20-(33); peduncles moderately to densely hispid-canescens, glandular, (4)-10-**23**-35-(48) mm long; bracts few, linear-oblong, usually reduced, not foliar, indument like leaves. INVOLUCRES cylindrical to narrowly campanulate when fresh, campanulate-hemispheric upon drying, (5.4)-6.2-**7.3**-8.4-(9.0) mm high; phyllaries in 4-5 imbricate series, outer and mid series, narrowly triangular-lanceolate, sparsely to moderately densely strigose, sparsely to densely glandular, margins hyaline narrow, fimbriate-ciliate, sometimes anthocyanotic apically; inner ones similar. RAY FLORETS (11)-13-**16**-19-(22), strap yellow, (3.5)-6.9-9-11-(12) mm long, (0.5)-0.8-**1.1**-1.4-(1.8) mm wide, tube glabrate. DISC FLORETS (17)-19-**28**-39-(52), yellow, glabrous or a few minute hairs, corolla barely ampliate, (4.8)-5.1-**5.5**-6.0-(6.6) mm long, lobes (0.45)-0.5-**0.6**-0.7-(0.75) mm long, hairs usually absent or very few, 0.1-**0.1**-0.25 mm long. ACHENES (1)-1.3-**1.8**-2.3-(2.6) mm long, sparsely to moderately strigose; pappus off-white, double, outer whorl of linear scales 0.2-1 mm long, inner whorl of 35-45 barbellate bristles (5)-5.0-**5.7**-6.3-(7.3) mm long. Chromosome numbers: $2n = 18$, many reports; triploid, one report.

Flowering Period: (May)-JUNE-AUGUST-(October).

Distribution and habitat: Western Great Plains and lower to mid elevations in the central Rocky Mountains from southeastern Wyoming to southern New Mexico and west to eastern Arizona and Utah (Fig. 40B); short-grass grassland, dry areas with sage brush, open mixed conifer forests at lower elevations, pinyon-juniper-cholla brush; sandy and gravelly limestone, sandstone and granitic soils, fissures in lava surfaces, igneous cliffs; 1300-2700-(2900) m (4300-9000-(9500) ft.) elevation.

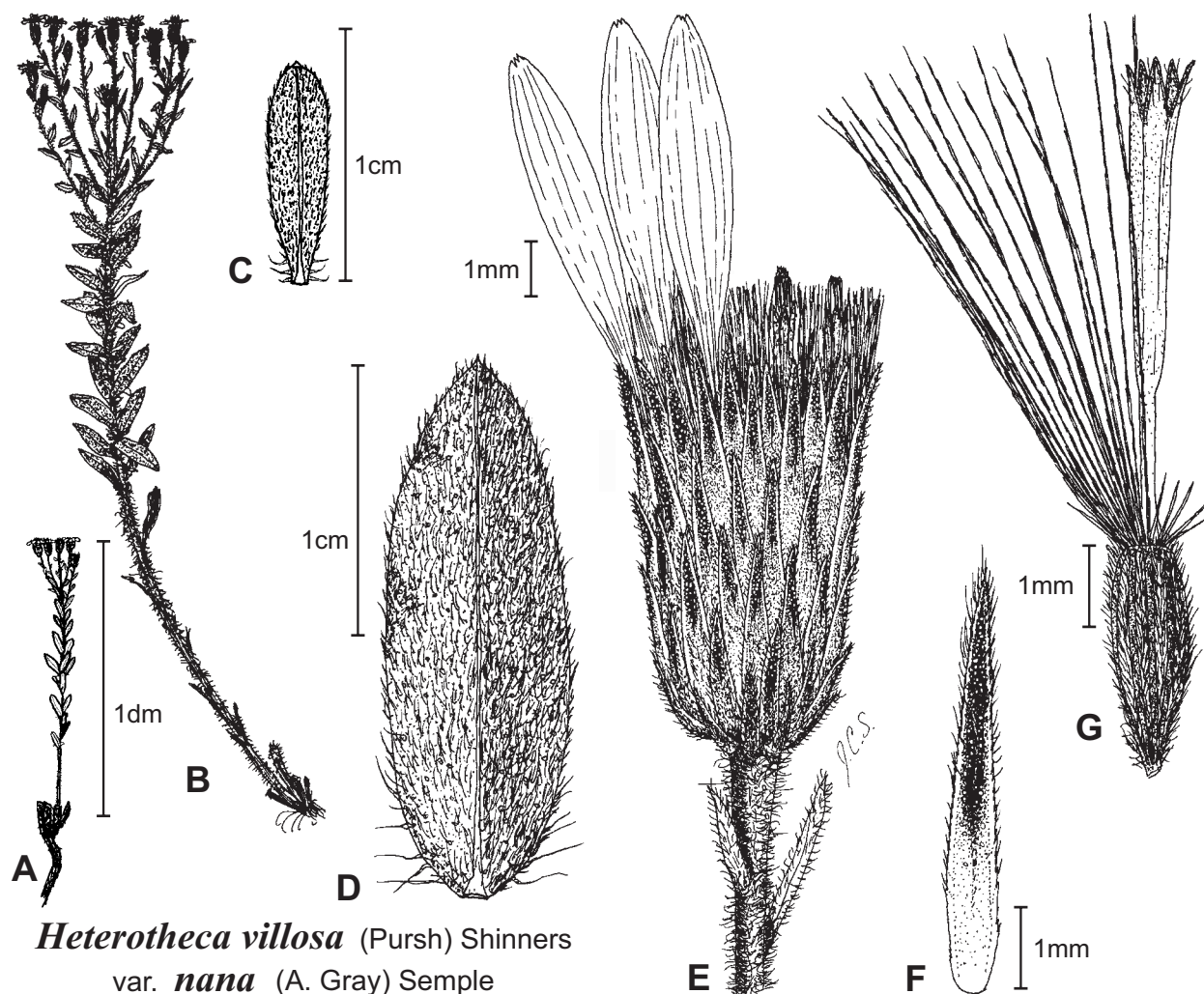
Discussion: Variety *nana* is distinguished by its linear to broad oblong, often patent, upper stem leaves and stems with short internodes (Fig. 48) versus narrowly to broadly oblanceolate upper stem leaves in var. *minor* on stems with longer internodes (Fig. 46). Forms of var. *minor* with oblong to ovate leaves generally have stems with longer internodes and fewer leaves. Plants at higher elevation in the foothills approach narrow leaved forms of *H. fulcrata* in general appearance, and may even hybridize with these, especially in the Laramie Hills of Wyoming. Possible hybrids between *H. villosa* var. *foliosa* and var. *nana* have also been collected and observed in the field; these have the general appearance of var. *foliosa* but with very sparsely to sparsely glandular upper stem leaves. In Colorado and Wyoming where the two varieties are sympatric, var. *foliosa* is tetraploid and var. *nana* is diploid, thereby greatly reducing the possibility of successful

hybridization. In the greater Four Corners area var. *nana* grades into var. *scabra* and collections are often difficult to place into one of these two races; both have broader leaf bases than var. *minor* as it occurs in the region.

The determination that the type of *Chrysopsis horrida* was more similar to the type of *Diplopappus hispidus* than previously realized resulted in the recommendation that the two be treated as conspecific and possibly even convarietal (Semple 1990). Discovery of the type of var. *minor* makes even that work out-of-date. Thus, the name *Heterotheca horrida* is removed from active use at the species level, after several decades of effort to get the name adopted, beginning with the work of Harms (1963, 1968) and my own earlier studies on the genus (Semple 1977, 1987). Semple (1992) proposed varietal level combinations in *H. villosa* for both var. *horrida* and var. *nana*. Field work in 1995 and additional analysis of the morphology of plants of the *nana-horrida* morphotype have led me to conclude that var. *horrida* belongs in synonymy under var. *nana*. Population samples from the high plains in central New Mexico included a range of plants that were similar to the very small size of the holotype of var. *nana* (Figs. 48A, C) and larger plants more similar to plants I previously would have assigned to var. *horrida*. Thus, the holotype of var. *nana* is representative of the extreme low end of the range of variation in stature encountered in the variety.

Harms in Correll and Johnston (1970) noted that var. *nana* (treated as *H. horrida* by Harms) might be present in Texas, but he had not seen collections confirming its presence in the state. No typical specimens of the variety from Texas were encountered in this study. A few collections assigned to other taxa as "aff." had some traits suggestive of var. *nana*, and only one collection is listed below as aff. var. *nana*; *Hinckley 4024* (NY). This latter collection is very atypical, but does not fit well into other taxa occurring in the area. It is tentatively assigned to var. *nana*, whose presence in Texas may be due only to a chance introduction. The variety is more likely to be found in the northwest corner of the panhandle near Oklahoma and New Mexico, if it exists in Texas.

Specimens examined: U.S.A. *Kuntze 3102* (NY). Valley of the Rio Grande below Donana, Terrajo de San Esteban, *Bigelow 510* (NY(2)). ARIZONA. Apache Co.: AZ-180 at Little Colorado crossing, *Lehto 7245* (ASU). Cyn. de Chelly Nat. Mon., Chinle P.O., *Demaree 38585* (RSA). Carnero Lake, *Lehto, Pinkava, Keil, & Pase L19121* (ASU). SE in Eager, *Pinkava, Lehto & Reeves P12689* (ASU). W of Eager, *Deaver 6421* (ASU). W of Eager, *Pinkava, Keil, Pase & Lehto L19087* (ASU). Green's Mt. Rd., *Lehto, McGill, Nash & Pinkava 11498* (ASU). Navajo Ind. Res., E of Ganado, *Harms 19131* (KANU, SASK); W of St. Michaels, *Harms 1897* (SASK), *Harms 19130* (KANU, SASK); near St. Michaels, *Klinger 189* (NMC). W of Springerville, *Shreve 8289* (DAO). White Mts. above Eagar, *Moldenke & Moldenke 27748* (LL). Coconino Co.: top of Walnut Cyn., North Rim, *Mishler 1305* (ASU). Navajo Co.: Lakeside, *Rhoton s.n.* (ASU). COLORADO. *Beckwith 228* (DS), *Sheldon 3556* (NY). "Powell's Expedition," *Vasey 274* (NY). *Woolson s.n.* (NY). Cyn. of the Arkansas, *Greene s.n.* (NDG). Luplin, *Johnston 824A* (RM). Wooton, *Rusby s.n.* (NY). Near Forks Hotel, *Osterhout s.n.* (RM(2)). Adams Co.: E of 104th Ave. and McKay Rd., *Semple & K.Shea 2226* (WAT). SW of Hoyt, *Stephens 56038* (KANU). Watkins, *Harriman 1436* (WIS). Arapaho Co.: Denver, *Harms 20230* (KANU), *Redfield 481* (NY), *Semple & K.Shea 2222* (NY, WAT), *Smith s.n.* (NY), *Smith s.n.* (NY, PH), *Wisler s.n.* (WTU). Baca Co.: SW of Pritchett, *Stephens & Brooks 21876* (KANU). Boulder Co.: Boulder, *Henry s.n.* (WIS), *Moldenke & Moldenke 27550* (LL), *Ramaley 9560* (RM), *Ramaley 9868* (WTU), *Vestal s.n.* (CAS, DS)s, *Vestal 464* (DS). Near Boulder, *Ramaley 173* (RM), *Ramaley 174* (RM), *Ramaley 1265* (RM), *Ramaley 1302* (RM), *Robbins 4014* (RM), *Robbins 4031* (NMC, RM), *Tweedy 4899* (NY, RM), *Vestal s.n.* (POM); Bear Cyn, *Robbins 1816* (RM). N of Boulder, *Wiegand & Upton 4363* (NY). S of Boulder, *Welsh & Charette 1291* (DAO, MIN, UNCC). SW of Boulder, *Wagenknecht 2969* (KANU, SASK), *Wagenknecht 2970* (KANU). Boulder Cyn., *Baker 3485* (POM). W of Lyons, *Harms 2103* (KANU, SASK(2)). Flagstaff Mt., *Salamun & Erdman 2045* (CAS). Four Mile Cyn *Hoover 10779* (CAS, OBI). Mesa, *Robbins 1656* (RM). Roosevelt N.F., *Moldenke & Moldenke 27489* (LL). St. Vrain River, SW of Deadman Gulch, *Wilken 14298* (NY). Chaffee Co.: S of Buena Vista, *Harms 2086* (KANU, SASK(2), WAT), S of Buena Vista, *Keil 17538* (OBI). Cascade Cyn. *Harper & Harper* (UC). Nathrop, *Harms 2083* (KANU, SASK). Salida, *Ewan 11571* (LL). Cheyenne Co.: E of Kit Carson, *Stephens 54791* (KANU). W of Wild Horse, *Semple & Brammall 2716* (WAT). Conejos Co.: Aspen Glade Camp Area, *Wagenknecht 2918* (KANU(2), SASK). Costilla Co.: W of Russell, *Harms 2047* (KANU, SASK(2), WAT). Veta Pass, *Rydberg & Vreeland 5401* (NY, RM). Custer Co.: E of Westcliffe, *Stephens & Brooks 26694* (KANU). Denver Co.: Denver, *Bethel s.n.* (CAS), *Bates 6594* (RM), *Bates 7013* (RM), *Bates 7014* (RM, TEX), *Bethel & Payson s.n.* (RM), *Clokey 2821* (CAS, DS, NY, RM, TEX, UC), *Clokey 2953* (CAS, DS, NY, RM(2), UC), *Clokey 3882* (CAN, CAS, LL, MIN, NY, POM, RM, UC, WS, WTU), *Clokey 3883* (CAN, CAS, DS, GH, LL, MIN, PH, POM, RM, UC, WS), *Eastwood 26* (CAS, DS, UC). Near Denver, *Holm s.n.* (WIS). North Denver, *Payson s.n.* (RM). Douglas Co.: E of Castle Rock, *Sauleda & Sauleda 6288* (WAT). S of Parker, *Semple & K.Shea 2224* (NY, TEX, WAT), *Semple & A.Shea 2260* (WAT). El Paso Co.: Colorado Springs, *Clarke 209 & 206* (NY), *Smith s.n.* (PH), *Williamson s.n.* (PH). N of Colorado Sprs *Stevens & Brooks 43091* (KANU, UC). NW of Colorado Sprs, "The Mesa", *Bacigalupi 684* (DS, UC). S of Colorado Springs, *Semple et al. 5440* (WAT),



Heterotheca villosa (Pursh) Shinners
var. *nana* (A. Gray) Semple

Figure 48. Morphology of *Heterotheca villosa* var. *nana*. A. Habit of holotype, Fendler [391c] GH. B. Shoot of robust plant. C-D. Upper stem leaves of holotype and average plant. E. Head of robust plant with only some florets drawn. F. Mid series phyllary with chlorophyllous zone dark. G. Mature achene with disc corolla attached.

Semple et al. 5459 (WAT). SW of Colorado Springs, Stephens & Brooks 27007 (KANU). Garden of Gods, Harms 2024 (KANU, SASK). Glen Eyrie, Martindale s.n. (KANU). Manitou, anon. (NY). N of Manitou Springs, Harms 2017-C (KANU). W of Manitou Springs, Harms 2005 (KANU, SASK(2), WAT), Harms 2007 (KANU, SASK). Elbert Co.: SW of Limon Hill 1269 (NY). N of Matheson, Dorr 541 (TEX). Fremont Co.: Canon City, Brandegee 498 (NY, UC). Florence, Eggleston 15425 (NY). S of Florence, Stephens & Brooks 26881 (KANU), Stephens & Brooks 42928 (KANU). Royal Gorge Park, Semple, K.Shea & K.Shea 2244 (NY, WAT). E of Texas Cr, Bacigalupi 1017 (DS, GH). Garfield Co.: E of Coffee Pot Springs, Miller 54 (DAO). Gilpin Co.: SE of Black Hawk, Wagenknecht 2956 (KANU, SASK). Near Central City, Gillett & Taylor 11511 (DAO). CO. Huerfano Co.: N of La Veta, Harms 2037 (KANU, SASK), Harms 2041 (KANU, SASK), Stephens & Brooks 26603 (KANU). SW of La Veta, Wagenknecht 2893 (KANU, SASK). etween Pueblo and Walsenburg, Mathias 523 (POM). NE of Walsenburg, Stephens & Brooks 22237 (KANU). W of Walsenburg, Harms 2033 (SASK(2)), Harms 2043 (KANU, SASK), Harms 2044 (KANU, SASK). Jefferson Co.: Coors, Eggleston 15232 (GH, POM). W of Denver, Semple & K.Shea 1322 (WAT), Golden, Fisher s.n. (CAS), Fisher 6 (WIS). Near Golden, Jones 276 (NY, POM, RSA). Morrison, Smith s.n. (PH). N of Morrison, Reeves R1943 (ASU). Near Mt. Morrison, Constance & Rollins 1923 (UC, WS), Zobel s.n. (MIN(2)). US-285 S of CO-8, Semple & K.Shea 1385 (WAT) US-6 E of Co. line, Semple & K.Shea 2256 (NY, WAT). Kit Carson Co.: Flagler Recreation Area, Brooks 3793 (KANU). La Plata Co.: N of Durango, Wagenknecht 2944 (KANU(3), SASK). South Ute Res., Iron Springs Gulch, Lusher s.n. (ASU). Larimer Co.: Big Thompson Cyn., anon. 4570 (WTU), Baker 4751a (LL), Osterhout 3646 (RM), Osterhout 5566 (RM). Dale Cr.,

Osterhout 5129 (RM), *Osterhout 5521* (RM), *Osterhout 5539* (RM), *Osterhout 5540* (RM), *Osterhout 5522* (BRY, RM), *Osterhout 5542* (BRY, POM, RM). W of Drake, *Harms 2111* (KANU(2), SASK(2)). Fossil Cr. Reservation, *Osterhout 4855* (RM). Ft Collins, *Baker s.n.* (POM), *Sheldon 5* (DS). Loveland, *Johnston 699* (NY). Horsetooth Rd., *Warnock 850* (TEX). E of Livermore, *Osterhout 5712* (RM). Near Long's Peak, *Holm s.n.* (WIS). E of Poudre Park, *Semple et al. 1305* (WAT). Poudre River Cyn., *Brooks 286* (KANU), *Ginter 597* (USFS), *Osterhout s.n.* (UC). N of Three Forks, *Harms 2115-B* (KANU, SASK(2), WAT). Las Animas Co.: W of Bacca Rds PP & QQ, *Kuhn 513* (KANU). NW of Branson, *Weber & Arp 14182* (DAO, NY, SD). W of Gulnare, *Stephens & Brooks 42774* (KANU). Barela Mesa, *Robertson 39* (NY). W of Kim, *Stephens & Brooks 42575* (KANU). N of Stonewall, *Stephens & Brooks 26522* (KANU). Trinidad, *Beckwith 191* (NY), *Beckwith 221* (NY), *Beckwith 230* (DS), *Osterhout 5759* (RM). Lincoln Co.: E of Arriba, *Semple & Heard 7714* (WAT). W of Genoa, *Birkholz 2466* (KANU). S of Hall Station, *Ownbey 1316* (LL, NY, RM, WS, UC, WTU). S of Hugo, *Iltis & Iltis 18671* (WIS). E of Limon, US-40-287 2.5 km S of I-70, *Semple & Brammall 2714* (WAT). S of Punkin Center, *Stephens 54605* (KANU). Logan Co.: SE of Sterling, *Stephens 5229* (KANU). Mesa Co.: W of Gateway, *Harrington 4353* (ASU). Mineral Co.: NW of Creede, *Lewis s.n.* (ASU). Moffat Co.: E of Dinosaur, Skull Creek, *Higgins 8240* (ASU, NY). E of Elk Springs, *Semple et al. 5768* (ASU, COLO, MO, WAT, UTC). E of Sunbeam, *Hermann 5346* (LL). Montezuma Co.: Mesa Verde N.P., *Haas 6* (RM). Park Co.: S of Hartsell, *Stephens & Brooks 26978* (KANU). Morgan Co.: E of Fort Morgan, *Semple & Brammall 2701* (WAT). Phillips Co.: 5 mi S of Holyoke, *Stephens & Brooks 24074* (ASU, KANU). Pueblo Co.: N of Beulah, *Stephens & Brooks 42864* (KANU). E of Colorado City, *Stephens & Brooks 42792* (KANU). S of Nepesta, *McGregor 13325* (KANU). Pueblo, *Woodward s.n.* (GH). S of Pueblo, *Harms 2031* (SASK(2)), *Semple & K.Shea 1419* (WAT). W of Siloan, *Stephens & Brooks 26851* (KANU). NE of Walsenburg, *Stephens & Brooks 22280* (KANU). Rio Grande Co.: Masonic Park, *Pinkava 4897* (ASU). Rio Grande N.F., *Mooers 420* (NY). Routt Co.: between Milner and Hayden, *Atwood & Higgins 5844* (BRY, RM). Sedgewick Co.: Julesburg, *Osterhout 5147* (BRY, RM). S of Julesburg, *Stephens & Brooks 24045* (KANU), *Stephens 55734* (KANU). W of Ovid, *Weber 6414* (WTU). Sedgewick Hill, *Semple & Brammall 2700* (WAT). Teller Co.: NE of Victor, *Dix, Barrau & Rhodes 21* (ASU). Washington Co.: N of Akron, *Wilken 13901* (NY). NW of Akron, *Richardson & Robertson 1328* (KANU, NY). E of Cope, *Weber 12949* (DAO, WIS). E of Elba, *Stephens 56098* (KANU). S of Otis, *Stephens 5052* (KANU). Weld Co.: Antelope Hill, *Osterhout 5870* (RM). E of Buckingham, *Harrington 2236* (ASU). E of Berthoud, *Semple 2257* (WAT). N of Nunn, *Brooks 3692* (KANU, UNCC). NE of Nunn, *Harrington 463* (ASU). New Windsor, *Moyer s.n.* (MIN, NY), *Osterhout 1330* (RM), *Osterhout 2362* (NY), *Osterhout 2484* (NY, RM). Windsor, *Osterhout s.n.* (RM), *Osterhout 2316* (RM), *Osterhout 5573* (RM(2), UC), *Osterhout 6049* (RM). N of jct. hwy-71 and 52, *Welsh, Moore, Matthews 9330*, (BRY, NY). US-85 S of state line, *Dzikanowski & Dunn 2627* (BRY, CAS, NY). NEBRASKA. Banner Co.: NE of Harrisburg, *Churchill & Loveless 12196* (NY). SE of Harrisburg, *Stephens & Brooks 40870* (KANU). S Harrisburg, *Stephens & Brooks 24776* (ASU, KANU, NY). Pumpkin Seed Valley, *Rydberg 146* (NY), *Rydberg 147b* (NY). Box Butte Co.: W of Alliance, *Jones s.n.* (WIS). Chase Co.: NW of Imperial, *Stephens & Brooks 40914* (KANU). Deuel Co.: Big Springs, *Kraus s.n.* (WIS). E of Chappell, *Stephens & Brooks 40913* (KANU). Greeley Co.: Spalding, *Nolte s.n.* (WIS). Keith Co.: NE of Ogallala, *Bare & McGregor 1419* (KANU). W of Roscoe, *Semple & Brammall 2699* (WAT). Kimball Co.: SSW of Bushnell, *Stephens & Brooks 40863* (KANU). W of Dix, *Stephens 50129* (KANU). Perkins Co.: E of Grant, *Stephens & Brooks 13953* (KANU). N of Grant, *Stephens 50202* (KANU). Scotts Bluff Co.: S of Goring, *Stephens & Brooks 24763* (KANU). NEW MEXICO. *Fendler s.n.* (NY(2), PH, UC), *Fendler 360* (PH). *Vasey s.n.* (NY). E of Mesa Prieta, *Hendricks & Bond 1049* (ASU). Pine Springs Cyn., *Talbot s.n.* (LL). Near Water Cyn., *Herrick s.n.* (NMC). Bernalillo Co.: Near Alameda, *Clothier 91* (ASU). E of Albuquerque, *Clothier 77* (ASU). Sandia Mts., *Ellis 350* (NY), *Herrick 1017* (NMC). Las Huertas Cyn., *Ellis 211* (NY). Catron Co.: SW of Horse Springs, vicin. Bat Cave, *Smith 32* (DAO, GH). Cibola Co.: Grand Malpais, *Ward & Spellenberg 81-514* (NMC, NY). NE of Grants, *Harms 1903* (KANU, SASK(2), WAT). W of Grants Station, *Wooton s.n.* (NMC). Colfax Co.: E of Abbot, *Harms 19112* (KANU). N of Black Lake, *Stephens & Brooks 26334* (KANU). E of Eagles Nest, *Lucas 129* (LL, TEX). Philmont Scout Ranch, *Hartman 200* (RM), *Hartman 2478* (RM, TEX). SE of Raton, *Turner & Melchert 4814* (TEX). S of Springer, *Harms 1946* (KANU, SASK). Ute Park, *Standley 13957* (NY), *Standley 14282* (NY). Dona Ana Co.: Rio Grande valley, below Donana, *Parry 510d* (NY). Harding Co.: E of Mosquero, *Stephens 79758* (KANU). Lincoln Co.: *Iwen & Iwen 263* (WIS). N of Angus, *Harms 1806* (KANU, SASK), *Harms 1808* (KANU, SASK). S of Corona, *Semple & Heard 8091* (WAT, NMC, TEX). Gray, *Earle & Earle 167* (RM, MIN, NMC, NY, POM). Jicarilla Indian Res., *anon. s.n.* (ASU). N of Ruidosa, *Semple & Heard 8145* (WAT). White Mts., *Wooton 263* (DS, GH, MIN, NMC, NY(2), POM, RM, UC). Los Alamos Co.: Jemez Mts. W of Bandelier N.M., *Harms 1917* (KANU, SASK), *Harms 1919* (KANU, SASK). Near White Rock, *Harms 1920* (KANU, SASK). SW of White Rock, *Harms 19124* (KANU, SASK). McKinley Co.: S of Ambrosia L., *Faulkner & Martin 167* (BRY). NM-400 between I-40 and Ft. Wingate, *Helmkamp 4-4* (TEX). Santa Fe Old Tr Hwy, 47 mi E of Gallup, *Goddard 721* (UC). Ojo Caliente, Zuni Reservation, *Wooton 2612* (NMC). E of Thoreau, *Harms 1901* (KANU, SASK, WAT). Mora Co.: NW of Holman, *Semple & Heard 8074* (WAT, NMC). S of La Cueva, *Semple & Heard 8077* (WAT, NMC). W of Mills, *Spellenberg & Soreng 6016* (NMC, NY). Near Mora, *Shuly 44-13* (TEX). N of Wagon Mound, *Harms 1937* (KANU, SASK), *Harms 1941* (KANU, SASK(2), WAT). NW of Wagon Mound, *Stephens & Brooks 26184* (KANU). Watrous, *Arsène et al. s.n.* (NY), *Arsène & Benedict 17486* (LL, POM, UC). NE of Watrous, *Harms 1934* (KANU, SASK). Otero Co.: W of Cloudcraft, *Harms 1838* (KANU, SASK). SW of Ruidoso, *Semple & Heard 8155* (WAT). Toward Weed, *Soreng & Spellenberg 594* (NY). Rio Arriba Co.: W of Chama, *Harms 19122* (KANU, SASK), *Harms 19123* (KANU). W of Conjilon, *Wagenknecht 2934* (KANU). NW fo El Vado, *Harms 19119* (KANU, SASK). Rio Arriba Co.: Carson N.F., Jicarillo Dist., *Parker s.n.* (ASU). Near Espanola, *Correll & Martinez 50862* (NY). N of Lindrith, *Springfield 402* (USFS). Rito de los Frijoles, *Robbins 8124* (RM). WSW of Truchas, *Bennett 8117* (BRY, KANU, TEX). E of Vallecitos, *Wagenknecht 2929* (KANU, SASK). San Juan Co.: near Red Rock, *Eastwood & Howell 6776* (CAS). S of Blanco, *Peabody & Sears 1812* (BRY). NE of Bloomfield, *Shultz & Shultz 1285* (GH, NY, WTU). Cutter Cyn., *Wynhoff KL-11* (ASU). SE of Cuba, *Harms 1916* (KANU, SASK). S of Jemez Springs Cyn., *Harms 1911* (KANU, SASK). NE of

Jemez Springs, *Harms 1915* (KANU, SASK). San Miguel Co.: Gallinas, *Arsène 18794* (DS, LL, POM). Gallinas R. Valley, Terrell Ranch, *Lundell & Lundell 14448* (GH, LL). Las Vegas, *Plank s.n.* (NY), *Rose & Fitch 17567* (NY); Cyn. Bonito, *Arsène 19210* (LL, DS). E of Las Vegas, *Hill 14535* (NY). SE of Las Vegas, *Bacigalupi 608* (DS, UC). N of Las Vegas, *Higgins 9108* (ASU, BRY, NY). S of Las Vegas, *Arsène 18536* (LL, POM), *Harms 1930-A* (KANU, SASK(2), WAT). SSW of Las Vegas, *Harms 1928* (KANU, SASK). Las Vegas Hot Springs, *Grant 5745* (DS). E of Montezuma, *Sanders 1274* (TEX). Montezuma Mt., *Millinger 10* (TEX), *Milliger 18* (TEX), *Millinger 20* (TEX), *Millinger 27* (TEX). Pecos, *Eastwood 15438* (CAS), *Standley 4906* (GH, NMC, NY). N of Pecos, *Sundberg 1612* (ASU, WAT). NW of Rowe, *Harms 1924-A* (KANU, SASK). SE of Rowe, *Harms 1927* (KANU(2), SASK(2), WAT). N of Sapella, *Semple & Heard 8087* (WAT, NMC). S of Tecolote, *Stephens & Brooks 26099* (KANU). Sandoval Co.: Bernalillo, *Harms 19128* (KANU). W of Bernalillo, *Harms 1909* (KANU, SASK, WAT). SE of Cuba, *Sears & Peabody 315* (BRY). Jemez Biology Camp, *Castetter 646* (USFS). N of Jemez Pueblo, *Harms 1910* (KANU(2), SASK, WAT). SE of Cuba, Silver L. Fish Hatchery, *Weber 66* (MIN). Jemez Pueblo, *Castetter 1103* (RM). Jemez Springs, *Hershey s.n.* (CAS, NMC), *Nelson 11688* (RM, UC). S of Jemez Springs, *Harms 1912* (KANU). Los Alamos, *Clear s.n.* (CAS). SW of San Ysidro, *Pase 2465* (RM). San Juan Co.: NW of Aztec, *Munz 13040* (DS, RSA, UC). Sante Fe Co.: Big Tesuque Ski Area, *Lepper s.n.* (WIS). S of Golden, *Hitchcock, Rethke & van Raadshooven 4217* (CAS, DS, GH, UC, WS, WTU). W from Glorieta, *Bennett 8784* (BRY). La Bajada, *Arsène & Benedict 15516* (WIS). La Cienega, *Plowman & Kilham s.n.* (GH). Santa Fe, *Bennett 8307* (BRY), *Boyle s.n.* (NMC), *Castetter 1040* (RM), *Cockerell s.n.* (NMC), *Harms 1922* (KANU, SASK(2)), *Harms 19126* (KANU), *Mulford 1288* (NY), *Parker s.n.* (ASU), *Standley 4503* (NMC), *Thompson 24* (WIS). E of Sante Fe, Cerros Negros area, *Crosby 14689* (DAO). Santa Fe Cyn., *Eastwood s.n.* (CAS), *Eastwood 15592* (CAS), *Smith 4053* (UC). Santa Fe Cr. valley, *Fendler s.n.* (GH). NE of Santa Fe, *Mosquin & Gillett 5414A* (DAO, WS). S of Santa Fe, *Harms 1923-A* (KANU, SASK, WAT). Socorro Co.: Magdalena Mts., Puertocito Gap, *Willson & Edwards 4266* (NMC, NY). WSW of San Antonio, *Willson & Edwards 4248* (NY). Taos Co.: NW of Holman, *Semple & Heard 8068* (WAT, NMC). S of Pilar, *Semple & Heard 8052* (WAT). S of Ranchos de Taos, *Jakle s.n.* (ASU). S of Red River, *Holland 6104* (KANU). Taos R. Cyn, *Nelson 11469* (RM, UC); Webbers Ranch, *Copple 160* (RM). Tres Piedras, *Lane 3074* (KANU), *Stephenson 9* (RM). W of Tres Piedras, *Anderson & Barkley 2483* (NY). N of Vadito, *Semple & Heard 8061* (WAT, NMC). Torrance Co.: SE of Cedarvale, *Stephens & Brooks 25971* (KANU), *Stephens & Brooks 26013* (KANU). E of Clines Corners, *Dziekanowski & Dunn 2384* (BRY, NY). NE of Duran, *Semple & Semple 10518* (NMC, WAT). Manzano N.F., *Carter s.n.* (NMC), *Sherman S-44* (USFS). Union Co.: Capulin Mt., *Waterfall 11483* (UC). between Clayton and Grenville, *Wetter 505* (NY, WIS). E of Gladstone on hwy 26, *Harms 1956* (KANU), *Harms 1957* (KANU, SASK). Moses, *Demaree 13283* (MIN). E of Raton, *Morrow s.n.* (RSA). N of Seneca, *Stephens 79594* (KANU). Valencia Co.: E of Grants, *Harms 19129* (KANU), *Keil K11117* (ASU). Leaguna Indian Village, *Lemmon & Lemmon s.n.* (UC(4)). E of New Laguna, *Harms 1905* (KANU, SASK, WAT). N of Trechado, *Cutler 2112* (CAS, GH). **WYOMING.** Crow Creek, *Nelson 2019* (NY, RM). Albany Co.: *Nelson 735* (RM). Chug Creek, *Nelson 7354* (MIN, NDG, NY, POM, RM). Hartville, *Nelson 503* (NDG). Laramie, *Greene s.n.* (NDG), *Nelson s.n.* (RM), *Pammel et al. 1885* (IND). Laramie Hills, *Jack 1028* (GH), *Nelson 1418* (NY, POM, RM(2), UC), *Nelson 5333* (POM, RM). SE of Rock River, *Stephens 70624* (KANU). Carbon Co.: *Nelson & Nelson 8399* (NY). Carbon Co.: Slater, *Goodding 1738* (NY, RM). Laramie Co.: W of Cheyenne, *Finzel 362* (RM). N of Meriden, *Semple & K.Shea 2260* (WAT), *Semple & K.Shea 2261* (WAT), *Semple & K.Shea 2262* (WAT), *Stephens 70950* (KANU). Platte Cyn., *Nelson 8644* (GH, NY, RM, UC), *Semple & K.Shea 2259* (WAT).. E of Chugwater, *Long & Von Loh s.n.* (RM). SW of Wheatland, *Stephens 70734* (KANU).

aff. var. nana

U.S.A. ARIZONA. Apache Co.: above Eagar, *Moldenke & Moldenke 27748* (LL). W of St. Michaels, *Harms 1897* (SASK). **COLORADO.** Costilla Co.: Veta Pass, *Rydberg & Vreeland 5401* (NY, RM). Las Animas Co.: N of Stonewall, *Stephens & Brooks 26522* (KANU). **KANSAS.** Seward Co.: NE of Hayne, *Harms 809* (KANU, SASK). **NEBRASKA.** Greeley Co.: Spalding, *Nolte s.n.* (WIS). **NEW MEXICO.** Bernalillo Co.: Sandia Mts., Allens Ranch, *Ellis 350* (NY). Los Alamos Co.: SW of White Rock, *Bennett 8297* (NY, TEX, WIS). San Juan Co.: Aztec, *Griffin s.n.* (NMC). San Miguel Co.: Red Aurora Camp, Pecos River, Santa Fe N.F., *Fleetwood 86* (NMC). Sandoval Co.: *Welsh, Peabody & Sears 15653* (BRY, NY). Santa Fe Co.: Sangre de Cristo Mts., *Bennett 8121* (BRY, KANU, TEX). Socorro Co.: Laro Mts. W of San Antonio, *Wooton 3880* (NMC). **OKLAHOMA.** Cimarron Co.: E of Kenton, *Stephens & Brooks 17319* (KANU). **SOUTH DAKOTA.** Jackson Co.: between Kadoka and the Badlands, *Petrak 50144* (NY). **TEXAS.** Culberson Co.: E Van Horn, *Hinckley 4024* (NY). **UTAH.** S of Monticello, *Allan 216* (BRY).

aff. var. nana (approaching var. *foliosa*)

U.S.A. COLORADO. Elbert Co.: N of Matheson, *Dorr 541* (TEX). **NEW MEXICO.** Guadalupe Co.: NW of Santa Rosa, *Higgins 8988* (ASU, BRY, NMC, NY). San Miguel Co.: Las Vegas, *Arsène 17757* (LL), *Vasey s.n.* (NY), *Wooton s.n.* (NMC). Santa Fe Co.: E of Santa Fe, *Heller & Heller 3807* (DS, GH, MIN, NY(2)).

aff. var. nana (approaching var. *minor* or mixed collections)

U.S.A. COLORADO. Boulder Co.: Sunshine Cyn., *Starr 117* (WIS). Clear Creek Co.: Georgetown, *Jones s.n.* (LL, DS, POM). **IDAHO.** Fremont Co.: Willow Creek R.N.A, *Wellner 3586* (NY). **NEW MEXICO.** Sandoval Co.: N of Jemez Springs, *Harms 1913* (KANU, SASK). Rio Arriba Co.: Chama R, Abiquin, *Wolf 2901* (CAS, DS, GH, RSA). Rito de los Frijoles, *Robbins 8192* (CAS, RM, RSA, TEX). Sandoval Co.: Gallinas Cyn., Trout Sprs., *Sagalyn 83* (GH). **WISCONSIN.** Adams Co.: N of WI-82, *Semple 8845* (WAT, WIS).

aff. var. nana (approaching var. *scabra*)

U.S.A. NEW MEXICO. Sandoval Co.: SE of San Ysidro, *Higgins 10473* (BRY, NY). Valencia Co.: E of New Laguna, *Harms 1905* (KANU, SASK, WAT).

aff. var. nana (approaching *H. stenophylla* var. *angustifolia*)

OKLAHOMA. Cimarron Co.: Kenton, Black Mesa, *Demaree 13362* (MIN, NY, PH).

17.9 *Heterotheca villosa* (Pursh) Shinnery var. *sierrablancensis* Semple, var. nov. TYPE: U.S.A. NEW MEXICO. Lincoln Co.: Sierra Blanca, NM-532 8.5 km W of NM-48, rocky outcrop and face of road cut at switchback directly below scenic overlook, 2 Oct 1995, *Semple & Semple 10513-A* (Holotype: WAT!; isotypes: MO!, NMC!, RM!; all specimens from same plant). Paratypes: *Semple & Semple 10513-B* (ASU!, NY!, WAT!), *Semple & Semple 10513-C* (WAT!), *Semple & Semple 10513-D* (GH!, UC!, WAT!).

Heterothecae villosae var. *nanae accedens sed foliis ovatis lanceolatis vel oblongis dense hispido-strigosis pilis brevibus et sparsim ad dense glandulosis, ligulis flosculorum radiorum 9-10.7-14 mm longis.*

Perennial from stout woody taproots, STEMS several to many, ascending-erect, 22-28.3-34-(46) cm tall, moderately to densely hispid-strigose, long spreading hairs numerous; 18-26-33-(46) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (20)-22-26-30 mm long, (3)-4.5-5.8-7.8-(9.7) mm wide, petiolate, cuneate, rarely somewhat mucronate, moderately hispid-strigose and moderately to densely glandular (rarely sparsely) on both surfaces; margins entire, strigose, longer spreading hairs along margins basally. UPPER STEM LEAVES lanceolate to ovate, (13)-15.1-17.8-20.5-(23) mm long, (3)-3.7-4.8-6.0-(6.5) mm wide, sessile, somewhat reduced upward, broadly acute to obtuse, indument similar to lower or denser, (2)-4-21-37-(50) glands/mm², (29)-42-68-93-(118) hairs/mm², margins flat, a few longer hispid hairs along margins basally. CAPITULESCENCE congested cymose-corymbiform to subumbelliform, heads (1)-3-6-12-(17); peduncles moderately to densely hispid-canescens, glandular, (6)-10-20.6-31-(49) mm long; bracts few, linear-lanceolate to oblong, greatly reduced, not foliar, indument like leaves. INVOLUCRES narrowly campanulate when fresh, campanulate-hemispheric upon drying, (5)-5.7-6.7-7.8-(8.7) mm high; phyllaries in 4-5 imbricate series, outer ones 1/5-1/4 the length of the inner, narrowly triangular-lanceolate, moderately short-strigose, eglandular to very sparsely glandular, margins hyaline narrow, fimbriate-ciliate, often anthocyanotic apically; inner ones similar. RAY FLORETS (10)-13-15-17-(20), strap yellow, (8.5)-9-10.7-12-(14) mm long, 1-1.6-1.9-(2.2) mm wide, tube glabrate. DISC FLORETS (19)-24-34-43-(49), yellow, glabrous or a few minute hairs, corolla barely ampliate, (4.4)-4.8-5.4-6.1-(6.7) mm long, lobes 0.5-0.6-0.66-(0.75) mm long, hairs usually absent. ACHENES (1.4)-1.7-2.1-2.6-(2.8) mm long, moderately strigose; pappus off-white, double, outer whorl of linear to linear-lanceolate scales 0.25-1 mm long, inner whorl of 35-45 barbellate bristles (4.3)-4.6-5.3-5.9-(6.1) mm long. Chromosome number: $2n = 18$.

Flowering Period: SEPTEMBER-OCTOBER.

Distribution and habitat: Rocky slopes of Sierra Blanca, Lincoln County, New Mexico and peaks to the south; (Fig. 40C); slopes in forests of *Abies*, *Pinus ponderosa*, and/or *Pseudotsuga*; open disturbed areas, exposed igneous rocky slopes, rocky granitic outcrops, road cuts; 2250-3500 m (7400-11500 ft.) elevation.

Discussion: Variety *sierrablancensis* is distinguished by its ovate-oblong, moderately densely strigose and sparsely to usually moderately densely glandular leaves, its rather umbelliform capitulescence, and its showy ray florets (Fig. 49). It is close to var. *nana*, but it has a usually denser indument and more often ovate than oblong leaves. Some plants from the White Mts. approach *H. fulcrata* var. *fulcrata* (Fig. 71) in leaf shape but lack the distinct large foliar bracts of the latter. Less pubescent plants with oblong leaves are similar vegetatively to *H. villosa* var. *nana* (Fig. 48), but usually have longer showier rays. Collections made in 1985 and 1995 from the type area differed somewhat in leaf size and indument density indicating that growing conditions influence these traits.

The variety is endemic to the White Mts. of southeastern New Mexico at higher elevations than var. *nana* occurs in the area. The type collections and other specimens collected at the same time all came from a single rock formation crossed at several elevations by the access road up the southeast side of Sierra Blanca. The variety was not seen elsewhere along the road. Whether this was due to chance or reflects some obligate soil requirement is not known. Further field work is needed to clarify the distribution of this new variety.

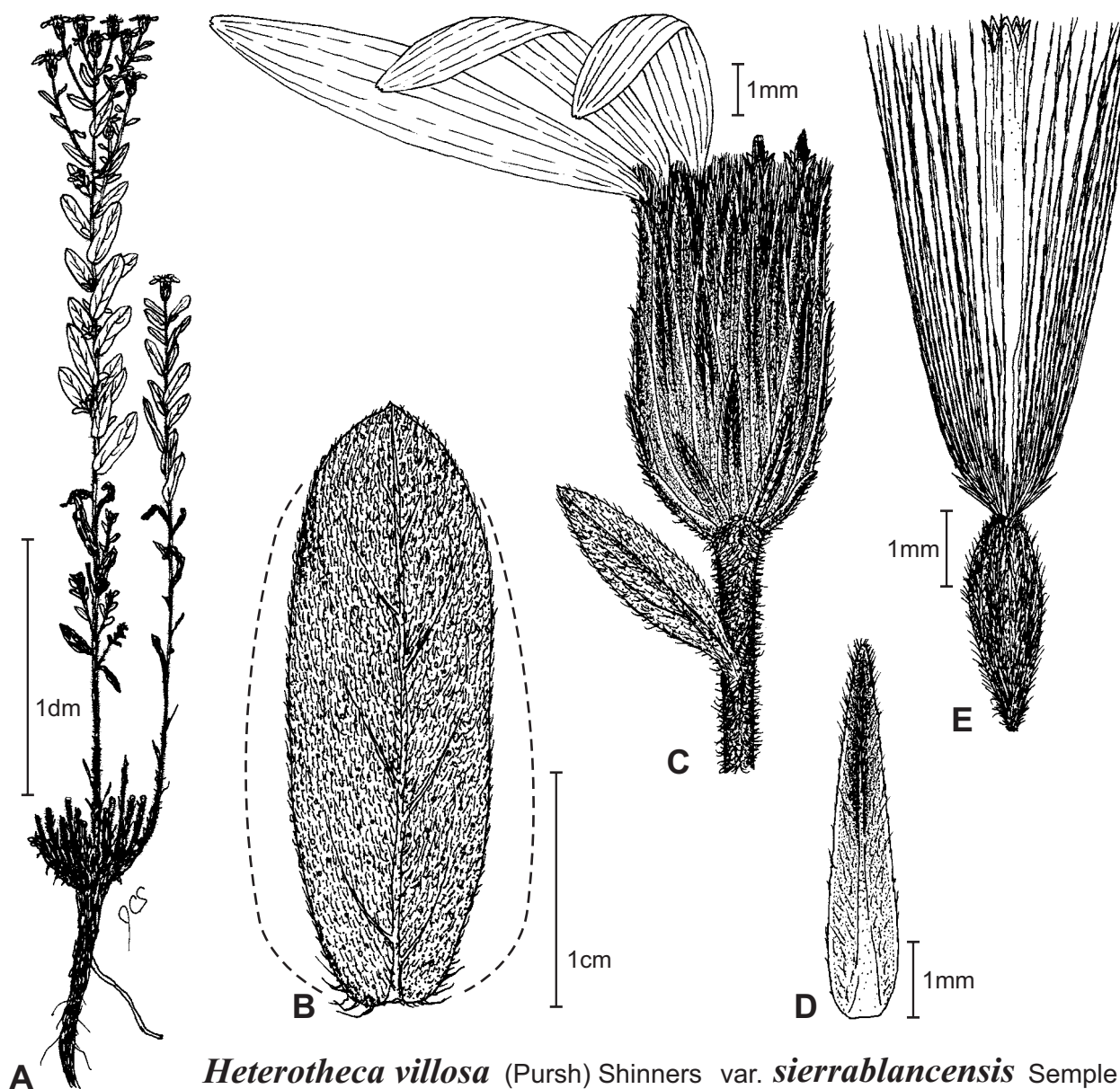


Figure 49. Morphology of *Heterotheca villosa* var. *sierrablancensis*. A. Habit of holotype *Semple & Semple 10513A*. B. Mid-upper stem leaf, may be more ovate (broken line). C. Head with only some florets drawn. D. Mid series phyllary with chlorophyllous zone dark; apical margins can be anthocyanotic. E. Mature achene with disc corolla attached.

Specimens examined: U.S.A. NEW MEXICO. Lincoln Co.: W of Alto, *Semple & Heard 8140* (WAT). Sierra Blanca, *Roszbach & Hodgdon {8844}* (GH); Eagle Cr. Cyn., *Soreng & Ward 1608* (NMC); at N border of Mescalero Ind. Res., *Baad 948* (WIS, WTU); Windy Point Vista, *Semple & Heard 8113* (WAT, NMC), *Semple & Semple 10512* (WAT); below Windy Point Vista, *Semple & Heard 8116* (DAO, MO, MT, NMC, RM, TEX, WAT), Guadalupe Ridge near large cave, *Chapline 698* (NMC). White Mts., *Wooton 366* (NY, MIN), *Wooton & Standley 3419* (DS, MIN, NMC, RM). White Mt. Peak, *Wooton s.n.* (NMC), *Wooton 366* (NY, MIN). White Mt. Trail, *Ewing 58228* (RM). Otero Co.: SW of Ruidoso, *Keil 14159* (OBI). Sacramento Mts., Tularosa Cr., *Wooton s.n.* (NMC). White Sands Missile Range, E of San Antonio, *Spellenberg, Brozka & Hoban 10596* (NMC).

aff. var. *sierrablancensis* (approaching var. *nana*)

U.S.A. NEW MEXICO. Lincoln Co.: Gray, *Earle & Earle 167* (RM, MIN, NMC, NY, POM). Ruidosa, *Semple & Heard 8148* (WAT). N of Ruidosa, *Harms 1801-1* (KANU(2), SASK(2), WAT). White Mts., *Wootton 263* (DS, GH, MIN, NMC, NY(2), POM, RM, UC), *Wootton & Standley 3419* (DS, MIN, NMC, RM); White Mt. Trail, *Ewing 58228* (RM).

- 18. *Heterotheca shevockii* (Semple) Semple, comb. et stat. nov.** *Heterotheca villosa* (Pursh) Shinnery var. *shevockii* Semple, *Phytologia* 73: 453. 1992. TYPE: U.S.A. CALIFORNIA. Kern Co.: Kern R. Canyon, Bodfish, CA-178 at Bodfish-Havilah Rd., off of off-ramp, ca. 850 m el., 16 Nov 1981, *Shevock 9110* (Holotype: CAS!; isotype: WAT!). PARATYPES: U.S.A. CALIFORNIA. Kern Co.: Kern R. Canyon, CA-178 8.2 km SE of CA-155, edge of rd. below rock cut, 26 Sept 1987, *Semple & Chmielewski 8953* (CAS!, JCS-personal herbarium!, NY!, RSA!, UC!, WAT!); CA-178 25.4 km SW of CA-155, Democrat Hot Springs, Democrat Raft Removal Area, 26 Sept 1987, *Semple & Chmielewski 8954* (CAS!, RM!, RSA!, WAT!); just E of Miracle Hot Springs, Sequoia Nat'l For. - NE end of Hobo Campground, 18 Aug 1990, *Semple, Suropto & Ahmed 9363* (WAT!); CA-178, ca. 1.5 mi E of Rich Bar, 1000 ft. el., 16 Nov 1981, *Shevock 9105* (CAS!).

Perennial from stout woody taproots; STEMS several to many, ascending-erect, (28)-36-75-113-(131) cm tall, sparsely strigose, moderately hispid (hairs often broken off in older stems), becoming densely glandular and sparsely hispid-strigose above, long spreading hairs numerous; (15)-16-37-58-(82) nodes below capitulescence. LOWER STEM LEAVES oblanceolate to lanceolate, (25)-28-39-50-(55) mm long, (5)-5.5-8.8-12-(16) mm wide, subpetiolate to sessile, cuneate, acute, mucronate, moderately hispid-strigose on both surfaces; margins entire, strigose, longer spreading hairs near base. UPPER STEM LEAVES linear-lanceolate to lanceolate-triangular, (17)-31-43-55-(65) mm long, (6)-7-9-12-(15) mm wide, sessile, base abruptly tapering to sometimes subclasping, reduced upward, moderately glandular, 0-5-11-(21) glands/mm², sparsely hispid-strigose, (5)-13-46-80-(130) hairs/mm², margins entire, often inrolled, few long spreading hairs near base; rameal leaves much reduced upward, becoming linear to linear oblanceolate. CAPITULESCENCE cymose-paniculiform, heads (3)-5-13-20-(70), branches elongated in robust shoots; peduncles long, densely glandular, sparsely hispid-strigose, bracts few, lower ones leaf-like, greatly reduced upward, becoming linear to oblanceolate, 2-3-4.1-(6) mm long, 0.4-0.7-0.8-(1.1) mm wide, margins with long spreading hairs. INVOLUCRES cylindrical to turbinate when fresh, campanulate upon drying, (9)-9.4-10.7-12-(13) mm tall; phyllaries in 5-6 imbricate series, outer 1/5-1/4 length of inner, narrowly triangular, densely glandular, sparsely strigose especially along the pronounced midvein, margins hyaline, fimbriate-ciliate apically; mid series linear-lanceolate to linear-oblanceolate, moderately hispid apically, margins similar to outer series. RAY FLORETS (9)-11-13-15-(18), strap yellow, (5)-5.5-6.8-8.2-(10) mm long, (0.8)-1.0-1.4-1.8-(2.0) mm wide. DISC FLORETS (31)-41-55-68-(77), yellow, glabrous, corolla barely ampliate, (5)-5.5-6.0-6.6-(7) mm long, lobes (0.3)-0.5-0.6-0.8-(1.1) mm long, glabrous or very sparsely strigose, hairs 0.04-0.27 mm long. ACHENES (2.0)-1.8-2.4-3.1-(4.5) mm long, moderately strigose; pappus off-white, double, outer whorl of a few linear scales 0.25-1 mm long, inner whorl of 35-45 barbellate bristles 5-7 mm long. Chromosome number: $2n = 36$, several reports.

Distribution and habitat: The lower Kern R. Canyon in the Greenhorn Mountains of Kern Co., California (Fig. 50H); sandy, gravelly soils and rock crevices 400-900 m (1310-2950 ft.) elevation.

Discussion: *Heterotheca shevockii* is distinguished from other species by its usually tall stems and lanceolate-triangular leaves with sometimes inrolled margins, its large heads and floral parts, and pappus bristles usually

Figure 50. Morphology and distribution of *Heterotheca shevockii*. A-B. Shoots of very robust and very diminutive plants, difference environmentally induced. C. Mid-upper stem leaf; adaxial surface on left side, abaxial surface on right. D. Upper stem and head (only some florets drawn). E-F outer and inner series phyllaries with chlorophyllous zone dark and brown tip. G. Mature achene with disc corolla attached; upper corolla can be glabrous. H. Distribution in southern California. →

only about 90% the length of the disc corollas at anthesis (Fig. 50). Smaller plants are similar to *H. villosa* var. *scabra* to which *H. shevockii* is probably closely related. In California, var. *scabra* is known only from a few locations in the Little San Bernardino Mountains (1200-1300 m elevation), *H. villosa* var. *minor* occurs in the Sierra Nevadas, the Cascade Mountains and on lava flows in Lassen and Modoc Counties (600-3100 m elevation), while *H. shevockii* is endemic to the Greenhorn Mts. portion of the Kern River Canyon (400-800 m elevation). As with all races of *H. villosa* (Semple 1990), in usual form *H. shevockii* is readily recognized, but depauperate and atypical individuals are not easily separated from sometimes similar taxa, i.e., var. *minor* (Fig. 46) and var. *scabra* (Fig. 47). The type material is spring blooming and somewhat unusual for the taxon; shoots of the holotype are tall, those of the isotype short.

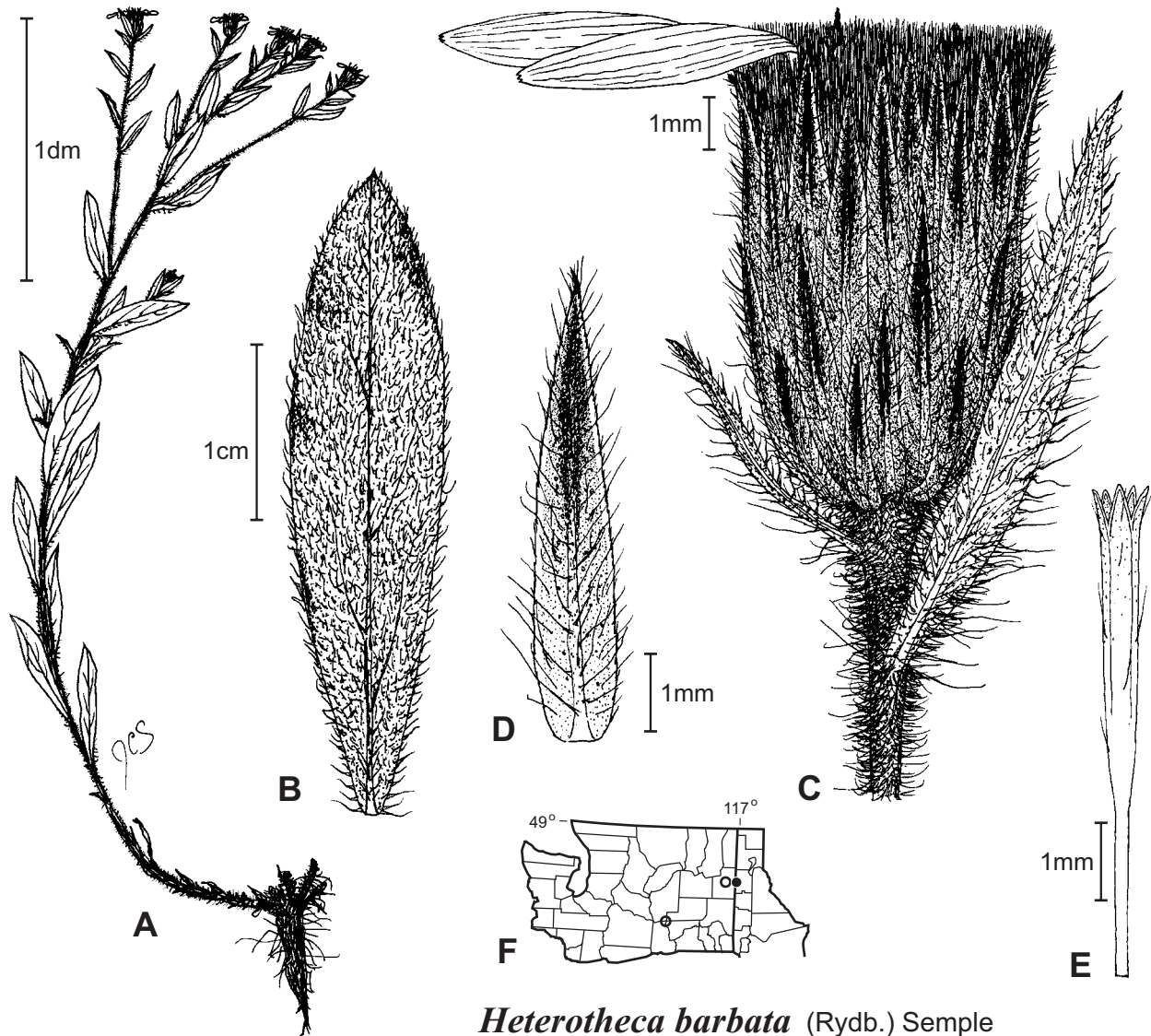
Shevock's Goldenaster was named for James Shevock, an expert on the flora of Kern County, California, who collected the taxon several times in the Kern River Canyon area and who provided valuable personal communication on its habit and habitat.

Heterotheca shevockii was first described as a variety of *H. villosa*, but species status was found to be more appropriate even if this rank makes *H. villosa* paraphyletic. Rieseberg and Brouillet (1994) presented arguments supporting the need for recognizing that when new species arise from marginal populations of wide spread species, there will be a period of time during which both the parental species and the daughter species exist synchronously. Because *H. shevockii* is geographically isolated from *H. villosa*, it could have been retained within the latter species at the subspecies level with the remainder of the species in a second subspecies. The same could have been done for *H. camporum*, another probable derivative of *H. villosa*. Morphologically, *H. shevockii* and *H. camporum* are typically as distinct from *H. villosa* as the latter is from *H. fulcrata*, *H. mucronata* and *H. stenophylla*, for example. These have all been treated within a broadly defined *H. villosa* whose limits end up essentially becoming those of sect. *Phyllotheca*. However, doing this while recognizing a few distinctive endemics like *H. jonesii* undoubtedly does not avoid the problem of *H. villosa sensu lato* being paraphyletic. Short of dividing *H. villosa* as treated here into a number of poorly delimited and frequently hybridizing species, the problem of paraphyletic taxa in sect. *Phyllotheca* may be unavoidable because the section has been actively evolving and producing distinctive new taxa from marginal populations.

Specimens examined: U.S.A. CALIFORNIA. Kern Co.: Kern R Cyn, *Shevock 11028* (CAS), *Alexander 35* (POM), *Benson 4057* (DS, POM, RM), *Benson 5714* (POM), *Howell 38692* (CAS), *Kraws 39* (POM). E of cyn. mouth, *Cohen 25* (POM), *Cohen 30* (POM), *Twisselmann 5948* (CAS). E of Bakersfield, *MacFadden 13527* (CAS), *McGregar 27* (DS), *Patterson & Patterson 162* (ASU, TEX), *Semple, Suario & Ahmed 9361* (WAT). W of Bodfish, *Breedlove 3827* (CAS, DS), *Semple & Chmielewski 8953* (WAT). Delonhega Hot Springs, *Smith 1333* (JEPS, UT, WS). Democrat (Hot Springs) Raft Removal Area, *Semple & Chmielewski 8954* (WAT). E of Democrat Spring, *Semple & Chmielewski 8955* (WAT). E of Miracle Hot Springs, Hobo Campground, *Semple, Suario & Ahmed 9366* (WAT). Richbar, *Twisselmann 16351* (CAS, JEPS, TEX). E of Richbar, *Twisselmann 3256* (CAS(2)). W of Richbar, *Twisselmann 6506* (CAS).

19. *Heterotheca barbata* (Rydb.) Semple, Brittonia 39: 379. 1987. *Chrysopsis barbata* Rydb., Bull. Torrey Bot. Club 37: 129. 1910. TYPE: U.S.A. IDAHO. Kootenai Co.: Valley of Spokane R., 17 Jul 1893, *Sandberg, MacDougal & Heller 664* (Holotype: NY!; isotypes: CAS!, GH!, US!).

[Description based on type specimens only.] Perennial from stout woody taproots, STEMS several ascending, 38-54-43 cm tall, moderately to densely hispid, hairs sometimes slightly reflexed, long spreading hairs numerous; 9-15-20 nodes below capitulescence. LOWER STEM LEAVES oblanceolate, 43-46-50 mm long, 9-10-11 mm wide, petiolate, cuneate, moderately hispid-strigose, sparsely glandular on both surfaces; margins entire, strigose, longer spreading hairs along margins basally. UPPER STEM LEAVES lanceolate-elliptic, 34-36-38 mm long, 8-8.4-9 mm wide, sessile, little reduced upward, acute, indument similar to lower, 0-4-11 glands/mm², 11-18-30 hairs/mm², margins flat to very slightly undulate, a few longer spreading hairs along margins basally. CAPITULESCENCE open cymose-corymbiform, heads 4-8-13; peduncles moderately densely hispid-strigose, sparsely glandular, 31-60-77 mm long; bracts few, linear-lanceolate, reduced, indument like leaves. INVOLUCRES campanulate, 9.4-9.6-9.8 mm high; phyllaries in 4-5 imbricate series,



Heterotheca barbata (Rydb.) Semple

Figure 51. Morphology of *Heterotheca barbata*. A. Habit of holotype, one shoot shown. B. Mid stem leaf. C. Head with only some florets drawn. D. Mid series phyllary with chlorophyllous zone dark. E. Disc corolla at anthesis. F. Distribution; Washington and northern Idaho (○ aff. *H. barbata*).

narrowly triangular-lanceolate, sparsely to moderately hispid-strigose, eglandular to very sparsely glandular, margins hyaline narrow, fimbriate-ciliate and often anthocyanotic apically; inner ones similar. RAY FLORETS 14-17-20, strap yellow, 10-10.5-11 mm long, 1 mm wide, tube glabrate. DISC FLORETS 28-33-41, yellow, a few thin hairs (to 1.5 mm long) along tube, corolla barely ampliate, 6-6.1-6.2 mm long, lobes 0.75-0.8-0.9 mm long, hairs few, 0.1-0.25-(0.4) mm long. ACHENES not seen in a mature state, moderately to densely strigose at anthesis; pappus off-white, double, outer whorl of linear scales 0.25-1 mm long, inner whorl of 35-45 barbellate bristle longer than the corollas at anthesis mm. Chromosome number: $2n =$ unknown.

Flowering Period: JULY-(August).

Distribution and habitat: Spokane River Valley E of Spokane in Idaho, very rare in down river locations (Fig. 51F); sandy plains; ca. 800 m (ca. 2600 ft.) elevation.

Discussion: *Heterotheca barbata* has large lanceolate-elliptic leaves, long branches each with one to a few very large heads and disc corollas with a few very long hairs along the tube (Fig. 51). It is most similar to *H. villosa* var. *minor*, which lacks these traits (Fig. 46). The species is known to me only from the type material. A search at my request of the general area of the type locality and vicinity by Constance Brown (Pullman, Washington) was unsuccessful. The taxon may be extinct. A second collection, *Baird 1087* (BRY, NY) from along the Columbia River in northeastern Washington has traits approaching typical *H. barbata* and is tentatively assigned to this species, as is a third collection, *Suksdorf 9061* (GH, WS) from the Spokane R. in Spokane, Washington. All three collections could be included in *H. villosa* as a separate variety or as aberrant forms within var. *minor*. The distinctiveness of the type material, however, is emphasized here in order to highlight the problem. Cronquist annotated *Suksdorf 9061* as “*C. villosa* var. *hispidula* Hook. Gray” in 1949. In this case, Dr. Cronquist’s lumping may be the most reasonable way to deal with the entire *H. barbata* problem.

Specimens examined: *H. aff. barbata* U.S.A. WASHINGTON. Benton Co.: NE of White Bluffs ferry site, Columbia R., *Baird 1087* (BRY, NY). Spokane Co.: by Spokane R. at Spokane Bridge, *Suksdorf 9061* (GH, WS).

20. *Heterotheca camporum* (Greene) Shinnery, Field & Lab. 29: 71. 1951. *Chrysopsis camporum* Greene, Pittonia 3: 88. 1896. *Chrysopsis villosa* (Pursh) Nutt. var. *camporum* (Greene) Cronquist, Bull. Torr. Bot. Club 74: 150. 1947. *Heterotheca villosa* (Pursh) Shinnery var. *camporum* (Greene) Wunderlin, Ann. Mo. Bot. Garden 59: 471. 1972. TYPE: U.S.A. ILLINOIS. prairies, *Short s.n.* (Holotype: NDG!; isotypes: GH!, NY(2)!, US!).

Perennial from stout woody taproots, spreading by rhizomes; STEMS several to many, ascending-erect, (45)-50-**82**-114-(154) cm tall, appressed strigose, large spreading hairs few to many. LOWER STEM LEAVES oblanceolate, (38)-46-**60**-73 cm long, (6)-8-**11**-15-(18) mm wide, subpetiolate to sessile, cuneate, moderately long-strigose on both surfaces; margins sparsely serrate, strigose, a few longer spreading hairs near base. UPPER STEM LEAVES narrowly to broadly oblanceolate, rarely (ob)ovate, sessile, little reduced upward, very sparsely to moderately glandular, 0-5-11-(21) glands/mm², moderately strigose, (5)-12-**46**-80-(130) hairs/mm², margins sparsely serrate, a few long spreading hairs near base. CAPITULESCENCE open to congested cymose-corymbiform, heads (2)-5-**13**-20-(24), sometimes solitary on long peduncular branches; peduncles short-hispid-strigose, sometimes glandular; bracts few, lower ones like leaves, becoming linear and less pubescent and more glandular near heads, (3)-4-**6.5**-9-(11) mm long, 0.3-**0.8**-1.4-(2.2) mm wide. INVOLUCRES cylindrical to turbinate when fresh, campanulate-hemispheric upon drying, (7)-7.3-**8.3**-9.3-(10.4) mm high; phyllaries in 4-5 imbricate series, outer and mid series narrowly triangular, eglandular to moderately glandular, sparsely strigose, margins hyaline, fimbriate-ciliate apically; inner ones. RAY FLORETS (16)-18-**24**-29-(38), strap yellow, (10.5)-11-**14**-17-(21.5) mm long, 1-**1.5**-2-(2.6) mm wide. DISC FLORETS (23)-32-**45**-58-(66), yellow, glabrous, corolla barely ampliate, (5)-5.1-**5.6**-6.1-(6.6) mm long, lobes (0.5)-0.6-**0.7**-0.8- (1.0) mm long, glabrous to very sparsely glabrate. ACHENES (1.7)-1.8-**2.4**-3.0-(3.9) mm long, moderately strigose; pappus off-white, double, outer whorl of linear scales 0.2-1 mm long, inner whorl of 35-45 barbellate bristles (4.9)-5.4-**6.1**-6.8-(7.2) mm long. Chromosome number: $2n = 36$; more than a dozen reports.

Flowering Period: JULY-OCTOBER-(December).

Distribution and habitat: Ozark Plateau eastward to eastern Tennessee and adjacent states, range expanding in eastern U.S. in disturbed areas in Michigan, North Carolina, Virginia and New Jersey, (Fig. 52H); prairies, limestone glades, roadsides, fields, railroad rights-of-way, open oak woods, disturbed areas; sandy soils, cracks in limestone bluffs and pavements; (30)-120-300-(760) m ((100)-400-1000-(2500) ft.) elevation.

Discussion: *Heterotheca camporum* is distinguished by its serrate stem leaves and sometimes tall stature (Fig. 52). No other species has well developed serrations along the margins of its upper stem leaves, although basal leaves may have one or two serrations near the apex.

The species is divided into two varieties differing in indument features and distribution. The typical variety is usually not glandular and may be densely hairy, while var. *glandulissimum* is glandular and less hairy generally. The ranges of the two taxa did not overlap until quite recently. The rapid expansion of the range of var. *glandulissimum* in this century has resulted in potential sympatry of the two varieties in southern Missouri and Arkansas.

20.1 *Heterotheca camporum* (Greene) Shinnars var. *camporum*

Perennial from stout woody taproots, STEMS several to many, ascending-erect, (33)-41-54-68-(71) cm tall, moderately to densely hispid-strigose, long spreading hairs numerous; 17-33-51-(63) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, (37)-39-55-70-(72) mm long, (6)-7.1-11.8-15.7-(18) mm wide, petiolate, cuneate, densely hispid-strigose, eglandular to rarely very sparsely glandular on both surfaces; margins with 1-3-(5) serrate teeth per side, strigose, longer spreading hairs along margins basally. UPPER STEM LEAVES lanceolate, rarely narrowly ovate, (17)-23-40-56-(66) mm long, 6-8.7-12-(15) mm wide, sessile, little reduced upward, acute, indument similar to lower, usually eglandular, 30-68-106-(130) hairs/mm², margins flat, becoming twisted during senescence, 1-3 serrate teeth per side, a few longer spreading hairs along margins basally. CAPITULESCENCE congested to open cymose-corymbiform, heads (2)-4-6-7; peduncles moderately to densely hispid-strigose, usually eglandular, 23-40-56-(65) mm long; bracts few, linear-lanceolate, reduced, indument like leaves. INVOLUCRES narrowly campanulate when fresh, campanulate-hemispheric upon drying, (7.5)-7.7-8.5-9.2-(9.5) mm high; phyllaries in 4-5 imbricate series, outer and mid series narrowly triangular-lanceolate, eglandular to very sparsely glandular, densely strigose, margins hyaline narrow, fimbriate-ciliate; inner ones similar. RAY FLORETS (16)-17-25-33-(38), strap yellow, (10)-10.6-12.7-14.7-(16) mm long, 1-1.3-1.6-(2) mm wide. DISC FLORETS (23)-26-39-52-(55), yellow, glabrous or a few minute hairs, corolla barely ampliate, (5)-5.1-5.5-5.8-(6.1) mm long, lobes 0.5-0.66-0.74-(0.8) mm long, hairs absent or very rare and short. ACHENES (1.7)-1.8-2.1-2.4-(2.8) mm long, sparsely to moderately strigose; pappus off-white, double, outer whorl of linear scales 0.2-1 mm long, inner whorl of 35-45 barbellate bristle (4.9)-5.2-5.9-6.6-(6.8) mm long. Chromosome number: $2n = 36$; several reports.

Distribution and habitat: Eastern Missouri and northern Arkansas to western Indiana (Fig. 52G); prairies, sandy plains, limestone bluffs and glades, railroad rights-of-way, sandy disturbed areas; 100-300 m (300-1000 ft.) elevation.

Discussion: Variety *camporum* is distinguished by its usually large lanceolate-oblanceolate, hispid-strigose and eglandular (or very rarely very sparsely glandular) stem leaves with several serrate teeth along the margins (Fig. 52). The branch leaves may be serrate but often are entire. The variety can be similar in stature and general appearance to *H. villosa* var. *minor* (Fig. 46) and *H. villosa* var. *villosa* (Fig. 41), whose ranges just reach the northwestern limits of distribution of var. *camporum* in northern Illinois (Figs. 39 and 40, respectively). Usually the more robust stature and serrate leaves make identification easy. When plants are short and the leaf serrations are small and present on only some stem leaves, misidentification is more likely.

The species is endemic to limestone bluffs and glades and sandy prairies in the Prairie Peninsula region of the midwestern United States. It was first collected by John Bradbury in 1810-1811 probably near St. Louis, Missouri (Semple 1990). Collection data suggest the variety was well established on the eastern prairies when European settlers arrived, unlike var. *glandulissimum*.

Two collections from Nebraska listed below are not shown on the map (Fig. 52H): *Pepoon s.n.* (WTU) and *Bates s.n.* (MIN) collected in 1884 and 1912 respectively. Both are atypical and possibly just aberrant forms of *H. villosa*, but they are too much like *H. camporum* to be dismissed without comment. The lack of

more recent collections suggests that the species is not established in Nebraska.

Specimens Examined: U.S.A. *Bas s.n.* (NY). ARKANSAS. Boone Co.: W of Harmon, *Semple & Heard 8305* (WAT). Carrol Co.: NE of Oak Grove, *Semple & Suario 9947* (WAT). IOWA. Clinton Co.: Camanche, *Shimek s.n.* (MIN, WIS), *Shimmers S-44-679* (MIN, ND, RM). Campbells L., *Cooperrider 2187* (DAO, MIN, PH, WIS). ILLINOIS. "Prairies of Illinois," *Torrey s.n.* (UC). *Hall s.n.* (NY). Alexander Co.: Hwy-127 N of Cache, *Bailey & Swayne 493* (UNCC). Hodge Park, *Evers 70332* (UNCC), *Harper 4097g* (NY). N of Unity, *Evers 18700* (WIS). Carroll Co.: *Steyermark 40842* (F). N of Thomson, *Shinners S-44-682* (MIN, ND). W of Thomson, *Wunderlin 299* (UNCC). Cass Co.: Beardstown, *Benke 2035* (F), *Geyer s.n.* (MO), *Geyer s.n.* (GH, PH). E of Beardstown, *Chase 11341* (WAT). SE of Chandlerville, *Mibb 293* (WAT). Fulton Co.: US-136 W of Illinois R., *Semple & Chmielewski 7380* (NY, WAT). Henry Co.: NW of Annawan, *Sears 1055* (UNCC). Jersey Co.: *Christ 280* (WAT). Lawrence Co.: *Winterringer 6186* (F). E of Lawrenceville, *Bailey & Swayne 1750* (SIU, UNCC). Lee Co.: Dixon, *M.B.W. s.n.* (NY). Madison Co.: Alton, *Sherff 905* (F). N of Alton, *Sherff s.n.* (MO). Mason Co.: *Bebb s.n.* (F, NY, PH), *Chase 10024* (KANU, WAT), *Lee s.n.* (MIN). *Pepoon s.n.* (F). Bath, *Gleason s.n.* (GH). Havana, *Burrill (2745)* (GH). E of Havana, *Evers, Jones & Jones 587* (NY), *Gleason 9190* (NY). Kilbourne, *Semple & Chmielewski 5326* (WAT). Menard Co.: *Hall s.n.* (F). Athens, *Hall s.n.* (F), *Hall s.n.* (MO). Monroe Co.: S of Renault, *Evers 63015* (UNCC). Morgan Co.: *Steele s.n.* (MO). Ogle Co.: Rock R., Grand Detour, *Spongberg 63/78* (GH). Peoria Co.: *McDonald s.n.* (UNCC), *McDonald s.n.* (F), *McDonald s.n.* (F), *McDonald s.n.* (F), *Rothrock s.n.* (F), *Stewart s.n.* (F). Limestone Twp., *Chase 15391* (UBC). Peoria Co.: Peoria, *Chase 3487* (F, UNCC, WS, WTU(2)), *McDonald s.n.* (F), *McDonald s.n.* (NMC, UC), *McDonald s.n.* (NY), *McDonald s.n.* (UC). near Peoria, *Donald s.n.* (NY). Pulaski Co.: Mounds, *Evers 51696* (WIS). Rock Island Co.: E of Cordova, *Evers 57290* (UNCC). Scott Co.: Bluffs, *Eggert s.n.* (MO). St. Clair Co.: Belleville, *Herzog s.n.* (NY). Cahokia, *Martidale s.n.* (NY). Fairview Heights, *Semple & Suario 9405* (MO, WAT). French Village, *Eggert s.n.* (MO(7)), *Thompson s.n.* (MO). Tazewell Co.: Pekin, *Chase 10543* (F, KANU, NY), *Chase 13527* (KANU, LL, WIS). Whiteside Co.: *Fuller 13690* (F), *Moffat 547* (UC). E of Fulton, *Thieret 1629* (RSA). INDIANA. Daviess Co.: N of Washington, *Deam 53277* (IND). Gibson Co.: *Schneck s.n.* (IND). Knox Co.: *Kriebel 3922* (MO), *Schneck s.n.* (IND). Oaktown, *McCoy 1598* (NY). N of Oaktown, *Buser 2575* (IND(2)), *Tryon 3232* (MIN). S of Oaktown, *Friesner 6618* (RM, RSA, UC). Vincennes, *Ellis 145* (IND), *Palmer 42185* (MO). NE of Vincennes, *Semple & Heard 8334* (WAT). SE of Vincennes, *Deam 50983* (WIS). SW of Vincennes, *Deam 17078* (IND, MIN). Lagrange Co.: Bloomington, *Huff 87* (IND), *Jones 289b* (IND). Cult. possibly SE of Ontario, *Deam s.n.* (IND). Porter Co.: N of Furnessville Blowout, *Tryon 4272* (F, US). Sullivan Co.: W of Carlisle, *Deam 18254* (IND). S of Sullivan, *Bechtel 15210* (NY). Tippecanoe Co.: SW of West Lafayette, *Grady 7053* (UNCC). Vigo Co.: *Blatchley s.n.* (NY). S of Terra Haute, *Deam 18211* (IND, MIN). MISSOURI. *Eggert s.n.* (ND). Dunklin Co.: Campbell, *Bush s.n.* (MO). Franklin Co.: *Christ s.n.* (WAT). Pacific, *Chandler 4532* (MO), *Kellogg s.n.* (MO), *Kellogg 25988* (MO). Howell Co.: N of West Plains, *Semple & Suario 9925* (MO, WAT). Mississippi Co.: W of Charleston, *Palmer & Steyermark 41513* (MO, NY). New Madrid Co.: Malden, *Bush s.n.* (MO). Scott Co.: *Eggert s.n.* (MO), *Eggert s.n.* (MO), *Kellogg s.n.* (MO), *Steyermark 6628* (F), *Steyermark 66171* (F). Shannon Co.: Round Springs, *Redfearn et al. 1684* (UNCC). St. Louis Co.: *Emig s.n.* (MO). Allenton, *Kellogg s.n.* (MO), *Letterman s.n.* (MO), *Letterman s.n.* (MO), *Letterman s.n.* (MO, NY), *Letterman s.n.* (MO). St. Louis, *Eggert s.n.* (F), *Engelmann {651}* (MO, PH), *Engelmann s.n.* (WIS(2))s, *Sherff 440* (F, MO(2)), *Steyermark 1262* (MO)s, *Steyermark 8997* (MO). Valley Park, *Glatfelter s.n.* (NY), *MacGregor s.n.* progeny (KANU). Webster Grove, *Woodson 566* (MO). Windsor Spring, *anonymous s.n.* (MO). Stoddard Co.: *Bush 66* (NY). Bernie, *Bush 167* (MO, NDG). Wayne Co.: *Steyermark 1190* (MO). Wayne Co.: Williamsville, *Bush 3655* (MO, NY), *Palmer 6157* (MO, POM), *Russell s.n.* (MO). Near Williamsville, *Palmer 19429* (MO, NY). W of Williamsville, *Semple & Suario 9902* (MO, WAT).

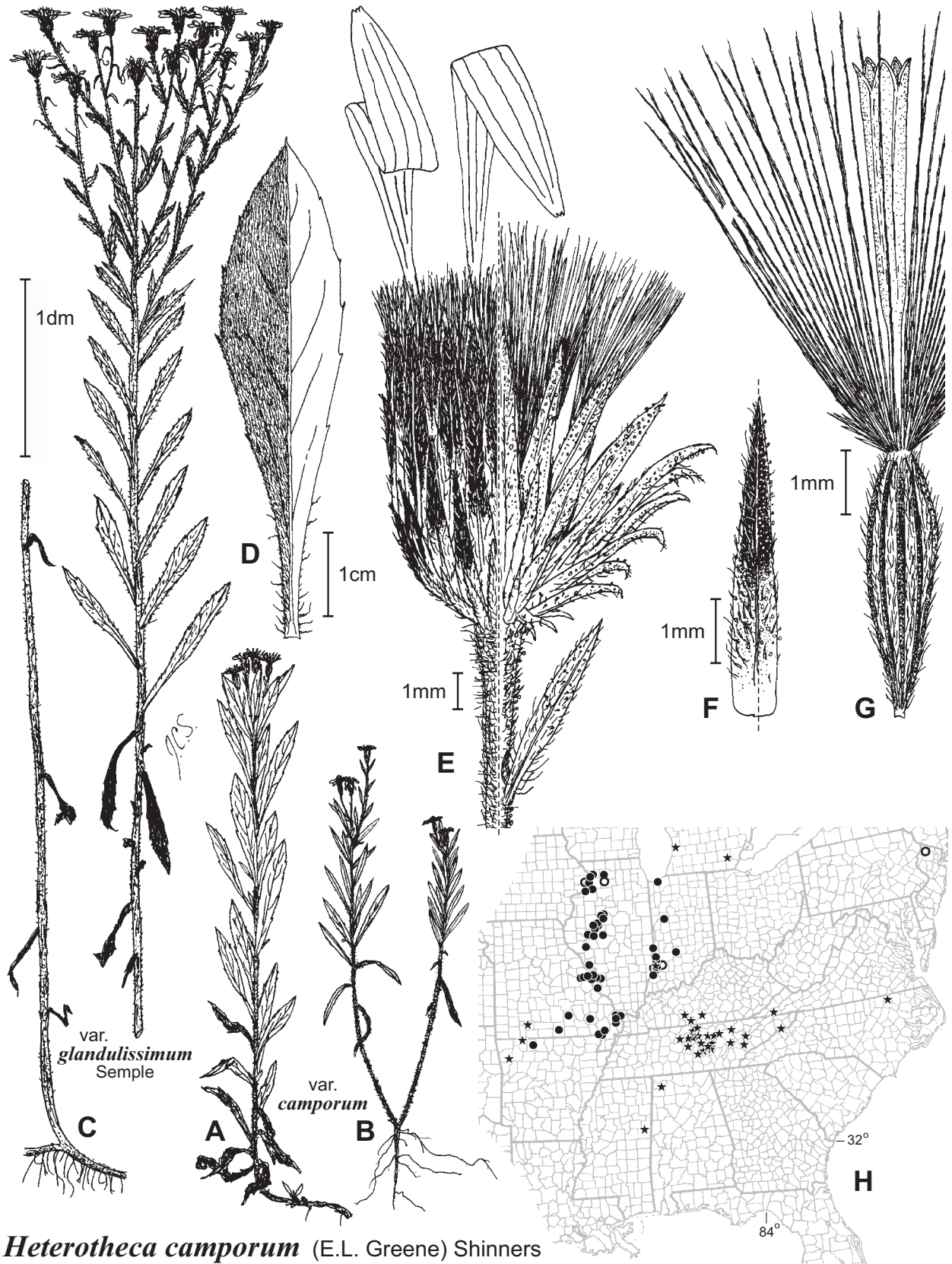
Aff. var. *camporum*

U.S.A. ILLINOIS. Rock Island Co.: Port Byron, *Harper s.n.* (F). NEW JERSEY. Sussex Co.: Ogdensburg, *Snyder 1084-3* (NY). NEBRASKA. Dodge Co.: *Pepoon s.n.* (WTU). Howard Co.: St. Paul, *Bates s.n.* (MIN).

Mixed collections of var. *camporum* and var. *glandulissimum* or intermediates

U.S.A. INDIANA. Daviess Co.: N of Graham elevator, *Friesner 23797* (GH(2), IND, KANU, NSSC, WIS). Knox Co.: N of Oaktown, *Tryon 4267* (F, MIN, MO, PH, WIS). S of Oaktown, *Friesner 10141* (CAS, F, NY, S, UC, WS).

Figure 52. Morphology and distribution of *Heterotheca camporum*. A-B. Var. *camporum*. A. Shoot, lower stem in sand. B. Narrow leaved form (Iowa). C. Var. *glandulissimum*. D. Var. *camporum*; mid stem leaf, adaxial surface, hairs shown on left side only. E. Head with only some florets drawn; fresh var. *camporum*, left side; dried var. *glandulissimum*, right side dried. F. Mid series phyllary with chlorophyllous zone dark; var. *camporum* on left side, var. *glandulissimum* on right. G. Mature achene, disc corolla attached. H. Distribution, eastern U.S.; var. *camporum* (●; ○ - aff. var. *camporum*), var. *glandulissimum* (★). ➡



Heterotheca camporum (E.L. Greene) Shinnors

20.2 *Heterotheca camporum* (Greene) Shinnery var. *glandulissimum* Semple, Brittonia 35: 146. 1983. *Chrysopsis camporum* Greene var. *glandulissimum* (Semple) Cronquist. Man. V.P. N.E. 863. 1991. TYPE: U.S.A. TENNESSEE. Cumberland Co., US-127, just S of county line, *Semple, Brammall & Hart 3010* (Holotype: WAT!; isotypes: MO!, NY!)

Perennial from stout woody taproots, clones forming at the ends of long rhizomes, STEMS several to many, ascending-erect, (40)-65-**98**-132-(154) cm tall, moderately to densely hispid-strigose, long spreading hairs numerous; (21)-33-**54**-74-(86) nodes below capitulescence. LOWER STEM LEAVES oblanceolate, 59-**64**-70 mm long, 10-**11**-14 mm wide, petiolate, cuneate, moderately hispid-strigose, sparsely to moderately glandular on both surfaces; margins with a few serrate teeth, strigose, longer hispid hairs along margins basally. UPPER STEM LEAVES narrowly to broadly lanceolate, (36)-39-**45**-51-(56) mm long, (6)-7-**9.2**-11.5-(14) mm wide, sessile, sometimes little reduced upward, acute, indument similar to lower or more glandular, 1-**8**-15-(21) glands/mm², (5)-18-**30**-42 hairs/mm², margins flat, sparsely serrate to entire, a few longer hispid hairs along margins basally. CAPITULESCENCE open cymose-corymbiform, heads (8)-11-**17**-23-(25); peduncles moderately to densely hispid-strigose, sparsely to moderately glandular, (36)-41-**50**-58-(65) mm long; bracts few, linear-oblong, reduced, sometimes foliar, indument like leaves. INVOLUCRES campanulate when fresh, broadly campanulate-hemispheric upon drying, 7-**8.3**-9.5-(10.5) mm high; phyllaries in 4-5 imbricate series, outer and mid series narrowly triangular-lanceolate, moderately to densely glandular, sparsely hispid-strigose, margins hyaline narrow, fimbriate-ciliate, often anthocyanotic apically; inner ones similar. RAY FLORETS (18)-20-**23**-26-(30), strap yellow, 11-**14.5**-18-(22) mm long, (1)-1.2-**1.7**-2.2-(2.6) mm wide. DISC FLORETS (31)-37-**47**-60-(66), yellow, glabrous or a few minute hairs, corolla barely ampliate, 5.1-**5.7**-6.3-(6.6) mm long, lobes (0.5)-0.6-**0.7**-0.9-(1) mm long, hairs absent or very rare. ACHENES (1.7)-1.9-**2.6**-3.3-(4) mm long, sparsely to moderately strigose; pappus off-white, double, outer whorl of linear scales 0.2-1 mm long, inner whorl of 35-45 barbellate bristle (5)-5.6-**6.2**-6.9-(7) mm long. Chromosome number: $2n = 36$; about a dozen reports.

Distribution and habitat: Ridge and valley region of central and eastern Tennessee and adjacent states, scattered introduced locations further north and west in northern Arkansas and southern Missouri (Fig. 52H); limestone bluffs and glades, roadsides, fields, disturbed areas, stream banks; 30-760 m (100-2500 ft.) elevation.

Discussion: Variety *glandulissimum* is distinguished from typical *H. camporum* by its glandular leaves, peduncles and phyllaries and its often greater than one metre tall stems (Fig. 52). The variety appears to have evolved within historical times in Tennessee, or only recently evolved the traits necessary to make it a successful roadside weed. Semple (1983) discussed the range expansion of var. *glandulissimum* in the last 100 years. Field observations and data on additional collections indicate that the variety is continuing to expand its range in the eastern United States into the Ozarks and northward through Kentucky. Isolated collections undoubtedly representing chance introductions have been documented in southern Michigan and northern New Jersey. Potentially, the taxon could turn up almost anywhere in the eastern states, although it is likely that many introductions will not persist. The construction along the interstate highway system appears to have provided the habitats necessary for expansion. Other recently colonized areas have large disturbed areas associated with tourist site construction (southwestern Missouri and western Arkansas). The *Buckley s.n.* (GH, NY) collection from "Alabama" was cited by Torrey and Gray (1841) under "C. villosa". Its existence demonstrates that var. *glandulissimum* existed in some form decades before it established itself in Tennessee and began its range expansion early in this century. The details of the distribution of the taxon in the last century are unknown.

This is the only taxon in sect. *Phyllothea* that was successfully transplanted to the experimental garden at Waterloo and then establish itself and persist for more than a year or two. Plants of other taxa generally do not transplant successfully, although a few have survived for more than a decade in the experimental

greenhouse. One clone of var. *glandulissimum* derived from a plant native to Tennessee has been growing vigorously in a home garden in Waterloo, Ontario for 20 years. It has retained the trait of a late September-early October blooming peak typical of its original provenance. The plant may produce 50 or more 1 m tall shoots in a single season. The size of the heads and rays makes the taxon a rather spectacular ornamental that might be developed commercially.

Specimens Examined: U.S.A. ALABAMA. *Buckley s.n.* (GH, NYex Ham. Coll.; cited in F.N.A. 1841 under *C. villosa*). Colbert Co.: Littleville, *Semple & Suario 10178* (MO, WAT). Sheffield, *McDowell 555* (DUKE). NE of Sheffield, *Harper 3279* (NY). Jackson Co.: Larkinsville, *Kral 44585* (NY). Sumter Co.: S of Tuscaloosa, *Thomas 106, 266* (WAT). ARKANSAS. Benton Co.: *Williams 63350* (NY). Washington Co.: N of Brentwood, *Semple & Suario 9958* (WAT). ILLINOIS. Cook Co.: Cult, Garwell Garden Perennial Bed, Chicago Botanic Garden, Glencoe, *Jarantoski s.n.* (UBC). KENTUCKY. Allen Co.: S of Petroleum, *Semple & Chmielewski 9109* (CAN, MO, MT, NLU, UC, WAT). Campbell Co.: Alexandria, *Thieret 52664* (NY). Metcalfe Co.: W of Edmonton, *Semple & Suario 9443* (DAO, MO, UC, WAT). Rockcastle Co.: *Semple & Suario 9599* (DAO, MO, UC, WAT). Warren Co.: SE of Bowling Green, *Semple & Chmielewski 9103* (RM, VDB, WAT). MICHIGAN. Ottawa Co.: Holland, *Gillis 14306* (GH). Washtenaw Co.: Ann Arbor, *Reznicek 7088* (WAT). MISSISSIPPI. Lowndes Co.: Columbus, *Sargent s.n.* (LL). Noxubee Co.: 1.5 mi S of Brookville alg US-45. *Wilkens 11864* (UNCC). MISSOURI. Christian Co.: Ozark, *Semple & Suario 9939* (MO, WAT). NORTH CAROLINA. Halifax Co.: W of Whitakers, *Leonard & Radford 3376* (ASU, BRY, KANU, LL, MIN, NY, RSA, UBC, UC, UNCC, USCH, WIS, WTU), *Semple & Brammall & Hart 3059* (NY, WAT). TENNESSEE. Blount Co.: Maryville, *Rogers 33931* (KANU, TENN). Bradley Co.: Cleveland, *Semple et al. 5331* (WAT). Coffee Co.: W of McMinnville, *Ford & Russell 2311* (TENN). Cumberland Co.: Ozone, *Morton 1417* (NY). Davidson Co.: *Semple & Chmielewski 9122* (GA, MIN, TEX, WAT, WIS). Nashville, *Flexner 168* (WAT). E of Nashville, *Svenson 3767* (WIS). De Kalb Co.: Caney Fork Gorge, *Shanks, Sharp & Clebsch 3780* (TENN). Fentress Co.: W of Clarkrange, *Kral 41487* (RSA, WAT, WIS). Franklin Co.: Cowan, *Magee 62* (UNCC). Jackson Co.: N of Gainsboro, *Shanks, Woods & Cooley 14257* (TENN). Knox Co.: near E Tenn St. Hospital, *Sharp 22639* (TENN), *Sharp 24942* (TENN). Macon Co.: Red Boiling Springs, *Beatley 26795* (TENN). Pickett Co.: Cookeville, *Hollister s.n.* (KANU, not seen). Putnam Co.: S of Cookeville, *Fairchild, Clebsch & Sharp 7518* (TENN). W of Cookeville, *Kral 41429* (GH, KANU). Monterey, *Rogers 31451* (TENN, UNCC). E of Monterey, *Morton 4074* (NY(2)). W of Monterey, *Sharp & Iwatsuki 21624* (DS, DUKE, NY, TENN, UNCC). Monterey Lake, *Norris & Shanks 2477* (TENN). Roan Co.: E of Kingston, *Semple & Brammall & Hart 3012* (WAT, LL). Between Rockwood and Harriman, *Morton 3789* (NY). Rutherford Co.: Murfreesboro, *DeSelm 32D* (TENN). NE of Murfreesboro, *DeSelm 714* (TENN). Smith Co.: NW of Carthage, *Sharp & Clebsch 47-461* (TENN). N of Walling, *Mahler 4561* (UNCC). Smith Co.: Riddleton, *Beatley 26798* (TENN). Turners Hill, *Demaree 51758* (UNCC). Trousdale Co.: Hartsville, *Clebsch s.n.* (TENN). N of Lebanon, *Skorepa 6739* (TENN). Unicoi Co.: *James 18032* (TENN). Limestone Cove, *Morton 4371* (NY). E of Unicoi, *Semple & Suario 9638* (CAS, BRY, WAT). Van Buren Co.: W of Spencer, *Wood, Cooley & Sharp 9107* (TENN, UNCC). Warren Co.: N of McMinnville, *Kral 41460* (RSA, WAT, WIS). Nicholson Springs, *Fairchild, Clebsch & Sharp 11516* (TENN). White Co.: *Adams s.n.* (UNCC). S of Falling Water R., *Beatley 25959* (TENN). SE of Sparta, *Deam 61654* (IND). Wilson Co.: N of Lebanon, *Kral 41447* (GH, KANU). VIRGINIA. Montgomery Co.: Mt. Tabor, *Nicely 770* (UNCC). Scott Co.: W of Gate City, *Semple & Suario 9624* (ASU, DAO, GA, MO, WAT).

Cultivated: CANADA. ONTARIO. Waterloo Co.: Waterloo, cult., transplanted from Tennessee, *Semple s.n.* (WAT).

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