REGIONAL KEYS TO SPECIES OF *HETEROTHECA* (ASTERACEAE, ASTEREAE): NORTHWESTERN USA, THE NORTHERN GREAT PLAINS, AND SELECTED STATES OF THE WESTERN USA

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ABSTRACT

Keys to species of *Heterotheca* are presented for 7 individual USA states (Arizona, Colorado, Kansas, Nevada, New Mexico, Utah, and Wyoming, and for 2 multistate regions, the northwestern USA and the northern Great Plains. These are based on recent treatments of *Heterotheca* sects. *Heterotheca* and *Chrysanthe* (Nesom 2019, 2020) and include additional comments by the author.

Recent taxonomic treatments of *Heterotheca* have been published by Semple (1996, 2006) and Nesom (2019, 2020). In Nesom's view, the genus includes 60 species, all in North America (Mexico, USA, Canada): sect. *Ammodia* – 3 species; sect *Chrysanthe* – 49 species; sect. *Heterotheca* – 8 species.

Semple provided inclusive keys but Nesom did not, noting (2019, p. 4) that "Because of infraspecific variation, parallelism and convergence, and the apparent frequency of hybridization, I have not attempted to provide a key that includes all of the taxa," and suggesting that the distribution maps and diagnostic descriptions would be of practical use.

For further help with identification, a series of regional keys is presented here, based on species delimitations by Nesom. These were written from approximately November 2021 through February 2022 and originally posted on my personal website < https://polyploid.net/blog/?p=556 >. To familiarize myself with Nesom's taxonomy, I worked through ± 3800 photographic observations of *Heterotheca* on iNaturalist, $\pm 95\%$ of these in sect. *Chrysanthe* < https://www.inaturalist.org/taxa/57989-Heterotheca >.

My usage of the term "hispido-strigose" may benefit from a definition: having short, coarse trichomes that are \pm perpendicular from the leaf or stem surface at the base but curved antrorsely to become \pm parallel to the surface at the tip. I use "strigose" without further modification to mean the trichomes are appressed, while "loosely strigose" indicates the trichomes are strongly ascending from their bases but not appressed. "Glandular" without modification implies sessile glands.

The keys begin with two multistate areas, the northwestern USA (Idaho, Oregon, and Washington) and the Northern Great Plains (Illinois, Iowa, Minnesota, Nebraska, North Dakota, South Dakota, and Wisconsin), followed by individual states in alphabetical order, Arizona, Colorado, Kansas, Nevada, New Mexico, Utah, and Wyoming. Personal observations on geography, morphological variation, and in some cases, disagreements or caveats regarding the taxonomy, are included within the keys. In the following two sections, I provide some commentary on evaluating taxonomies and my overall assessment of Nesom's taxonomy of *Heterotheca* sect. *Chrysanthe* in relation to Semple's.

Evaluation of taxonomies

The ideal taxonomy maximizes information content, which we might separate into three axes: cohesion, differentiation, and utility. These can be conceptualized in terms of measures that are, in principle, quantifiable and objectively measurable. In practice, we will rarely have access to reliable,

quantitative estimates of the various measures. Even with subjective estimates, I think this provides a conceptual framework to compare taxonomies in a more meaningful and granular way than the usual "lumpers vs. splitters" dichotomy. Some "lumped" taxonomies are better even if one has a bias toward "split" taxonomies, and vice-versa.

For simplicity, I use "taxa" as a shorthand here and in the following section to mean the set of lowest-level taxa recognized within the scope of a particular taxonomy, regardless of their rank. I also use "genus" as shorthand for the scope of a particular taxonomy. In more sophisticated frameworks, intervening ranks would be considered and, of course, scopes vary widely among monographic and floristic works. Another simplifying assumption is that we must assign all individuals to a species.

Cohesion—Suppose we partition the total variation among individuals of a genus into within- and between-species components. A species is more cohesive as the variance within that species decreases. Cohesion increases the predictive value about the total characteristics of an individual or set of individuals that is provided by assigning them to a particular species. Across the set of species in a genus, we could take the average of the variances within each. All else equal, this average cohesion will improve as more taxa are recognized. We could also correct cohesion for the number of species recognized, at least in principle.

Differentiation—The between-species proportion of total variation increases as the taxonomy explains more of the total variation in the genus. We can also conceptualize differentiation on a per-character basis for a pair of species. Differentiation is higher when the boundary between species corresponds with the minimum between two peaks in a bimodal (ideally, non-overlapping) distribution for variation in a particular character. We could then aggregate across characters and across species pairs.

Utility—We could conceptualize utility on a between-taxonomy basis and subdivide it into accuracy and efficiency. Suppose we have two botanists, of equal overall ability. Each botanist learns one of two taxonomies and the two arrive at equal levels of familiarity. We could then give each botanist the same set of specimens and measure their error rates in assigning individuals to species with reference to the taxonomy each has learned. A taxonomy with a lower error rate has higher utility. For efficiency, we start again with two botanists but this time we train them until they achieve equal error rates. We could measure efficiency in terms of how long it takes to learn each taxonomy, and how long it takes to assign each individual, in order to achieve equal error rates.

Comparing taxonomies of *Heterotheca* sect. *Chrysanthe*

I think all taxonomies of the section are likely to be problematic. Regardless of how many taxa are recognized, at what ranks, the taxa have fuzzy boundaries. Consequently, cohesion will be poor and within-species variation annoyingly high (even if we correct for differences in the number of taxa recognized). Differentiation as measured on a pairwise, per-character basis will be poor, for the same reason. So in comparing the two, I assume both will present us with problems.

I think Semple's taxonomy prioritizes utility at a cost in differentiation. His taxonomy has fewer taxa, making it easier to learn. All else equal, fewer taxa reduce the between-species variation explained by the taxonomy. If recognizing a greater number of taxa conveyed only modest gains in explanatory differentiation, without improvement in per-character differentiation or within-species cohesion, or perhaps with a substantial improvement in accuracy, I think this tradeoff could be generally favorable. I don't think these conditions hold.

Compared to Semple's taxonomy, I think Nesom's provides better per-character differentiation, though given the nature of the section this is still problematic. I think Nesom's treatment provides dramatic improvements in cohesion amd explanatory power. I think accuracy is probably equivalent or better, though I have greater facility with Nesom's treatment than Semple's so I am in a poor position to evaluate this. There is a substantial utility cost in learning Nesom's taxonomy, perhaps in applying

it as well, but I think it performs much better than we would expect relative to the baseline tradeoffs we should expect from generic "splitter vs. lumper" comparisons. I hope the present keys reduce the utility costs.

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Key 1. NORTHWESTERN USA (Idaho, Oregon, and Washington)

1. Ray flowers present.

2. Pubescence of the stems mostly ascending to appressed (strigose, hispido-strigose, or occasionally villous), sometimes also with a sparse overstory of long, spreading trichomes.

3. Plants tall (usually > 40 cm, unless the plants stunted under harsh conditions); cauline leaves elliptic to oblong, 2–3 times longer than wide; leaves sericeous; plants of southeastern Idaho.

4. Plants silver below the inflorescences but becoming greener above; adaxial surfaces of most cauline leaves silver, glandular but the glands obscured, the distalmost cauline leaves and bracts densely and conspicuously glandular and only sparsely strigose or hirsutulous; stem pubescence 2-storied below the inflorescences, with an overstory of long, spreading trichomes above a dense, short, silver understory, but becoming uniformly hirsutulous to hirsute above, the trichomes predominately spreading; phyllaries glandular and with sparse, ascending to occasionally spreading, eglandular trichomes as well . **Heterotheca utahensis**

This species is found around the northern Wasatch Range and Uinta Mountains, barely entering Idaho in Franklin County. Nesom associates sericeous leaves with *Heterotheca zionensis* and long, spreading trichomes on the stems with *Heterotheca utahensis*, but so far as I can tell the main stems and most of the cauline leaves are indistinguishable between the two. These features become useful on the distalmost leaves and in the inflorescences.

4. Plants silver throughout; adaxial leaf surfaces silver throughout the plant, eglandular or the glands obscured; stem densely strigose, silvery, often with a sparse overstory of long, spreading hairs below the inflorescence; in the inflorescence the short, silver hairs often ascending rather than appressed and the long, spreading overstory absent or nearly so; phyllaries eglandular, with short, ascending trichomes like those of the peducles

This species is widespread across Utah, Arizona, New Mexico, and western Texas but in Idaho Nesom reports it only in Bear Lake and Franklin counties. I differ a little from Nesom in the characters separating *Heterotheca zionensis* from *Heterotheca utahensis*, as described above. The cauline leaves of both species are typically oblong to elliptic and spreading to deflexed at least at the base.

3. Plants short (< 40 cm); cauline leaves narrowly elliptic to oblanceolate, 3–6 times longer than wide; either leaves not sericeous or plants not in southeastern Idaho.

This species is found in northern Idaho, eastern Washington, notheastern Oregon, and west along the Columbia River to near Portland. The closely strigose, often \pm silvery, oblanceolate leaves are distinctive among the *Heterotheca* of the northwestern USA. The heads are not directly subtended by leafy bracts but there are usually narrow bracts on the peduncles and these can get within a few mm of the heads.

5. Stems glandular or not; leaves usually glandular; both stems and leaves hispido-strigose to loosely strigose; long, spreading trichomes or long marginal cilia absent or very few

2. Pubescence of the stems spreading to deflexed.

6. Stems with dense, dimorphic, 2-storied pubescence: a sparser overstory of long, spreading trichomes and a much shorter, denser, hirsutulous to hispido-strigose understory

Plants of southeastern Idaho, with stem pubescence always dimorphic but the understory varying from

predominately ascending to predominately spreading. Additional discussion above, first lead of couplet 3. 6. Stems hirsute, the trichomes often varying in length but not in two distinctly different classes.

7. Phyllaries glandular and without eglandular pubescence; heads not subtended by leafy bracts.

8.. Stems hirsutulous to minutely hispido-strigose; bases of cauline leaves widely spreading to deflexed; some of the heads subtended by inconspicuous bracts shorter than the phyllaries

Byrawling plants of rock outcrops in southeastern Idaho, also found throughout Nevada and western Utah. The leaves are small but very numerous, gradually reduced in size toward the heads. The leaves are usually prominently glandular and sparsely hispido-strigose, often with a few long cilia or sparsely hirsute on the surfaces.

8. Stems hirsute to hirsute-villous; bases of cauline leaves ascending; capitular bracts absent

This is a narrow endemic to the general vicinity of the Rogue River in Douglas, Jackson, and Josephine counties, southwestern Oregon. In general appearance it most resembles *Heterotheca orovillosa*.

7. Phyllaries eglandular-pubescent, sometimes glandular as well; heads subtended by leafy bracts or not.

9. Heads not subtended by leafy bracts; plants of southwestern Oregon

This species is found primarily in California. In Oregon, Nesom reports it only in Josephine County. The stems and leaves are eglandular or glandular; when glandular, the glands are usually inconspicuous amid the denser eglandular pubescence. Capitular bracts are usually absent, occasionally linear, 1–3, about equalling or a little shorter than the phyllaries. Plants are often ± rhizomatous or decumbent, forming loose mats from which arise many short, erect stems. 9. Heads subtended by leafy bracts; plants of northern Oregon, northern Idaho, and

10. Stems and leaves both eglandular; stems hirsute; leaves and bracts densely hispido-strigose on the surfaces; margins of the capitular bracts usually not ciliate

This is a widespread species, from northern Colorado north to southern Saskatchewan and northwest to southern British Columbia. Plants are usually eglandular throughout, though Nesom mentions a glandular-leaved form in Wyoming. Capitular bracts are linear to oblanceolate and generally about equalling the phyllaries, present but few (1–3) on at least some of the heads but often absent from some heads as well.

This is a widespread species with about the same overall range as *Heterotheca hispida*. Most or all heads have 2–6 linear, linear-oblong, or oblanceolate bracts about equalling or a little longer than the phyllaries. Although stems and leaves are almost always prominently glandular as well as eglandular-pubescent, the glands and trichomes vary quite in density. Occasional plants may be densely glandular and nearly devoid of eglandular pubescence at one extreme, or sparsely hirsute and nearly eglandular at the other extreme.

Key 2. <u>NORTHERN GREAT PLAINS</u> (Illinois, Iowa, Minnesota, Nebraska, North Dakota, South Dakota, and Wisconsin)

This species is uncommon in Illinois, Iowa, and Nebraska. The proximal cauline leaves are usually petiolate, with ovate blades and the bases of the petioles auriculate-clasping. The distal cauline leaves are sessile, auriculate-clasping, and usually ovate.

1. Plants perennial; bases of cauline leaves not auriculate-clasping; pappus present on ray and disk flowers.

2. Leaf surfaces eglandular or inconspicuously glandular and the glands obscured beneath eglandular pubescence.

This species is relatively widespread in the eastern United States. It is found throughout Illinois and probably reaches the northwestern extent of its native range in the northwest corner of the state. It may be found sporadically elsewhere in the northern Great Plains, though. Both Semple (in the Flora of North America treatment) and Nesom indicate that it is spreading along transportation corridors and sometimes becomes established beyond its native range. Serrate leaf margins are often given as the defining feature of *H. camporum*, but this is unreliable in Illinois. Plants to the south and east, *H. camporum* var. *glandulissima*, are densely glandular, ± hispid, sometimes have bracts nearing or subtending the heads, and at least the larger cauline leaves are serrate. The plants in Illinois, *H. camporum* var. *camporum*, are more densely strigose, less glandular, less bracteate, with narrower and more entire leaves. These features become more

Washington.

pronounced as you move north in the state, and in northern Illinois the leaves are nearly linear, evenly strigose or almost sericeous, and only rarely serrate.

3. Heads subtended by leafy bracts or on leafy peduncles, < 1 cm above the uppermost leaves or bracts; leaves entire.

4. Stems strigose, trichomes predominately ascending to appressed, sometimes with a sparser overstory of long, spreading trichomes.

5. Leaf surfaces finely to loosely strigose, the trichomes not stiff and pustulose-based; cauline leaves usually broadly oblanceolate and with rounded apices

Heterotheca villosa Prior to Nesom's revision, this has been treated as a very widespread, polymorphic species found throughout western North America and eastward through much of the Great Plains and Midwest. *Heterotheca villosa* sensu stricto is restricted to the northern Great Plains and is found throughout the Dakotas, Nebraska, and western Minnesota. The heads are usually subtended by one or more broadly lanceolate to oblong bracts longer than the phyllaries. The difference in pubescence between this and *H. angustifolia* is easily recognizable once seen a few times.

Found throughout Nebraska, uncommon in South Dakota and the west edge of Iowa. The heads are usually ebracteate but may have small, oblanceolate, and usually prominently and stiffly ciliate bracts about as long as the phyllaries. This species is more silvery than *Heterotheca villosa*. Nesom describes this and *H. scabrifolia* as having narrowly revolute leaf margins, but I find that I cannot recognize this feature reliably in either species.

4. Stems hirsutulous to hirsute, the trichomes spreading to deflexed

2. Leaf surfaces conspicuously glandular, the glands at most partially obscured.

7. Cauline leaves entire.

8. Stems glandular, along with eglandular pubescence; heads often subtended by 1–3 leafy bracts.

- 9. Eglandular pubescence of the stems stiffly hirsute Heterotheca wisconsinensis This is a narrowly-distributed and distinctive species of the Central Sand Plains of Wisconsin. It has often been included in *H. villosa* but resembles some of the more hispid and glandular forms of *H. camporum* in the Ozark Mountains and on the Cumberland Plateau more than it does *H. villosa*.

Key 3. ARIZONA

1. Plants annual or biennial; lower cauline leaves petiolate and the bases of the petioles auriculateclasping; pappus absent on ray flowers, present on disk flowers.

1. Plants perennial; lower cauline leaves sessile or petiolate but not auriculate-clasping; pappus present on ray and disk flowers.

3. Leaves prominently glandular; eglandular pubescence often present as well, but sparser than the glands and not at all obscuring them; leaves green.

- 4. Stems eglandular; heads not subtended by leafy bracts.

4. Stems glandular, usually with eglandular pubescence as well; heads subtended by leafy bracts or not.

5. Stems and leaves strigillose, eglandular pubescence minute and tightly appressed; plants of east-central Arizona, on and a little north of the Mogollon Rim Heterotheca nitidula Though usually included with the prominently bracted plants of *Heterotheca fulcrata* s.l., the bracts do not seem to be a reliable feature of this species. There may be a single large, leafy bract immediately subtending the head or the cauline leaves may simply diminish in size up the stem, the uppermost relatively small & narrow, a few mm to 1 cm below the head. When present, the subtending bracts are usually sparsely but prominently ciliate. The strigillose pubescence of the leaf surfaces is usually sparse enough to place these plants in my first lead of couplet 1. Sometimes the eqlandular pubescence is a little

denser and the glandular pubescence sparser, so *Heterotheca nitidula* is found under the second lead as well.

5. Stems and leaves sparsely strigose to hirsute or villous; plants throughout the state, rarely around the Mogollon Rim in east-central Arizona.

6. Stems and leaves both prominently hirsute; leaves with long-ciliate margins; plants of central Arizona from the Pinal Mountains north to the Payson area

This species will usually key under the second lead of couplet 12. Plants are usually on rock outcrops and have long, mostly unbranched stems with numerous, small, ascending leaves. The heads are usually subtended by short, linear to linear-lanceolate bracts, but these are often very inconspicuous or absent.

6. Plants not as above: either the leaves or the stems not prominently hirsute, or the leaves not with long-ciliate margins, or plants not in central Arizona.

7. At least some of the heads subtended by leafy bracts equalling or exceeding the phyllaries.

7. Heads not subtended by leafy bracts.

9. Plants stipitate-glandular throughout; plants of southeastern Arizona

A distinctive plant of rocky sites in Cochise and Santa Cruz counties, though it might occasionally be confused with plants of *Heterotheca arizonica* in which the capitular bracts are inconspicuous or absent from some of the heads. The leaves are typically oblong, coarsely ciliate on the margins but with few or no eglandular trichomes on the surfaces. 9. Glands sessile throughout, or occasionally stipitate in part; plants of central to

northern Arizona.

9. Phyllaries densely glandular and without eglandular trichomes

Heterotheca cinerascens Found in northwestern Arizona, mostly north of the Grand Canyon on sand-stone. This species is sometimes difficult to distinguish from *Heterotheca polothrix*. Plants are usually in many-stemmed clumps with small, closely-spaced, oblanceolate leaves that are widely spreading to reflexed basally but bent upwards about midlength. Eglandular pubescence of both stems and leaves is usually puberulent to hirsutulous.

9. Phyllaries with eglandular pubescence and sessile-glandular or not.

This is a poorly known species and apparently rare. In general appearance is resembles *Heterotheca fulciens*, but without capitular bracts.

3. Leaves usually glandular, but inconspicuously so; eglandular pubescence more abundant than the glands and generally obscuring them to some degree; leaves usually grayish to silver.

11. Stems and leaves both prominently hirsute; leaves with long-ciliate margins.

12. Heads ebracteate or with linear to linear-lanceolate bracts usually shorter than the phyllaries; plants of central Arizona from the Pinal Mountains north to the Payson area

Plants are usually on rock outcrops and have long, mostly unbranched stems with numerous, small, ascending leaves.

11. Plants not as above; either the stems or the leaves not prominently hirsute, or the leaves not with long-ciliate margins.

13. Some or all of the heads subtended by leafy bracts equalling or exceeding the phyllaries.

Although I do not like to rely on capitular bracts for this species at couplet 13, neither do I wish for it to appear in triplicate. *Heterotheca nitidula* is easily recognizable once its aquaintance has been made, so I hope the reader comes to know it first by plants that key more easily. 14. Stems and leaves loosely strigose, sericeous, or hirsute.

15. Leaves silver, the surfaces densely long-sericeous Heterotheca rutteri This is a narrowly distributed species found in Santa Cruz County, adjacent parts of Cochise and Pima counties, and adjacent Mexico. Nesom quotes Semple as "It is one of those species that once seen is never confused with another taxon," but also mentions occasional plants that are greenish rather than silvery.

15. Leaves green or grayish, loosely strigose to hirsute.

This is the common member of the *Heterotheca fulcrata* complex in montane woodlands and forests, on most of the Mogollon Rim and northward. Plants are usually minutely glandular on the stems and at least the adaxial leaf surfaces, but the leaves are often sparsely pubescent and green as well, so this species is included under both leads of couplet 3.

13. Heads not subtended by leafy bracts.

This species is found in northeastern Arizona. Plants are usually \pm hemispherical, the central stems erect and the outer stems sprawling, and the leaves grayish-green.

17. Stem pubescence mostly or exclusively strigose; leaves eglandular or the glands wholly obscured.

Found in about the northeastern half of Arizona. Plants are typically large and silvery, sometimes reaching 150-200 cm under good conditions. The stems are strigose and sometimes have a sparse overstory of long, spreading trichomes.

18. Plants short (usually < 30 cm), more or less rhizomatous to decumbent, often forming low mounds or loose mats with most of the stems becoming erect distally; leaves mostly oblanceolate, ascending their entire lengths, sometimes twisted

...... Heterotheca pedunculata

Found in about the northeastern quarter of Arizona. Plants are often silvery, like *Heterotheca zionensis*, but low-growing, with longer peduncles and fewer heads on each stem. Stems are strigose and rarely have any long, spreading trichomes.

Key 4. COLORADO

1. Plants annual or biennial; mid-cauline leaves sessile or petiolate, either the base of the blade or the base of the petiole auriculate-clasping; pappus absent on ray flowers, present on disk flowers

Heterotheca subaxillaris Found at scattered sites in eastern Colorado. The lowest cauline leaves, often senesced by flowering, are petiolate with the base of the petiole auriculate-clasping and the blade ovate, 1–1.5 times longer than wide. The middle cauline leaves are sessile and auriculate-clasping at base, oblong to narrowly ovate, 2-4 times longer than wide, sometimes narrowed toward in the basal quarter or so between the auricles and the main body of the blade.

1. Plants perennial; mid-cauline leaves sessile or petiolate but never auriculate-clasping; pappus present on ray & disk flowers.

2. Plants stipitate-glandular throughout, otherwise very sparsely hirsute; heads not subtended by leafy bracts (though often with a lone, linear bract shorter than the phyllaries)

A distinctive species known from only three collections in Archuleta County. It most resembles *Heterotheca resinolens*, but without capitular bracts and the glands mostly stipitate rather than sessile.

2. Plants not with the combination of features above; if densely glandular and with very sparse eglandular pubescence, then the heads subtended by leafy bracts equalling or exceeding the phyllaries.

3. Stem pubescence mostly appressed to strongly ascending.

4. Plants of the eastern plains.

5. Leaves pale green, prominently glandular, eglandular pubescence hispido-strigose (hairs short, spreading at base, then curved to parallel the surface); phyllaries prominently glandular, eglandular pubescence absent or very sparse

Heterotheca scabrifolia Nesom does not report this species in the state, but it is nearby in New Mexico and Kansas. Several iNaturalist observations from Colorado look like they may be *Heterotheca scabrifolia*. It is included here in case it may be found in southeastern Colorado.

5. Leaves grayish to silver, strigose to sericeous, eglandular or glandular but the glands obscured, sometimes with sparse, long, spreading marginal cilia; phyllaries loosely strigose to canescent, eglandular or glands mostly obscured.

Peripheral in southeastern Colorado. Both this and *Heterotheca angustifolia* usually have linear to linear-oblanceolate bracts subtending or just below but not directly subtending the heads. 6. Plants caespitose; leaf surfaces finely strigose with short, straight trichomes to loosely strigose with long, stiff, pustulose-based trichomes; leaves of the distal stems and peduncles usually oblanceolate to linear-oblanceolate.

7. Leaf surfaces finely to loosely strigose, the trichomes not stiff and pustulosebased; cauline leaves usually broadly oblanceolate and with rounded apices

Heterotheca villosa Found along the west edge of the eastern plains, in the vicinity of Fort Collins and south to Colorado Springs. Prior to Nesom's revision, this has been treated as a very widespread, polymorphic species found throughout western North America and eastward through much of the Great Plains and Midwest. *Heterotheca villosa* sensu stricto is restricted to the northern Great Plains. The heads are usually subtended by one or more broadly lanceolate to oblong bracts longer than the phyllaries. The difference in pubescence between this and *Heterotheca angustifolia* is easily recognizable once seen a few times.

describes this species as having narrowly revolute leaf margins, but I find that I cannot recognize this feature reliably.

- 4. Plants west of the eastern plains, in the mountains and intermontane basins.
 - 8. Some or all of the heads subtended by leafy bracts.
 - 9. Phyllaries and adaxial leaf surfaces eglandular Heterotheca hartmanii A plant of montane woodlands in northwestern Colorado. Both stems and leaves are usually finely and densely strigose, the leaf margins eciliate or occasionally with a few spreading cilia toward the base. Although the two occur in different habitats and do not overlap geographically, this species has a superficial similarity to *Heterotheca schneideri*. However, the phyllaries of *Heterotheca hartmanii* do not have the thickened, usually purplish margins of *Heterotheca schneideri*.
 - 9. Phyllaries and adaxial leaf surfaces glandular.

Found in alpine and subalpine habitats east and north of the San Juan Mountains. The distal cauline leaves and capitular bracts are typically spatulate to oblanceolate, with longattenuate bases and ciliate margins. This can help distinguish *Heterotheca pumila* from other species that may be stunted at high elevations. Separating it from *Heterotheca schneideri* is difficult where the two overlap in the Elk Mountains and West Elk Mountains. 10. Stems, leaves, and bracts finely & closely strigose; margins of leaves and bracts

eciliate; phyllaries in 4–5(–6) strongly graduate series, outermost series usually < 1/3 the length of the innermost; phyllaries finely short-strigose to hirsutulouspuberulent, margins thicker, not scarious, often purplish **Heterotheca schneideri**

Found in alpine and subalpine habitats, primarily in the San Juan Mountains. Nesom also cites two specimens from the vicinity of Crested Butte, "where *Heterotheca pumila* is abundant." From iNaturalist observations, though, my impression is that most plants in the Elk Mountains and West Elk Mountains are either *Heterotheca schneideri* or intermediate between the two species. Phyllaries may provide the most reliable characteristics in this area, though without spending a few days in the field with these plants I doubt I can get a satisfactory understanding of the situation. Outside of this area the two appear to be distinct.

8. Heads not subtended by leafy bracts.

11. Cauline leaves green or grayish, generally strigose but not densely so; at least the adaxial leaf surfaces evidently glandular, the glands readily visible.

12. Stems glandular; leaves sparsely but closely strigose, usually < 3 mm wide Heterotheca polothrix Plants of slickrock in southwestern Colorado, typically green, bushy, with many long stems and small, widely-spaced leaves. This species is very distinctive in its typical form but seems to intergrade more or less frequently with most of the other species of the Colorado Plateau.

11. Cauline leaves silver, densely strigose or sericeous; leaf surfaces glandular or not, but if glandular then the glands mostly or entirely obscured.

Found in southwestern Colorado. Occasional plants may appear intermediate between this species and *Heterotheca zionensis*, but most of the confusion surrounding this species involves *Heterotheca inflata* and affiliates, which have leaves glandular at least adaxially while those of *Heterotheca pedunculata* are eglandular on both surfaces.

13. Plants tall (usually > 30 cm), caespitose, stems mostly erect to ascending; inflorescences corymboid, often dense and compact early in development but in time usually becoming diffuse, with many heads on spreading branches.

14. Plants silver below the inflorescences but becoming greener above; adaxial surfaces of most cauline leaves silver, glandular but the glands obscured, the distalmost cauline leaves and bracts densely and conspicuously glandular and only sparsely strigose or hirsutulous; stem pubescence 2-storied below the inflorescences, with an overstory of long, spreading trichomes above a dense, short, silver understory, but becoming uniformly hirsutulous to hirsute above, the trichomes predominately spreading; phyllaries glandular and with sparse, ascending to occasionally spreading, eglandular trichomes as well

Heterotheca utahensis Peripheral in northwestern Colorado along the Utah border. Nesom associates sericeous leaves with *Heterotheca zionensis* and long, spreading trichomes on the stems with *Heterotheca utahensis*. However, so far as I can tell the main stems and most of the cauline leaves are indistinguishable between the two. These features become useful on the distalmost leaves and in the inflorescences.

14. Plants silver throughout; adaxial leaf surfaces silver throughout the plant, eglandular or the glands obscured; stem densely strigose, silvery, often with a sparse overstory of long, spreading hairs below the inflorescence; in the inflorescence the short, silver hairs often ascending rather than appressed and the long, spreading overstory absent or nearly so; phyllaries eglandular, with short, ascending trichomes like those of the peduncles . **Heterotheca zionensis** Northwestern Colorado along the Utah border, and perhaps sporadically southward on the west edge of the state. I differ a little from Nesom in the characters separating this species from *Heterotheca utahensis*, as described above. The cauline leaves of both

species are typically oblong to elliptic and spreading to deflexed at least at the base.

3. Stem pubescence predominately spreading.

15. Stem pubescence dimorphic, 2-storied: an overstory of long, spreading trichomes and an understory of much shorter spreading, ascending, or sometimes loosely appressed trichomes.

16. Heads subtended by ovate to oblong bracts exceeding the phyllaries

Heterotheca resinolens Plants of montane woodlands and forests in the Sierra Madre and Medicine Bow Mountains. Plants are generally erect, few-stemmed, with large green leaves. The pubescence at mid-stem is usually, perhaps always, of the 2-storied type similar to *Heterotheca hirsutissima*, but the overstory becomes sparser in the basal third of the stem, sometimes disappearing entirely. The more basal cauline leaves, also, are often attenuate to subpetiolar while those at mid-stem and above apparently never are. Though Nesom describes the leaf surfaces as "sessile-glandular with little other vestiture," so far as I can tell they are usually rather densely pilose with short, fine, clear, ± velvety trichomes. 16. Heads ebracteate or, occasionally, with a lone linear bract shorter than the phyllaries.

margins.

18. Phyllaries glandular; most cauline leaves ± silvery, densely strigose on the surfaces, glandular but the glands mostly obscured, the distalmost leaves and bracts becoming greener, less densely public public public sector, and prominently glandular **Heterotheca utahensis**

See above, first lead of couplet 13.

18. Phyllaries eglandular; cauline leaves not silvery, usually somewhat grayish, loosely strigose or hispido-strigose on the surfaces, glandular and the glands not much obscured.

Found throughout the mountains of western Colorado but apparently uncommon. This species resembles *Heterotheca hirsutissima* and apparently grades into it. It is usually a more sprawling plant of rockier sites, while *Heterotheca hirsutissima* is more hemispherical and more often in loamy to gravelly soils. There are usually capitular bracts on at least some of the heads, but this may not be a terribly reliable feature in this species. The leaves are often weakly conduplicate and a little twisted or contorted.

19. None of the heads subtended by leaflike bracts (occasionally one or two linear bracts are present, these not much larger than the outer phyllaries); eglandular pubescence of the leaf surfaces loosely strigose to hispido-strigose; larger cauline leaves usually obovate to elliptic Heterotheca hirsutissima

Found throughout Colorado, from the plains up to ponderosa woodlands, rarely higher. In its typical form the leaves of this species are loosely strigose and a little grayish, glandular but not conspicuously so. Plants with leaf surfaces hispido-strigose are also common, and seem to grade into *Heterotheca paniculata*, *Heterotheca hispida*, and *Heterotheca resinolens* to some extent, although all of thsoe species usually have leafy capitular bracts.

15. Stem pubescence not dimorphic; often varying in length but without a distinct overstory of much longer trichomes.

20. Some or all of the heads subtended by leafy bracts equalling or exceeding the phyllaries.

22. Taller plants (usually > 20 cm) mostly at lower elevations, occasionally subalpine; leaves oblanceolate or narrowly elliptic to oblong, sometimes \pm attenuate basally; pubescence of the leaf surfaces variable but not strigose: hirsutulous or pilose to hirsute, occasionally hispido-strigose; margins of the leaves and capitular bracts either eciliate or with coarse, stiff, widely spreading cilia.

23. Capitular bracts oblanceolate to elliptic, ≥ 2.5 times longer than wide; cauline leaves oblanceolate to elliptic (2.5–)3–6 times longer than wide, bases

either attenuate to subpetiolate or abruptly narrowing; leaf and bract surfaces various pubescent but not finely pilose.

Found in the mountains of western Colorado, mostly in the northwestern quarter of the state. This is generally a distinctive species, with sparsely hirsute but prominently glandular stems and leaves and narrow but prominently ciliate capitular bracts. It is sometimes difficult to distinguish from *Heterotheca resinolens*.

24. Heads usually numerous in \pm paniculate inflorescences, the peduncles mostly short or, when longer, very sparsely leafy; capitular bracts mostly \pm equalling or shorter than the phyllaries; margins of the distal cauline leaves and capitular bracts usually with coarse and stiff but short and relatively inconspicuous cilia, sometimes eciliate Heterotheca paniculata See above, first lead of couplet 19.

20. Heads not subtended by leafy bracts (rarely with a lone, linear bracts shorter than the phyllaries).

- 25. Stems glandular Heterotheca polothrix See above, first lead of couplet 14.
- 25. Stems eglandular.
 - 26. Phyllaries without scarious margins; leaves eglandular ... Heterotheca hispida See above, first lead of couplet 20.

26. Phyllaries with scarious, usually white to purplish margins; at least the adaxial leaf surfaces glandular.

27. Leaves strigose to loosely strigose; phyllaries minutely glandular and finely but loosely strigose; involucres 9-16 mm wide on pressed specimens

Plants of southwestern Colorado. occasionally as far north as the vicinity of Meeker.

typically on sandstone. I find this species particularly difficult. It seems to grade into *Heterotheca incensa, Heterotheca pedunculata,* and *Heterotheca polothrix* so frequently that it is difficult to identify the "core" of the species. However, it is equally difficult to accommodate these plants within those species. At present, I don't think there is a good solution.

27. Leaves hispido-strigose to hirsute; phyllaries eglandular or distally glandular and hispido-strigose; involucres 7-10 mm wide on pressed specimens

Plants of northwestern Colorado. As with *Heterotheca inflata*, above, I find this species confusing. The problem presented by *Heterotheca incensa* is more severe to the west, in Utah, and relatively manageable in Colorado.

Key 5. KANSAS

1. Plants annual or biennial; mid-cauline leaves sessile or petiolate, either the base of the blade or the base of the petiole auriculate-clasping; pappus absent on ray flowers, present on disk flowers

Kansas.

1. Plants perennial; mid-cauline leaves sessile or petiolate but never auriculate-clasping; pappus present on both ray and disk flowers.

 At least the larger cauline leaves sparingly serrate; leaves green Heterotheca camporum Not reported in the state by Nesom but well-documented in parts of adjacent Missouri. One specimen at KANU (Hansen 458) and one observation on iNaturalist appear to be this species. Both are near Kansas City. Nesom suggests this species may be spreading beyond its original range along highways and railroads.
All leaves entire; leaves usually ± silvery, sometimes green.

Not reported in the state by Nesom, but present in adjacent eastern Colorado. I include it here so that it might be identified if it does cross into the western edge of Kansas. The leaves are sessile-glandular and hispido-strigose to loosely strigose on the surfaces, and the larger leaves are usually sparsely long-ciliate on the margins.

3. Leaves linear to oblanceolate, usually \pm silvery, occasionally green; stems glandular or not, with eglandular pubescence 1-storied (long, spreading hairs absent or sparse) or \pm silvery, or both.

Apparently uncommon in Kansas and found primarily along the southern edge of the state. In Oklahoma, primarily around the Wichita Mountains, there is a form of this species that is prominently pustulose and has a dense whorl of linear bracts subtending each head. This form looks very different from the usual form on the plains, but apparently the two grade into each other.

4. Leaves \pm silvery; leaves strigose to sericeous, eglandular or glandular but the glands obscured, sometimes with sparse, long, spreading marginal cilia; phyllaries loosely strigose to canescent, eglandular or with the glands mostly obscured.

5. Plants caespitose; leaf surfaces strigose with long, straight, pustulose-based hairs; leaves of the distal stems and peduncles usually oblanceolate to linear-oblanceolate, usually spreading at base and bent upward about midlength, usually ciliate toward the base or along the entire margin, the cilia stiffly spreading Heterotheca angustifolia

Found throughout the western 2/3 of Kansas. Nesom indicates that the leaf margins of both this and *Heterotheca scabrifolia* are revolute, and he uses this feature in keys. I cannot recognize this feature reliably enough to use it for identification.

5. Plants rhizomatous, forming colonies; leaf surfaces sericeous, the hairs thin, silky and usually somewhat flexuous; stems usually without any long, spreading hairs; leaves of the distal stems and peduncles usually linear, sometimes linear-oblanceolate, usually ascending at base and \pm straight or gently recurved near the apex, usually eciliate or sparsely ciliate basally, the cilia often somewhat ascending Heterotheca canescens

Found primarily in south-central Kansas. This species appears to be consistently distinct from *Heterotheca angustifolia*, but when the rhizomatous habit is not obvious the differences between the two can be subtle and require familiarity with both species.

Key 6. NEVADA

1. Plants annual or biennial; lower cauline leaves petiolate and the bases of the petioles auriculateclasping; pappus absent on ray flowers, present on disk flowers.

Peripheral in southeastern Nevada. This species is widespread and variable, sometimes split into two or more species.

1. Plants perennial; lower cauline leaves sessile or petiolate but not auriculate-clasping; pappus present on ray and disk flowers.

3. Heads subtended by leaflike bracts, these often equalling or exceeding the phyllaries.

4. Distal cauline leaves and bracts strigose to hispido-strigose, minutely and inconspicuously glandular; bracts inconspicuously ciliate, the cilia < 1.5 mm long, weak, often ascending

4. Distal cauline leaves sparsely hispido-strigose to hirsute, prominently glandular; bracts prominently and coarsely ciliate, the cilia stiffly spreading, $mostly > 1.5 mm \log 1000$

Nesom reports a lone collection from Nevada, in the Granite Range of Washoe County.

3. Heads not subtended by leaflike bracts, or occasionally with a lone, linear, inconspicuous bract.

5. Stems glandular and sparsely hirsutulous; leaves many, closely spaced, linear to lanceolate, spreading to deflexed at the base; phyllaries glandular, lacking eglandular pubescence

5. Plants not as above: either the stems eglandular & sericeous or the leaves fewer, ascending, oblanceolate; phyllaries eglandular-pubescent, usually glandular as well.

6. Stems short (< 50 cm), often curved or branched; eglandular pubescence of the stems and leaves hirsute to hirsutulous or hirsute-strigose, stem and leaves usually glandular as well

Peripheral in Nevada, in the vicinity of Reno.

Key 7. NEW MEXICO

1. Plants annual or biennial; mid-cauline leaves sessile or petiolate, either the base of the blade or the base of the petiole auriculate-clasping; pappus absent on ray flowers, present on disk flowers

...... Heterotheca subaxillaris

Found in various more or less mesic habitats in west-central to southwestern New Mexico, in sandy habitats of eastern New Mexico, and at scattered sites in between. The lowest cauline leaves, often senesced by flowering, are petiolate with the base of the petiole auriculate-clasping and the blade ovate, 1–1.5 times longer than wide. The middle cauline leaves are sessile and auriculate-clasping at base, oblong to narrowly ovate, 2-4 times longer than wide, sometimes narrowed toward in the basal quarter or so between the auricles and the main body of the blade. The distal cauline leaves are sessile, ovate, cordate to auriculate-clasping at base. Some treatments separate *Heterotheca psammophila* and *Heterotheca subaxillaris* based on features of the leaves. While plants seem to vary

somewhat in how far up the stem transition points between the three leaf morphologies described above occur, I don't think separating species is tenable.

1. Plants perennial; mid-cauline leaves sessile or petiolate but never auriculate-clasping; pappus present on both ray and disk flowers.

2. Leaves prominently glandular; eglandular pubescence often present as well, but sparser than the glands and not at all obscuring them; leaves green.

3. Stems eglandular, with dimorphic, 2-storied pubescence: an overstory of long, spreading trichomes and an understory of much shorter spreading, ascending, or sometimes loosely appressed trichomes.

This species resembles *Heterotheca hirsutissima* and apparently grades into it. It is usually a more sprawling plant of rocky sites, while *Heterotheca hirsutissima* is more hemispherical and more often in loamy to gravelly soils. The cauline leaves are often weakly conduplicate and \pm contorted. The dimorphic pubescence of the stems in both this species and *Heterotheca hirsutissima* becomes \pm monomorphic on the peduncles.

In its typical form the leaves of this species are loosely strigose and a little gravish, glandular but

not conspicuously so. Nesom mentioned a collection from El Malpais, Cibola County, with "the habit of *Heterotheca hirsutissima* but atypical vestiture—densely glandular with reduced non-glandular vestiture." Plants fitting that description seem to be found occasionally throughout the range of the species and can be difficult to distinguish from *Heterotheca paniculata*.

3. Stems glandular and strigillose to hirsute with \pm monomorphic, eglandular pubescence; much longer, spreading trichomes absent or very sparse.

5. Eglandular pubescence hirsutulous to hirsute, sometimes very sparse.

6. Plants stipitate-glandular throughout; heads not subtended by leafy bracts

A plant of southwestern New Mexico and one of the most easily recognizable Heterotheca in the

state. It does not appear to intergrade with any of the others, though occasional plants of *Heterotheca* arizonica with poorly developed bracts might cause confusion.

6. Plants generally sessile-glandular, or if stipitate-glandular in part then at least the phyllaries sessile-glandular; heads subtended by leafy bracts.

7. Bracts subtending the heads elliptic to ovate, much longer than the phyllaries; bracts usually with only a few long, spreading cilia on the basal margins, or these absent; plants of the Sacramento Mountains / Sierra Blanca area, and Salinas Peak

As the name suggests, the heads are usually ± obscured by the bracts. The typical form of this species is very distinctive, but occasional plants are intermediate between it and *Heterotheca sierrablancensis*. There may also be intermediates with *Heterotheca fulcrata* along southern or lower elevation margins of the range of *Heterotheca cryptocephala*.

5. Eglandular pubescence strigillose, strigose, or hispido-strigose.

8. Plants hispido-strigose, on the eastern plains Heterotheca scabrifolia It is not clear if this species is truly present in the state. Nesom cited two questionable records in Union and Roosevelt counties, indicating he has not seen either. In Oklahoma, primarily around the Wichita Mountains, there is a form of this species that is prominently pustulose-hispid and has a dense whorl of long, linear bracts subtending each head. The typical form on the plains is hispido-strigose and has 0–2 bracts subtending each head.

8. Plants strigillose or strigose, in the western half of the state.

A distinctive slickrock plant, peripheral in northwestern New Mexico, more common to the west. Occasional plants appear intermediate between this species and *Heterotheca hirsutissima*, but confusion in identifying this species is otherwise unlikely. Plants in / near New Mexico seem to have strigose pubescence on both the stems and leaves, but pubescence of the stem varies across the range of this species.

9. Some or all of the heads usually subtended by large, leafy bracts; leaves strigillose, usually some of the leaves or bracts sparsely but conspicuously long-ciliate; plants few-stemmed, not bushy; leaves large, oblanceolate, 4-10 mm wide

Though usually included with the prominently bracted plants of *Heterotheca fulcrata* s.l., the bracts do not seem to be a reliable feature of this species, at least in plants I have seen in New Mexico. There may be a single leafy bract immediately subtending the head & exceeding the phyllaries, or the cauline leaves may simply diminish in size up the stem, the uppermost relatively small & narrow, a few mm to 1 cm below the head. When present, the subtending bracts are usually prominently ciliate. The strigillose pubescence of the leaf surfaces is usually sparse enough to place these plants in the first lead of couplet 2. Sometimes the eglandular pubescence is a little denser and the glandular pubescence sparser, so *Heterotheca nitidula* is found under the second lead as well.

2. Leaves usually glandular, but inconspicuously so; eglandular pubescence more abundant than the glands and generally obscuring them to some degree; leaves usually grayish to silver.

10. Leaves silvery, linear to narrowly oblanceolate; plants of the eastern plains.

distal stems and peduncles usually linear, sometimes linear-oblanceolate, usually ascending

This species appears to be consistently distinct from *Heterotheca angustifolia*, but when the rhizomatous habit is not obvious the differences between the two can be subtle and may require familiarity with both species.

10. Plants not as above; either the leaves not silvery, or broader, or plants not on the eastern plains.

11. Some or all of the heads subtended by leafy bracts equalling or exceeding the phyllaries.

12. Plants more upright; bracts and distal cauline leaves \pm elliptic, bases rounded to cuneate; plants often montane but neither alpine nor subalpine.

11. Heads not subtended by leafy bracts; occasionally with a lone, linear bract not much larger than the outer phyllaries.

14. Plants \pm silvery; both stems and leaves densely strigose; leaf surfaces either eglandular or the glands obscured.

This species is found primarily in the southern third of the state and along the western edge, but is also common around Santa Fe. Both the Santa Fe population and those in southern New Mexico are typically on roadsides and in other disturbed areas. Nesom suggested that at least the Santa Fe population is likely introduced. Plants can become quite large and robust, reaching 150-200 cm under good conditions. The leaves are typically elliptic to oblong and often widely spreading in the basasl half, but bent to become nearly ascending in the distal half. The stems often have a sparse overstory of long, spreading trichomes above the dense, strigose understory.

This species is found in the northern third of the state from montane wood-lands to subalpine or alpine habitats. It becomes more mound-forming at higher elevations.

14. Plants generally grayish, occasionally greenish; stems and leaves loosely strigose to hispido-strigose or hirsute; usually at least the adaxial leaf surfaces evidently glandular, the glands only partially obscured.

This species is found in a variety of habitats across the northern two-thirds of the state and is probably the most widely abundant *Heterotheca* in New Mexico. Nesom discussed several unusual forms that may be encountered, although the 2-storied pubescence should help clarify otherwise ambiguous plants. Plants can, occasionally, have linear, inconspicuous bracts subtending some of of the heads. The cauline leaves are often bent upward, sometimes contorted. 16. Plants few-stemmed, stems erect or ascending; stem pubescence hispido-strigose to hirsute, not dimorphic although occasionally with a few longer, spreading trichomes.

This species is most likely to be confused with *Heterotheca zionensis*. It is apparently rare in New Mexico; Nesom cites a single specimen in southwestern Chaves County; otherwise known from Texas.

17. Leaves finely and usually densely strigose on the surfaces; leaf apices rounded to acute, not or indistinctly apiculate; plants of the montane arc from the Capitan Mountains south to the Guadalupe Mountains Heterotheca sierrablancensis

This species is most similar to *Heterotheca hirsutissima*, but the ranges of the two do not overlap. *Heterotheca sierrablancensis* is endemic to roughly the same area as *Heterotheca cryptocephala* and, although in their typical forms the two can hardly be confused, occasional plants may be intermediate between them.

Key 8. UTAH

1. Plants annual or biennial; lower cauline leaves petiolate and the bases of the petioles auriculateclasping; pappus absent on ray flowers, present on disk flowers.

1. Plants perennial; lower cauline leaves sessile or petiolate but not auriculate-clasping; pappus present on ray and disk flowers.

3. At least some of the heads subtended by leafy bracts equalling or exceeding the phyllaries.

 This is a narrowly-distributed species on sandstone, in the vicinity of Zion National Park and in nearby parts of Iron, Kane, and Garfield counties. In its typical, cushion-forming aspect it can hardly be confused with any other *Heterotheca*. However, occasional taller plants muddy the waters enough that this feature can't be relied on in a key.

4. Plants not as above: capitular bracts usually differentiated from the cauline leaves; rays not drying purplish and never orange in life; phyllaries usually green; plants never cushion-forming.

5. Stems glandular (and with eglandular pubescence).

northwestern Emery County. It is apparently more common in Arizona to the south. 6. Phyllaries glandular, though perhaps minutely so; bases the capitular bracts neither

cosnpicuously paler nor bulged outward; glands of the distal stems and peduncles generally prominent, at most partially obscured.

entirely devoid of eglandular pubescence, making the two species difficult to distinguish. I believe such plants have to be included under *Heterotheca hirsuta*.

5 Stems eglandular.

8. Stems sparsely to densely hirsute or hirsute-villous, the trichomes predominately spreading to deflexed.

8. Stems densely strigose, occasionally with a few longer, spreading trichomes

This is an alpine and subalpine species primarily found in the San Juan Mountains of southwestern Colorado. There are subalpine/alpine plants in the La Sal and Abajo Mountains that look much like this species to me, but Nesom assigns these plants to *Heterotheca pedunculata* and does not report *Heterotheca schneideri* in Utah. When in doubt between the two, finding the plants to be minutely

glandular on either the adaxial leaf surfaces or on the peduncles might resolve the question in favor of *Heterotheca schneideri*. Or it might not!

3. Heads ebracteate, or occasionally a few heads with a long, linear bract not much larger than the outer phyllaries.

10. Cauline leaves silver, densely strigose or sericeous; leaf surfaces glandular or not, but if glandular then the glands mostly or entirely obscured.

12. Plants tall (usually > 30 cm), caespitose, stems mostly erect to ascending; inflorescences corymboid, often dense and compact early in development but in time usually becoming diffuse, with many heads on spreading branches.

Found in about the northern third of the state around the Wasatch and Uinta Mountains. Nesom associates sericeous leaves with *Heterotheca zionensis* and long, spreading trichomes on the stems with *Heterotheca utahensis*, but so far as I can tell the main stems and most of the cauline leaves are indistinguishable between the two. These features become useful on the distalmost leaves and in the inflorescences.

13. Plants silver throughout; adaxial leaf surfaces silver throughout the plant, eglandular or the glands obscured; stem densely strigose, silvery, often with a sparse overstory of long, spreading hairs below the inflorescence; in the inflorescence the short, silver hairs often ascending rather than appressed and the long, spreading overstory absent or nearly so; phyllaries eglandular, with short, ascending trichomes like those of the peduncles

This species is widespread across much of Utah. I differ a little from Nesom in the characters separating *Heterotheca zionensis* from *Heterotheca utahensis*, as described above. The cauline leaves of both species are typically oblong to elliptic and spreading to deflexed at least at the base, and outside the range of *Heterotheca utahensis* this is often a useful feature for separating *Heterotheca zionensis* from others with which it might be confused.

This species is found across about the eastern half of Utah. Occasional plants may appear intermediate between it and *Heterotheca zionensis*, but most of the confusion surrounding this species involves *Heterotheca inflata* and affiliates, all with leaves glandular at least adaxially while those of *Heterotheca pedunculata* are eglandular on both surfaces.

10. Cauline leaves green or grayish, with varying pubescence: sparsely strigose, evenly and loosely strigose, hispido-strigose, or hirsute; at least the adaxial leaf surfaces evidently glandular, the glands unobscured to partially obscured.

13. Stems glandular (and with eglandular pubescence).

14 Stem pubescence dimorphic, 2-storied: an overstory of long, spreading to deflexed trichomes and an understory of short, ascending to spreading trichomes

14. Stem pubescence not dimorphic, sparsely strigose to hispido-strigose or hirsutulous.

15. Phyllaries glandular and without eglandular pubescence; stems hirsutulous

Found at rocky sites throughout the western half of Utah. Plants are usually many-

stemmed and bushy, with small, closely-spaced, oblanceolate leaves that are widely spreading to reflexed basally but bent upwards about midlength.

15. Phyllaries glandular or not, but with eglandular pubescence; stem pubescence not hirsutulous.

Found across the southeastern half of Utah, mostly on sandstone. Although distinctive in its typical form, *Heterotheca polothrix* apparently intergrades with every other *Heterotheca* in its range.

13. Stems eglandular.

Nesom does not report this species in Utah, but it is found in adjacent Arizona, Colorado and New Mexico. I include it in case it may cross the state line.

17. Stems hirsute to hispido-strigose or loosely strigose; trichomes often variable in length or orientation (tending, especially, to become shorter and more strongly ascending distally) but not in two distinct classes.

18. Leaves strigose to loosely strigose; phyllaries minutely glandular and finely but loosely strigose; involucres 9-16 mm wide on pressed specimens

A plant of southeastern Utah, in Grand and San Juan counties, mostly on sandstone. These last two species are probably the most confusing in Utah. I am not very confident that they are good species or can be distinguished reliably from each other, from *Heterotheca polothrix*, or from *Heterotheca pedunculata*. Lumping them with one or more of these other species would not resolve the issue. What else one might do with these plants, though, I do not know.

18. Leaves hispido-strigose to hirsute; phyllaries eglandular or distally glandular and hispido-strigose; involucres 7-10 mm wide on pressed specimens

Relatively widespread in Utah, from the east side of the Uinta Mountains southwest to Kane County. As mentioned immediately above, I find this species and *Heterotheca inflata* confusing.

Key 9. WYOMING

1. Stem pubescence mostly appressed to strongly ascending, sometimes with a sparse overstory of long, spreading trichomes.

2. Some or all of the heads subtended by leafy bracts equalling or exceeding the phyllaries.

3. Leaves glandular.

3. Leaves eglandular.

5. Heads solitary or few and on long peduncles in a loosely corymboid inflorescence; plants of the Sierra Madre in Carbon County Heterotheca hartmanii

This species is peripheral in Wyoming, found primarily in northwestern Colorado. Although superficially similar to *Heterotheca villosa*, it is more likely affiliated with *Heterotheca depressa* and *Heterotheca pedunculata*.

5. Heads in a closely corymboid inflorescence; plants northeast or east of the Sierra Madre.

6. Leaf surfaces finely to loosely strigose, the trichomes not stiff and pustulose-based; cauline leaves usually broadly oblanceolate and with rounded apices

Prior to Nesom's revision, this has been treated as a very widespread, polymorphic species found throughout western North America and eastward through much of the Great Plains and Midwest. *Heterotheca villosa* sensu stricto is restricted to the northern Great Plains, including the eastern third or so of Wyoming.

6. Leaf surfaces strigose with long, stiff, pustulose-based trichomes; cauline leaves usually narrowly oblanceolate, the apices acute Heterotheca angustifolia See below, first lead of couplet 8.

2. Heads not subtended by leafy bracts, or rarely with a lone, linear bract shorter than the phyllaries.

species should key here, but occasional plants have capitular bracts or spreading pubescence on the stems. 7. Plants tall (usually > 40 cm); stems mostly erect; cauline leaves eglandular or glandular but the glands mostly obscured by strigose pubescence; phyllaries without scarious margins or these very narrow and translucent. 8. Leaves strigose with stiff, pustulose-based trichomes; plants of the eastern edge of Wyoming

Heterotheca angustifolia Nesom does not report this species in Wyoming, but it is found in adjacent counties of Nebraska and South Dakota. I include it and the following two species in case they may cross the border. 8. Leaves strigose but the trichomes neither stiff nor pustulose-based; plants of far southwestern Wyoming.

9. Plants silver below the inflorescences, greener above; adaxial surfaces of most cauline leaves silver, glandular but the glands obscured; distalmost cauline leaves and bracts densely & conspicuously glandular, only sparsely strigose or hirsutulous; stem pubescence 2-storied below the inflorescences, with an overstory of long, spreading trichomes above a dense, short, silver understory, becoming uniformly hirsutulous to hirsute with spreading trichomes above; phyllaries glandular and sparsely pubescent

9. Plants silver throughout; adaxial leaf surfaces silver throughout the plant, eglandular or glands obscured; stems densely strigose, silvery, often with a sparse overstory of long, spreading hairs below the inflorescence; in the inflorescence the short, silver hairs are ascending rather than appressed and the long overstory is absent or nearly so; phyllaries eglandular, with short, ascending trichomes like those of the peduncles

1. Stem pubescence predominately spreading.

10. Stem pubescence dimorphic, 2-storied: an overstory of long, spreading trichomes and an understory of much shorter spreading, ascending, or sometimes loosely appressed trichomes.

11. Heads subtended by ovate to oblong bracts exceeding the phyllaries

Heterotheca resinolens Plants of montane woodlands & forests in the Sierra Madre and Medicine Bow Mountains. Plants are generally erect, few-stemmed, with large green leaves. The pubescence at mid-stem is usually, perhaps always, of the 2-storied type similar to *Heterotheca hirsutissima*, but the overstory becomes sparser in the basal third of the stem, sometimes disappearing entirely. The more basal cauline leaves, also, are often attenuate to subpetiolar while those at mid-stem and above apparently never are. Though Nesom describes the leaf surfaces as "sessile-glandular with little other vestiture", so far as I can tell they are usually rather densely pilose with short, fine, clear, ± velvety trichomes.

11. Heads ebracteate or, occasionally, with a lone linear bract shorter than the phyllaries.

Plants of southeastern Wyoming, in the plains and foothill woodlands. This species can be difficult

to distinguish from *Heterotheca hispida*, though that species usually has small capitular bracts and this one does not.

10. Stem pubescence not dimorphic; often varying in length but without a distinct overstory of much longer trichomes.

13. Some or all of the heads subtended by leafy bracts equalling or exceeding the phyllaries.

14. Capitular bracts mostly oblanceolate to narrowly elliptic, ≥ 2.5 times longer than wide; cauline leaves oblanceolate to narrowly elliptic (2.5–)3–6 times longer than wide, bases either attenuate to subpetiolate or abruptly narrowing; leaf and bract surfaces variously pubescent but not finely pilose.

15. Taller (> 20 cm) plants of lower elevations, stems ascending to erect.

present but short and narrow. The leaves are usually hispido-strigose and eglandular, though Nesom mentions a glandular-leaved form in Carbon County & adjacent parts of surrounding counties.

13. Heads not subtended by bracts, or occasionally with one or two linear bracts shorter than the phyllaries.

17. Phyllaries without scarious margins; leaves usually eglandular Heterotheca hispida

See second lead of couplet 10 above. This species usually has evident but short & narrow capitular bracts. The glandular-leaved form apparently does not occur with *Heterotheca depressa* or *Heterotheca incensa*, so geography may be useful in uncertain cases.

17. Phyllaries with scarious, white to purplish margins; leaves glandular at least adaxially.

See above, first lead of couplet 7. Stem pubescence is usually strongly ascending to appressed, rarely spreading; most plants should be found under the first lead at couplet 1.

18. Phyllaries with narrowly acute apices; leaves hirsute to hispido-strigose on the

surfaces; stems erect or ascending, plants more upright Heterotheca incensa Peripheral in southwestern Wyoming, in the Flaming Gorge area. The narrowly triangular to

lanceolate, acute, scarious-margined phyllaries are distinctive.