Key to *Heterotheca* of Colorado, based on Guy Nesom's treatment of *Heterotheca* section *Chrysanthe* (Phytoneuron 2020-68). Written by Patrick J. Alexander, 26-28 Feb 2022. Couplet 8 closely follows Nesom, p. 306.

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) ..... *Heterotheca komarekiae*

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 & 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

6 Plants rhizomatous, forming colonies; leaf surfaces sericeous, the hairs thin, silky and usually somewhat flexuous; leaves of the distal stems and peduncles usually linear, sometimes linear-oblanceolate ..... *Heterotheca canescens*

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 pustulose-based; 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.

7 Leaf surfaces strigose with long, stiff, pustulose-based trichomes; cauline leaves usually narrowly oblanceolate, the apices acute ..... *Heterotheca angustifolia*

Found in southeastern Colorado and northeastward along the edge of the state. Nesom 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

10 Stems, leaves, and bracts strigoso-villous to villous-hirsute or hirsute; margins of leaves and bracts usually with long, spreading cilia, occasionally only weakly ciliate toward the base; phyllaries in 3–4 weakly

graduate series. outermost series rarely <1/2 the length of the innermost; phyllaries hirsute to hirsuto-villous and characteristically with long, fine hairs, margins thin-scarious, rarely purplish ..... *Heterotheca pumila*

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 long-attenuate 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 hirsutulous-puberulent, 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 silver, densely strigose or sericeous; leaf surfaces glandular or not, but if glandular then the glands mostly or entirely obscured

12 Plants short (usually >30 cm); plants usually with decumbent stems, sometimes ± rhizomatous, often forming low mounds or loose mats with the stems ascending to erect distally; inflorescences with few heads, these mostly on long, erect or strongly ascending peduncles ..... *Heterotheca pedunculata*

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.

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

13 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.

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 ..... *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.

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

14 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.

14 Stems eglandular; leaves densely but loosely strigose, usually >3 mm wide ..... *Heterotheca inflata*

See below, first lead of couplet 26.

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 & 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

17 Heads solitary or few, on long peduncles in a loosely corymboid inflorescence; phyllaries with scarious margins ..... *Heterotheca inflata*

See below, first lead of couplet 26. Nesom indicates this species may have 2-storied pubescence on the stems, but this seems to be unusual and I think few plants should key here.

17 Heads numerous in corymboid inflorescences; phyllaries without scarious 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 pubescent, 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

19 At least some of the heads usually subtended by leaflike bracts; eglandular pubescence of the leaf surfaces hirsutulous to hirsute, or (rarely) absent; larger cauline leaves usually oblanceolate ..... *Heterotheca paniculata*

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

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

20 Leaves eglandular ..... *Heterotheca hispida*

20 Leaves glandular

21 Low plants (usually <20 cm) of alpine and subalpine habitats; leaves oblanceolate to spatulate, long-attenuate basally or ± petioloid; leaves usually loosely strigose on the surfaces, sometimes hispido-strigose; margins of the leaves and capitular bracts usually with long but ± weak or flexuous cilia concentrated on the basal half or so ..... *Heterotheca pumila*

See above, first lead of couplet 10.

21 Taller plants (usually >20 cm) mostly at lower elevations, occasionally subalpine; leaves oblanceolate or narrowly elliptic to oblong, sometimes ± 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

22 Capitular bracts mostly ovate to oblong, the larger bracts 1.5–2.5 times longer than wide; cauline leaves oblong, 2-3 times longer than wide, abruptly narrowing at the base rather than attenuate; leaf and bract surfaces finely pilose ..... *Heterotheca resinolens*

See above, first lead of couplet 16.

22 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

23 Heads usually solitary or few in loosely corymboid inflorescences with long, leafy peduncles; at least the larger capitular bracts usually exceeding the phyllaries; margins of the distal cauline leaves and capitular bracts with prominent, long, stiff, coarse cilia ..... *Heterotheca hirsuta*

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*.

23 Heads usually numerous in ± paniculate inflorescences, the peduncles mostly short or, when longer, very sparsely leafy; capitular bracts mostly ± 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.

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

24 Stems glandular ..... *Heterotheca polothrix*

See above, first lead of couplet 14.

24 Stems eglandular

25 Phyllaries without scarious margins; leaves eglandular ..... *Heterotheca hispida*

See above, first lead of couplet 20.

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

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

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.

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

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.