

**TAXONOMIC SUMMARY OF *HETEROTHECA* (ASTERACEAE: ASTEREAE):  
PART 1, SECTS. *HETEROTHECA* AND *AMMODIA***

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**ABSTRACT**

Part 1 of an overview of the North American genus *Heterotheca* is presented. Included are 8 species of sect. *Heterotheca* and 3 species of sect. *Ammodia*. Species of sect. *Phyllothea* (the *H. sessiliflora* group) and sect. ***Heterotheca*** sect. ***Chrysanthe*** Nesom, **sect. nov.**, will be treated in forthcoming publications. ***Heterotheca mayoensis*** Nesom, **sp. nov.**, is recognized along with four new nomenclatural combinations: in sect. *Heterotheca* — ***Heterotheca rosei*** (Wagenk.) Nesom, **comb. et stat. nov.** and ***Heterotheca viridis*** (Nesom) Nesom, **comb. et stat. nov.**; in sect. *Ammodia* — ***Heterotheca rudis*** (Greene) Nesom, **comb. nov.**, and ***Heterotheca scaberrima*** (A. Gray) Nesom, **comb. et stat. nov.** Details of typification, a detailed distribution map, and at least a diagnostic description are provided for each species. A lectotype is designated for *Heterotheca* sect. *Gymnactis* DC. and an epitype is designated for *H. psammophila* Wagenk.

The North American genus *Heterotheca* has been divided in previous taxonomy into three main groups: (1) sect. *Heterotheca*, annuals and perennials that produce epappose ray achenes; (2) sect. *Ammodia*, perennials without ray flowers; and (3) sect. *Phyllothea* sensu lato, which has included the largest number of taxa in the genus, all perennial with pappose ray achenes. In the present study, the concept of sect. *Phyllothea* is limited to the 10 species of the *H. sessiliflora* group and the remaining species are conglomerated as sect. *Chrysanthe*.

***Heterotheca* sect. *CHRYSANTHE*** Nesom, **sect. nov.** **TYPE:** *Heterotheca villosa* (Pursh) Shinnars

Perennials; capitular bracts present or absent; ray florets present; disc corolla lobes glabrous or sparsely hairy with relatively short trichomes; ray and disc achenes both with inner and outer pappus.

Sect. *Chrysanthe* includes all species remaining after sects. *Ammodia*, *Heterotheca*, and *Phyllothea* have been segregated. It perhaps represents a plesiomorphic and non-monophyletic matrix of species from which specialized groups have arisen. Harms (1963, his Ph.D. dissertation) proposed a name at sectional rank for this heterogeneous group, typified by *Heterotheca villosa*, but the name was never effectively published.

Most of the taxa of sect. *Heterotheca* are Mexican endemics; the ranges of *H. grandiflora* and *H. subaxillaris*, and *H. psammophila* are primarily in the USA. Sect. *Ammodia* is limited to the Pacific Coast region (California, Oregon, and Washington). Sect. *Phyllothea* is mostly restricted to coastal and near-coastal regions along the Pacific from Baja California north into central California, with one outlier in northwestern Sonora and one in the California Sierra. Most of sect. *Chrysanthe* occurs in the central and western USA and Canada but one small group has radiated in Mexico and one species is primarily in the eastern USA.

The preliminary cladistic analysis of *Heterotheca* in Brouillet et al. (2009, p. 598; redrawn here as Fig. 1), which shows 12 species, suggests that while sects. *Ammodia*, *Heterotheca*, and *Phyllothea* (as treated here) may be monophyletic, sect. *Chrysanthe* probably is not. Instead, it perhaps is a plesiomorphic matrix from which specialized groups have arisen.

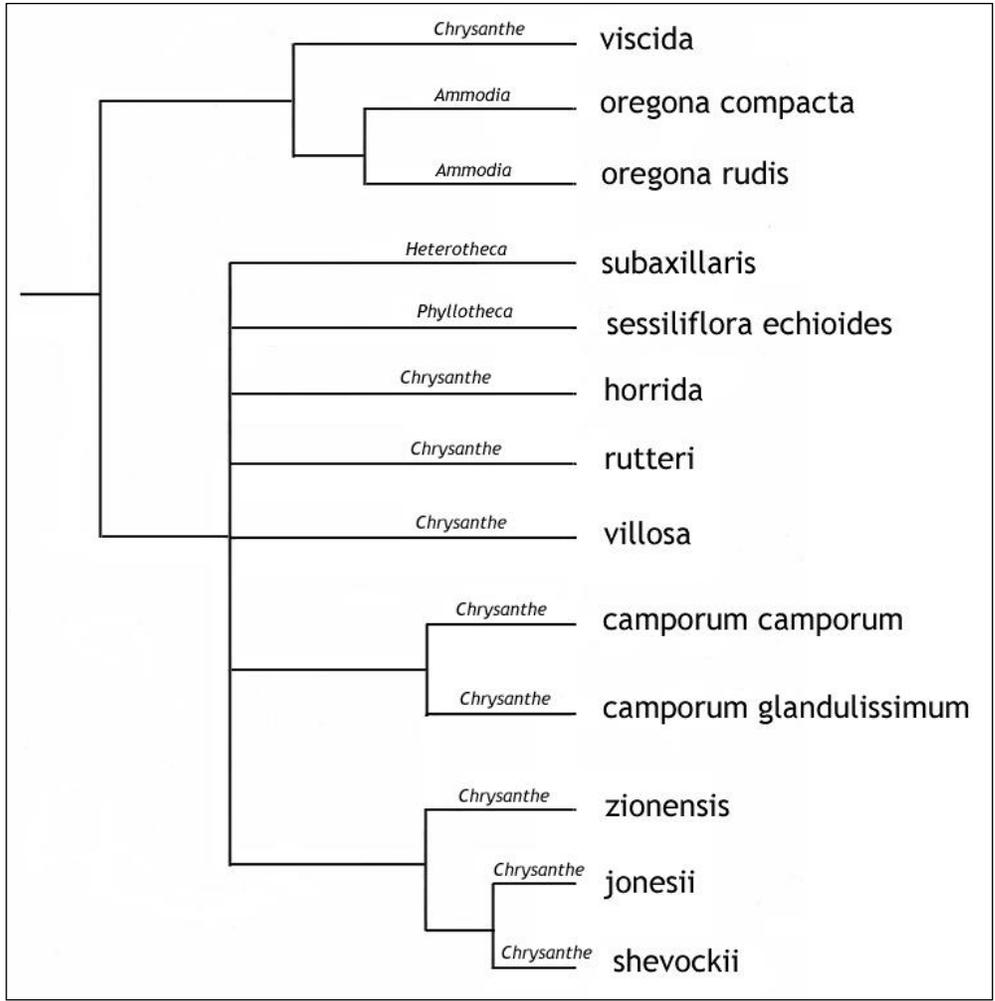


Figure 1. Cladistic relationship of 12 taxa of *Heterotheca* as determined from a parsimony analysis of ITS sequence data in Brouillet et al. (2009); extracted and redrawn from their Figure 37.1E. The taxon shown here as "subaxillaris" was labeled as "fulcrata subaxillaris" in the diagram by Brouillet et al., but the pertinent molecular data were taken from Morgan (1997), who identified that species as *Heterotheca subaxillaris*. Section names reflect the present taxonomy.

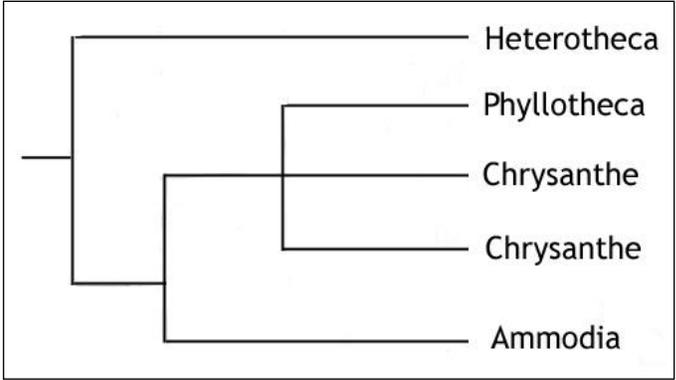


Figure 2. Relationships among sections of *Heterotheca* as intuitively hypothesized by Semple (1996, Fig. 3), using names as in the current study. Semple's "sessiliflora group" is identified here as sect. *Phyllotheca*, the larger part of his sect. *Phyllotheca* here as sect. *Chrysanthe*.

Taxonomic studies of *Heterotheca* have been published over the last 60 years (see Literature Cited and references in the text where pertinent), especially by Semple for sects. *Ammodia* and *Phyllothea*, for sect. *Heterotheca* by Wagenknecht, Harms, and Nesom, and for sect. *Phyllothea* by Shinnars, Harms, Nesom, and others. Chromosome counts have been published mostly by Harms and by Semple and colleagues (see Literature Cited). Semple included chromosome numbers as part of the description for most of the taxa in his 1996 revision; many of those counts have been documented in publication (Semple 2008). A large set of his chromosome vouchers is deposited at MO (as well as other herbaria) and has been examined during the present study.

Diploids and tetraploids occur within many species of *Heterotheca*; some species may be consistently diploid and a few apparently are consistently tetraploid. Many of the polyploids appear to be closely similar in morphology to diploids of the same species. No single widespread species has yet been studied in enough detail to characterize its overall ploidal constitution with high confidence.

The most comprehensive of prior taxonomic studies has been that of Semple (1996), which recognized 20 species and 20 additional (non-typical) varieties as comprising the genus. Semple commonly has used trinomials and quadrimomials to express the taxonomic structure — in his view, *Heterotheca sessiliflora* includes 6 entities at varietal rank divided among 4 subspecies; *H. oregona* includes 4 varieties; *H. fulcrata* includes 4 varieties; *H. villosa* includes 10 varieties. He allowed that infraspecific taxa of a single species may be sympatric, sometimes even in 4 geographically overlying "layers" (e.g., within *H. sessiliflora*, within *H. fulcrata*, within *H. villosa*).

For concepts of subspecific and varietal ranks, Semple referred (1996, p. 108) to his earlier study of the genus *Xanthisma* (Semple 1974). In his view, subspecies are discontinuously distinct in morphology, except for a few hybrids, and have allopatric distributions. Varieties are populations distinct within the species but characteristically sympatric with populations of different varieties and with populations of morphological intermediates. Variation is continuous among the varieties, although "the continuum would have pronounced modes."

For many of the taxa of sect. *Phyllothea*, Semple's maps and specimen citations show collections identified as "aff. [taxon] (close to or approaching [taxon]." For the most part, the implications of Semple's notation seem to be that the taxa are widely variable (plastic) and that hybridization and introgression have blurred earlier-established evolutionary boundaries (the present treatment also recognizes and cites variants and putative hybrids). For example, "Within species, intervarietal hybrids are common in areas of sympatry" (Semple 1996, p. 24). In *Heterotheca villosa* "Each variety mostly likely evolved in isolation and adapted to a different set of habitat parameters" but "The highly plastic nature of the species and undoubted hybridization [after secondary development of sympatry of the varieties] make identification to variety difficult in numerous cases" (p. 108). In *H. fulcrata* (with 4 sympatric varieties) "Many intermediate forms occur throughout the range, and pure and mixed populations occur in areas of sympatry" (p. 70).

Semple's interpretations also are constrained by his use of numerical analyses in developing concepts of taxa. "Multivariate morphological analyses were undertaken on more than 600 specimens including 76 type specimens" (1996, p. 2), but those studies are unpublished.

### **Taxonomic perspectives of the current study**

Distinct morpho-geographic entities can be discerned in *Heterotheca* and such entities are treated here mostly at specific rank. The degree of morphological distinction varies among species, and the genus includes widely distributed and narrowly distributed species. Despite a generally perceived difficulty in *Heterotheca* taxonomy, the morpho-geographic patterning recognized here does not seem extraordinary, because such is the case in most other genera, even in those thought to comprise many recently evolved species and probably with low overall genetic divergence among the species.

Perhaps the most significant problem in *Heterotheca* taxonomy has been that morphological and geographical boundaries of putative evolutionary entities simply have not previously been clearly discerned — this is reflected here in the revivification of various old names, description of previously unrecognized species, and modified definitions of previously accepted species. Other problems in the taxonomy of *Heterotheca* are related to several factors.

(1) Morphological differences among species involve relatively few classes of features.

Beyond features diagnostic at sectional rank, significant morphological features distinguishing *Heterotheca* taxa first are density and orientation of vestiture (especially on stems, including glands), presence/absence of capitular bracts, and arrangement of heads. Plant habit, degree of ciliation of leaf and bract margins, and head size also may be distinctive. As interpreted here, production of capitular bracts (foliaceous bracts immediately or closely subtending the involucre) is generally consistent within a species — but populational variation sometimes exists. Orientation of cauline vestiture also appears to be generally consistent within a species — hairs usually either are upwardly oriented (antrorsely, loosely to closely appressed) or spreading (irregularly so, stiffly patent, or sometimes deflexed at a slight angle); exceptions to this occur. Hairs sometimes appear to be distinctly "2-storied" — with a relatively dense understory and sparser, longer overstory, although this, too, sometimes is variable within a species.

(2) Intraspecific variation in morphology and ecology is considerable.

Knowledge of geographic boundaries closely underlies the validity of this observation, as recognition of the total geographic range of a species allows an understanding of its morphological and ecological variability. I have been aware of the potential for circular reasoning. Marked variability also may point to the possible existence of unrecognized entities or to the effects of hybridization. Or, in some species, especially those geographically isolated, it simply may point to an underlying matrix of genetic latitude.

(3) Parallel/convergent trends of variation among species are common.

This is a corollary of the relatively few classes of features that allow recognition of morpho-geographic entities and the numerous entities that can be recognized.

(4) Hybridization and introgression appear to be significant processes.

Recognition of putative hybrids (morphological variants outside the limits constrained by the genome of a particular species) is possible with knowledge of the distribution of species and their areas of sympatry. For example, in Colorado, the characteristically high-elevation *Heterotheca pumila* is a variable species apparently within the limits of its genome; further variation at lower elevations apparently often results from hybridization with other species. Where *H. "hispidia"* and *H. villosa* are sympatric, intermediates and intergrades apparently are extensive, although the consistent occurrence in both of plants of typical morphology implies that some degree of reproductive isolation is in effect. The same relationship apparently holds between the Great Plains species *H. villosa* and *H. "ballardii."* Other species exist in sympatry without apparent gene flow.

In sum, the taxonomy of *Heterotheca* has been perceived as difficult, and so it is, but evolution has produced relatively discrete morpho-geographic entities and their recognition is not an intractable problem. Widely distributed taxa exchanging genes with others in areas of sympatry are maintained here at specific rank (in contrast to recognizing conspecific sympatric entities). And to some extent, the account of the genus presented here reflects how underlying philosophy of approach and taxonomic tenets can affect perceptions of evolutionary patterning.

### **Identification of goldenasters using this treatment**

Because of intraspecific variation, parallelism and convergence, and the apparent frequency of hybridization, I have not attempted to provide a key that includes all of the taxa. It would have been a personally frustrating task and use of such a key at best probably would have been discouraging for others as well. Accuracy and expertise in identifications are possible, however, especially if correctly identified collections are available for reference. With the distribution maps and the diagnostic descriptions provided for each taxon, the present treatment should be of practical

use in identifying plants at hand. Once the morphology and geography of the species is understood, keys for smaller regions, where species occur in smaller numbers and with more apparent distinction among themselves, will be easier to construct.

### Remaining problems

Further study, especially at local and regional levels, will surely result in modifications of the taxonomy presented here. Interesting problems can be found in any corner of *Heterotheca* taxonomy or geography, and at least some of these are pointed out. Several species treated here as widespread and variable will be interesting for further study and it seems likely that it will be useful to recognize additional narrowly distributed endemics at specific rank. Detailed study of chromosome numbers may be a relatively simple way to discover evolutionary patterns.

### ACKNOWLEDGEMENTS

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**HETEROTHECA** Cass., Bull. Sci. Soc. Philom., s. 3, 1817: 137. 1817. *Hysterionica* sect. *Heterotheca* (Cass.) Baill., Hist. Pl. 8: 155. 1886. **TYPE:** *Heterotheca lamarckii* Cass., nom. illeg. (*Inula subaxillaris* Lam., *Heterotheca subaxillaris* (Lam.) Britt. & Rusby)

#### **HETEROTHECA SECT. HETEROTHECA**

*Calycium* Ell., Sketch Bot. South Carolina 2: 339. 1824 [1823], nom. illeg. **TYPE:** *Chrysopsis scabra* (Pursh) Ell. (= *Heterotheca axillaris* (Lam.) Britt. & Rusby).

Elliott included the description of *Calycium* after the entry for "9. SCABRA." of the genus *Chrysopsis* and intended *Calycium* as a potential alternate genus name for *Chrysopsis scabra*, noting this in prelude: "The two preceding species differ in habit from this genus and the *C. Scabra* very much, in the structure of the seed and pappus. If the double or exterior pappus should be found to form permanent generic distinctions, and to unite those species which in habit, symmetry and character agree, this plant must be separated from this genus. It may be distinguished by the following character."

*Diplocoma* Don in Sweet, Brit. Fl. Gard. 3: t. 246. 1828. **TYPE:** *Diplocoma villosa* D. Don ex Sweet (= *Heterotheca inuloides* Cass., var. indeterminate)

*Stelmanis* Raf., Fl. Tellur. 2: 47. 1836. **TYPE:** *Stelmanis scabra* Rafinesque, nom. illeg. (= *Chrysopsis scabra* Ell., nom. illeg.; *Inula scabra* Pursh, nom. illeg.; *Inula subaxillaris* Lam., *Heterotheca subaxillaris* (Lam.) Britt. & Rusby)

*Heterotheca* sect. *Chaetactis* DC., Prodr. 5: 317. 1836. **TYPE:** *Heterotheca chrysopsidis* DC. (= *H. subaxillaris* (Lam.) Britt. & Rusby)

*Heterotheca* sect. *Gymnactis* DC., Prodr. 5: 317. 1836. **LECTOTYPE** (designated here): *Heterotheca scabra* (Pursh) DC. (= *H. subaxillaris* (Lam.) Britt. & Rusby)

Under his sect. *Gymnactis*, DeCandolle included *H. inuloides*, *H. scabra*, *H. lamarckii*, and *H. leptoglossa*.

Plants of sect. *Heterotheca* are characterized by dimorphic achenes — disc achenes are compressed, strigose to sericeous, with a well-developed pappus; ray achenes are 3-angled, smaller, glabrous or much less pubescent, and completely epappose or rarely with a few short bristles or a minute corona. Phyllaries often are distinctly keeled. It is the only group of *Heterotheca* where an annual duration has evolved, and the plants tend to be erect from the base. Mostly following Wagenknecht (1960), Semple (1996) recognized 7 species and 4 non-typical varieties — the species recognized here form a considerably different set. Most of the diversity in sect. *Heterotheca* occurs in Mexico and was described in an earlier study (Nesom 1990), but here entities previously treated at varietal rank within *H. inuloides* are recognized as species, *H. psammophila* is recognized as distinctive, and a previously undescribed species is recognized. Morphological distinctions between species are relatively small (as in other goldenaster species groups), but the geographic boundaries generally appear to be sharply defined.

**1. HETEROTHECA SUBAXILLARIS** (Lam.) Britt. & Rusby, Trans. New York Acad. 7: 10. 1887. *Inula subaxillaris* Lam., Encycl. Meth. Bot. 3: 259. 1789. **TYPE:** USA. **Protologue:** "Croît dans la Caroline, le Maryland, & peut-être dans d'autres parties de l'Amérique septentrionale." (probable holotype: P, not seen).

Wagenknecht (1960, p. 73) noted that "Lamarck's (1789) description is somewhat vague and on its own would scarcely distinguish this species from several others in related genera. No indication is given as to where he acquired his specimen. The type specimen (P) bears only the notation "Walter, Carolina" and the reference to the Plukenet plate."

*Inula punctata* Muhl., Cat. 76. 1813 [nom. nud.; referred to by Elliott and deCandolle as a synonym of *Inula scabra* Pursh].

*Inula scabra* Pursh, Fl. Amer. Septent. 2: 531. 1814 [nom. illeg.; Pursh cited *Inula subaxillaris* Lam. as a synonym]. *Chrysopsis scabra* (Pursh) Ell., Sketch Bot. S. Carolina 2: 339. 1824 [1823]. *Heterotheca scabra* (Pursh) DC., Prodr. 5: 317. 1836. *Stelmanis scabra* (Pursh) Raf., Fl. Tellur. 2: 47. 1836.

*Heterotheca lamarckii* Cass., Dict. Sci. Nat. 21: 131. 1821 [nom. illeg.; Cassini cited *Inula subaxillaris* Lam. as a synonym]. *Chrysopsis lamarckii* (Cass.) Nutt., Trans. Amer. Philos. Soc. n.s. 7: 315. 1840.

*Heterotheca chrysopsidis* DC., Prodr. 5: 317. 1836. **TYPE: MEXICO. Coahuila.** Protologue: "in Mexico circa Saltillo januar. flor. legit cl. Berlandier ... v.s. comm. à cl. Berlandier." Saltillo, Jan 1828, *J.L. Berlandier 1368* (holotype: GDC; isotype: P 00742816; probable isotypes: P 00742813, P 00742814, NY 163188; possible isotype: GH 55886, right side). Digital images! of all collections. The holotype was annotated as such by Semple in 1984 — it shows a collection date of Jan 1828 from Saltillo and collection number of 1368. The isotype is similar. The probable isotypes have "1368" as collection number but show no date. The GH collection is labeled collection number "109," collected in Saltillo in Jan 1828.

*Heterotheca latifolia* Buckl., Proc. Acad. Nat. Sci. Philadelphia 13: 459. 1862. *Heterotheca subaxillaris* var. *latifolia* (Buckl.) Gandhi & Thomas, Sida Bot. Misc. 4: 110. 1989. *Heterotheca subaxillaris* subsp. *latifolia* (Buckl.) Semple, Sida 21: 759. 2004. **TYPE: USA. Texas.** Llano Co.: No other locality data, Jun 1861, *S.B. Buckley s.n.* (probable holotype: PH! digital image!).

*Heterotheca latifolia* var. *petiolaris* Benke, Rhodora 30: 201. 1928. **TYPE: USA. Texas.** Galveston Co.: Galveston, 12 Mar 1928, *H.C. Benke 4585* (holotype: F digital image!).

*Heterotheca subaxillaris* var. *procumbens* Wagenk., Rhodora 62: 75. 1960. **TYPE: USA. Alabama.** Mobile Co.: ca. 1 mi SW of Dauphin Island Post Office, flattish dunes, 29 Jul 1940, *R.M. Harper 3801* (holotype: GH digital image!; isotypes: F digital image!, MO! digital image!, PH! digital image!, US digital image!).

*Heterotheca latifolia* var. *macgregoris* Wagenk., Rhodora 62: 103. 1960. **TYPE: USA. Kansas.** Morton Co.: 9 mi N of Elkhart, bluffs along Cimarron River, dry sandy prairie, 27 Aug 1951, *R.L. McGregor 5163* (holotype: KANU!).

*Heterotheca latifolia* var. *arkansana* Wagenk., Rhodora 62: 105. 1960. **TYPE: USA. Arkansas.** Logan Co.: Magazine Mountain, 10 Sep 1930, *D.M. Moore 30142* (holotype: TEX!).

Annual or biennial; herbage drying green, erect to decumbent or procumbent. Upper cauline leaves usually at least slightly subclasping, becoming reduced in size but mostly remaining ovate; phyllaries densely glandular, usually without non-glandular hairs, innermost 5–8 mm long; disc corollas glabrous or nearly so; ray achenes usually completely glabrous, disc achenes usually with 1–3 resinous veins; outer pappus strongly developed. Chromosome number,  $2n = 18$  (many counts).

Within what is treated here as *Heterotheca subaxillaris*, Wagenknecht (1960) recognized *H. latifolia* and *H. chrysopsidis* as segregates at specific rank. Geographic trends can be observed and plants sometimes may be suspected of having originated in certain geographic areas, but plants occurring in broad areas of intergradation appear to be as numerous as those with names and said to have a distinctive combination of traits (see comments by Nesom 1990).

Semple (1996) recognized *Heterotheca subaxillaris* and *H. latifolia* as distinct species but later (2006) treated the same entities as subspecies — subsp. *subaxillaris* characterized as "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 Mexico." Burk (1961), however, found evidence that features of the coastal plain form are produced in response to environmental conditions. He transplanted North Carolina plants from a barrier island (Bogue

Barrier) and from an inland habitat to a common garden on the piedmont, where they "developed into virtually identical sets of plants." Using cloned individuals, he also observed that vestiture was significantly modified depending on the season and whether the plants were grown in a greenhouse or outdoors. Harms (1965) also documented the ease of environmental modification among plants of *H. subaxillaris*.

Burk also noted on the barrier island that most populations flowered in later summer and early fall but that one population flowered year-round. In January 1960, plants of the latter were in full flower while the others on the island were in winter-rossette form. In greenhouse experiments, he found that plants of the common winter-rossette form required long days to flower, while those flowering in January flowered under both long-day and short-day conditions. This difference in phenology has not been reflected in taxonomic proposals.

The name *Heterotheca chrysopsidis* has been applied to plants from Coahuila and adjacent Nuevo León that have woodier roots (perennial?) and shorter stature, petiolate, prominently thickened leaves (similar to coastal variants of *H. subaxillaris*), and deep reddish-brown pappus. These features are most pronounced in plants from gypsaceous areas of Nuevo León but intermediates are numerous.

**2. HETEROTHECA GRANDIFLORA** Nutt., Trans. Amer. Philos. Soc. n.s., 7: 315. 1840. **TYPE: USA. California.** Label: "Santa Barbara, in rupibus," [1836], *T. Nuttall s.n.* (holotype: BM digital image!).

*Heterotheca floribunda* Benth., Bot. Voy. Sulphur, 24. 1844. **TYPE: Protologue**: "San Pedro and San Quentin," no specimen cited (holotype: K?).

Along the Pacific coast, H.M.S. Sulphur visited the ports of San Pedro (Los Angeles Co., California) and San Quentin (Baja California) in October 1839. Bentham's description of *H. floribunda* is very brief and hardly diagnostic but Hall (1907), Wagenecht (1960), and others, followed here, have placed the name as a synonym of *H. grandiflora*.

Annual to biennial or short-lived perennial, plants to 2 m tall; stems and leaves sparsely to densely hispid-pilose to villous, herbage with a strong tendency to dry with a pronounced dark cast. Cauline leaves broadly lanceolate to triangular-lanceolate, narrowed to a sessile or subsessile, non-clasping, attenuate base, at least on the distal stems and commonly becoming linear-lanceolate to linear bracts. Phyllaries distinctly keeled (Fig. 3), with only glandular hairs or glandular and sparsely strigose, usually purple-tipped, innermost 7–9 mm long. Disc corollas prominently hairy on the throat. Ray achenes minutely strigose at least on the angles and commonly on the faces as well; pappus with a weakly developed outer series of scales or bristles. Chromosome number,  $2n = 18$  (many counts).

These are tall plants with large heads, broadly lanceolate to triangular-lanceolate leaves with a non-clasping base and acute apex. The leaves usually are densely villous and the herbage usually dries with a dark cast. Pappus tends to be reddish brown. With its distinctive habit and achene morphology, it rarely is misidentified — small plants have been identified as *H. subaxillaris*, but the leaves with non-clasping base and relatively dense vestiture usually are diagnostic.

*Heterotheca grandiflora* is native in California and Baja California, introduced in Arizona, Utah, and Hawaii. Common on sandy or disturbed soils at altitudes from sea level to 2000 feet.



Figure 3. *Heterotheca grandiflora*, from BM holotype. Reddish brown pappus and strongly keeled phyllaries.

**3. HETEROTHECA PSAMMOPHILA** Wagenk., *Rhodora* 62: 76. 1960. **TYPE: USA. Arizona.** Yavapai Co.: 1 mi S of Sedona, sandy soil along edge of roadside ditch, 23 Aug 1957, *B.L. Wagenknecht* 4824 (holotype: KANU, not located). **EPITYPE** (designated here): **Arizona.** Yavapai Co.: 0.5 km downstream from Granite Creek confluence and headwater springs of the Verde River, ca. 2.4 km upstream from Campbells Ranch, 4.7 km SE of Paulden, 1290 m, below an eroded terrace on the bank of the Verde River, roots partially in damp, gravelly soil with *Salix*, *Populus*, *Fraxinus*, *Baccharis*, 25 Jun 2011, *F.S. Coburn* 336b (ASU, Fig. 6).

Annual, thick-stemmed, up to 1.5(–2) m tall; stems and leaves sparsely to densely hirsute to hispid-pilose, herbage drying green, without a dark cast. Cauline leaves oblong to oblong-obovate, oblong-ovate, or triangular-ovate (commonly 3–4 times longer than wide, usually epetiolate and clasping to subclasping to nearly the base of the stem, vestiture reduced adaxially. Involucres 6–8(–9) mm high (innermost phyllaries); phyllaries densely glandular, without non-glandular hairs. Disc corollas glabrous or nearly so. Ray achenes usually completely glabrous; disc achenes usually with 1–3 resinous veins. Chromosome number,  $2n = 18$ .

Previously and through part of the current study, I treated *Heterotheca psammophila* as a synonym of *H. subaxillaris*, but further observations indicate there is rationale for its formal recognition. Such plants essentially are mostly restricted to Arizona, northern Sonora, and northwestern Chihuahua. Native populations edge into adjacent California and New Mexico.

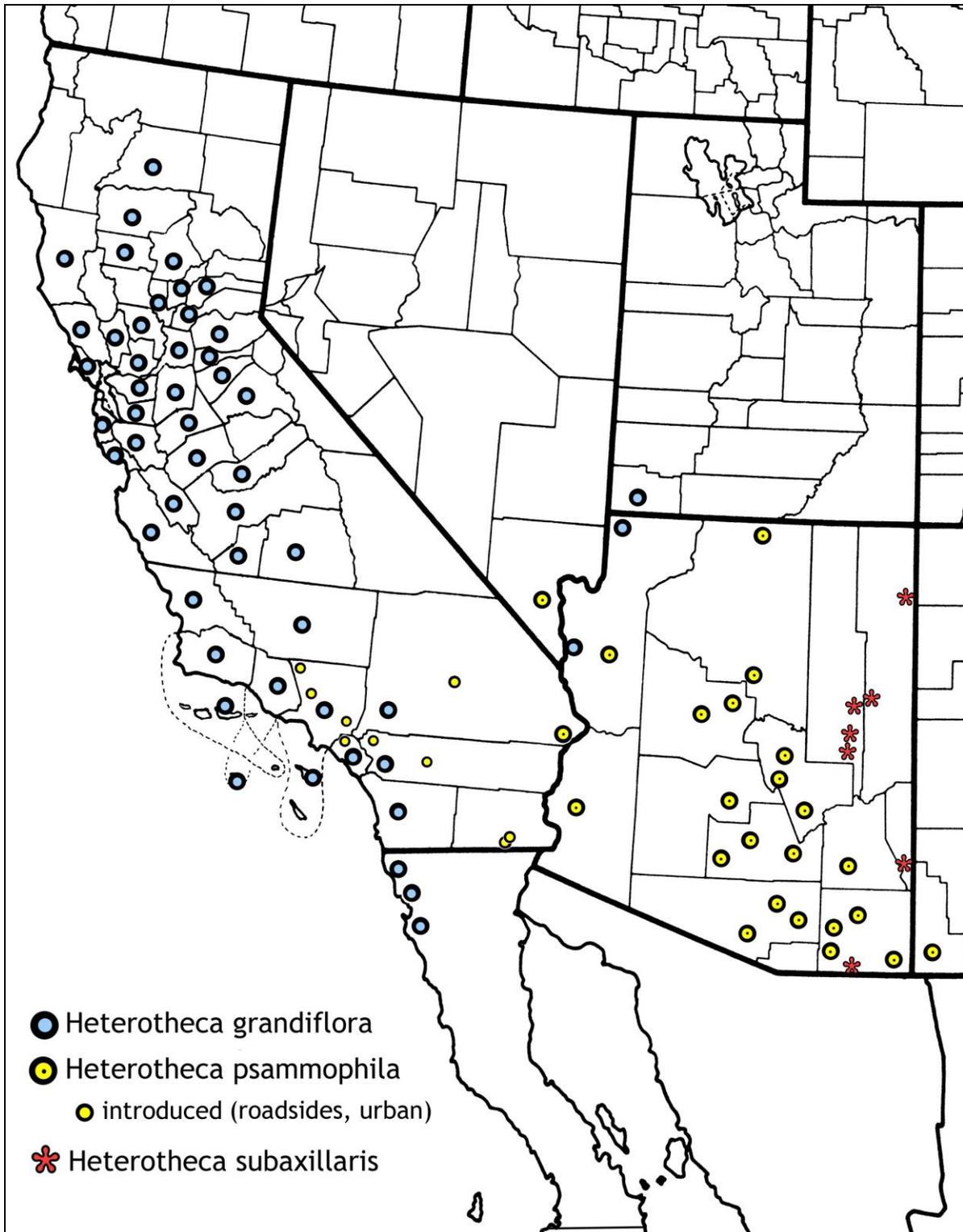


Figure 4. Distribution of *Heterotheca* sect. *Heterotheca*: *H. grandiflora*, *H. psammophila*, and *H. subaxillaris*.

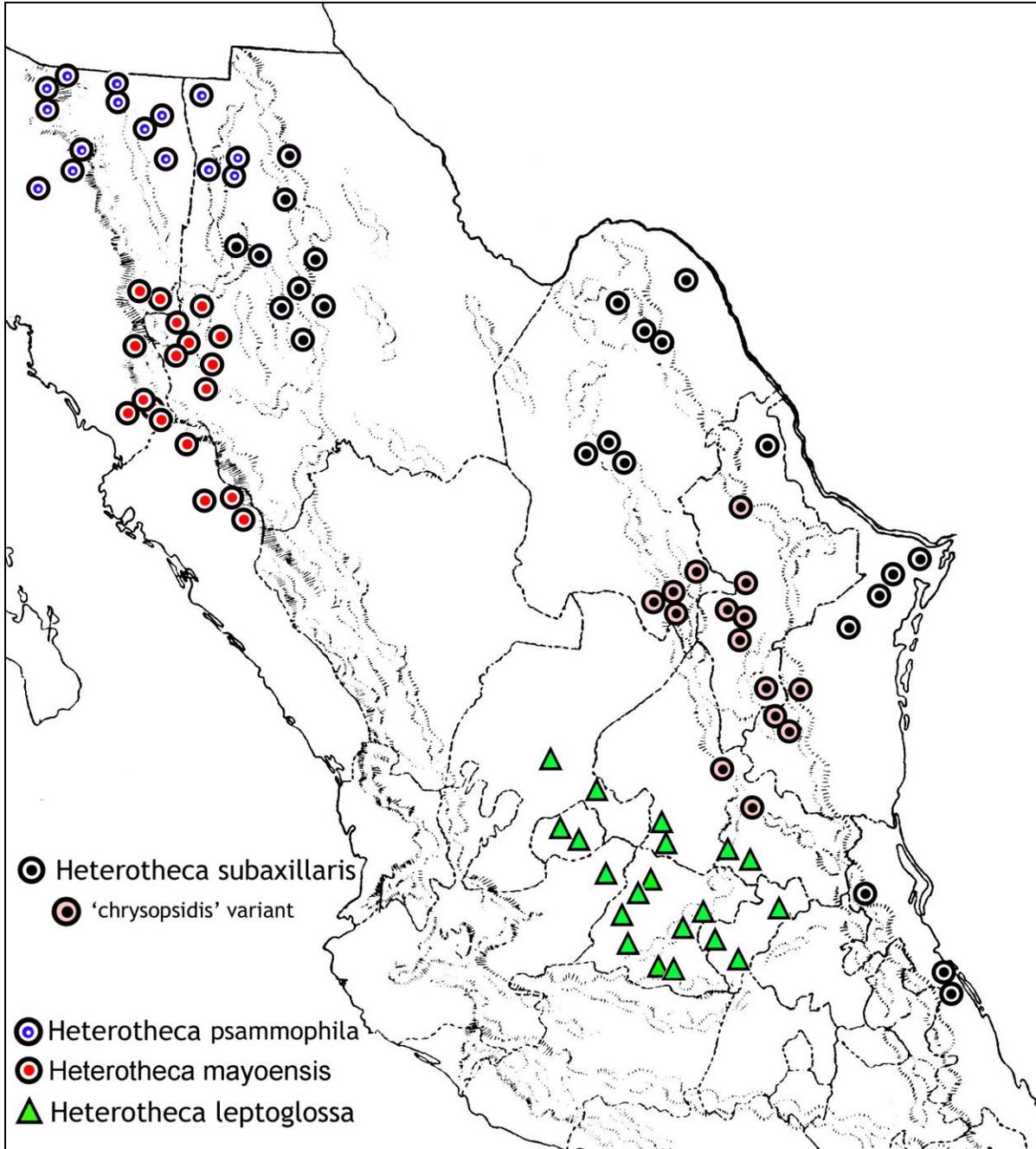


Figure 5. Distribution of *Heterotheca* sect. *Heterotheca*: *H. subaxillaris*, *H. psammophila*, *H. mayoensis*, and *H. leptoglossa*. *Heterotheca mayonensis* and *H. leptoglossa* also are shown in Figure 10, with the other Mexican endemics.



Figure 6. *Heterotheca psammophila*, epitype, Coburn 336b (ASU).



DET. *H. psammophila* Nesom 19 78  
 J. Harry Lehr 13/1/77  
 Annotation — Herbarium of Desert Botanical Garden

15970

No. ....

DESERT BOTANICAL GARDEN  
 Phoenix, Arizona

Ref. .... Family COMPOSITAE .....

Vol. & Page ..... Collection Date 23 Aug 1977 .....

Botanical Name *Heterotheca subaxillaris* (Lam.) Britt  
 Variety ..... & Rusby .....

Locality Rd. to Alchesay Fish Hatchery at crossing  
 N. fork White R. Navajo County, AZ .....

Cover Type ..... Open-Pond Pine .....

Slope ..... Soil Type .....

Abundance Frequent ..... Altitude 7500' .....

Other Data .....

Collector's Name ..... J. Harry Lehr ..... No. 1953 .....

Checked by .....

HERBARIUM  
 DES  
 DATABASE

DESERT BOTANICAL GARDEN  
 DES00015970

Figure 7. *Heterotheca psammophila*, Navajo Co., Arizona.



Figure 8. *Heterotheca psammophila*, Yavapai Co., Arizona.



Figure 9. *Heterotheca psammophila*, near Colonia Juárez in northwestern Chihuahua.

**Representative collections of native *H. psammophila* in the USA outside of Arizona.**  
**California.** San Bernardino Co.: Whipple Mts, along Colorado River at Big River SW of Earp, riparian woodland, sandy soil near river, 15 Nov 1980, *Sanders 2043* (UC, UCR). **New Mexico.** Hidalgo Co.: *Alford s.n.* (DES), *Dittmer 8575* (UNM), *Makings 3084* (DES), *Makings 3567* (TEUI), *Wagner 1391* (UNM), *Wagner 1678* (UNM), *Zimmerman 2274* (DES). Typical *Heterotheca subaxillaris* also occurs in Hidalgo Co.: *Dittmer 8574* (UNM), *Worthington 14879* (COLO).

Adventive populations of *Heterotheca psammophila* occur in southern California and perhaps in Brewster Co., Texas. Some California collections previously identified as *H. subaxillaris* have proved to be *H. psammophila* or *H. grandiflora* of small stature; all IDs of *H. subaxillaris* in California should be checked.

**Collections of apparently adventive *H. psammophila*.** **California.** Imperial Co.: Imperial Valley, ca. 10 mi E of El Centro, 13 Jun 1994, *Gruenhagen s.n.* (UCR, grown at UCR from field collection); 2 mi E of Calexico, border of California-Mexico, 7 Nov 1938, *Woglum 12645* (RSA). Los Angeles Co.: Irwindale, abandoned gravel pit adjacent to 210 Freeway, ca. 300 m E of Irwindale Ave, 31 Dec 1997, *Swinney 5890* (UCR); E Santa Susana Mts, Lyon Canyon area, W of I-5 Freeway, ca. 4 mi N of I-5/State Hwy 14 jct, 14 Jun 2004, *White 10498A* (UCR); SE Tehachapi Mts, Gorman area, Gorman Post Rd, scarce on roadside, 6 Jul 2006, *White 11608* (UCR). Orange Co.: Vicinity of city of Brea, immediately N of Carbon Canyon Rd and E of Placentia Ave, ca. 600 ft, heavily disturbed area, margin of *Quercus agrifolia* forest, 13 Oct 1992, *White 961* (UCR); city of Laguna Niguel, ridges and open slopes directly N of intersctn Crown Valley Pkwy and Pacific Island Drive, 17 May 2004, *White 10383* (UCR). Riverside Co.: UCR campus, well-watered planter beside Boyce Hall, solitary weed, 23 Sep 1999, *Provance 1680B* (UCR); Indio, 2 mi S of Jackson St., sandy flat, 26 Sep 1965, *Roos s.n.* (RSA, UCR). **Texas.** Brewster Co.: Santa Helena Canyon, Big Bend National Park, *Moore & Steyermark 3467* (as cited by Wagenknecht: GH, PH, UC); near the mouth of Santa Helena Canyon, 8 Aug 1938, *Warnock T505C* (FSU, TEX).

In his key to species, Wagenknecht (1960, p. 66) distinguished *Heterotheca psammophila* by its "Stems up to 1.2 cm in diameter, the lateral branches coarse; leaves cordate-clasping, sparsely pilose above; phyllaries densely glandular and pilose." None of these features, however, is effective in identifying the form, at least as seen on herbarium specimens. A more consistent distinction is the morphology and vestiture of the cauline leaves — oblong to oblong-obovate, oblong-ovate, or triangular-ovate (commonly 3–4 times longer than wide), usually epetiolate and clasping to subclasping to nearly the base of the stem (vs. the proximal petiolate), and with reduced vestiture adaxially. *Heterotheca psammophila* produces larger heads than *H. subaxillaris* (innermost phyllaries 6–8(–9) mm long vs. 5–6(–7) mm) and they are generally taller and thicker-stemmed.

Semple (1996), following Wagenknecht, included *Heterotheca psammophila* in his key to species of sect. *Heterotheca*. For FNA in 2006, however, he treated it within the synonymy of *H. subaxillaris* subsp. *latifolia*, noting that "Robust plants (to 2 m) occurring in Arizona, New Mexico, and adjacent Texas have been treated as *Heterotheca psammophila*, but they grade into those treated as subsp. *latifolia* farther east on the prairies and eastward." I agree with Semple that plants with *psammophila*-like leaves and other features occur within the range of *H. subaxillaris*, particularly in the southeastern USA and in west Texas, but my assessment here of the taxonomy is weighted by the observation that the geographic range of *H. psammophila* appears to be sharply defined in both the USA and Mexico (Figs. 4, 5). Outlying variants in the USA are regarded here as populational variants within *H. subaxillaris*.

### The *Heterotheca inuloides* group

*Heterotheca inuloides* has previously been treated inclusively. Wagenknecht (1960) treated *H. rosei* (in its initial description) as a variety of *H. inuloides*, noting its morphological distinction and (p. 70) that it "is geographically distributed in a manner to warrant its treatment as a variety." Some populational variants of *H. rosei* in the area of ne Nayarit-se Durango-sw Zacatecas and in the vicinity of Uruapan and Tancítaro, Michoacan, have inuloides-like vestiture and perhaps warrant formal recognition. *Heterotheca viridis* and *H. leptoglossa* were subsumed within *H. inuloides* without due consideration of their biology and geography. With numerous collections now available for study, these plants appear to comprise discrete entities in morphology and geography, identified as in the following key and including a newly described species.

In view of the geography, it would not be surprising to find that *Heterotheca subaxillaris* is evolutionarily sister to all the others or that *H. subaxillaris*, *H. psammophila*, and *H. grandiflora* as a group are sister to the Mexican endemics, which are identified here as the "*H. inuloides* group."

1. Outer phyllaries densely villous or hispid-pilose from base to tip with spreading to spreading-ascending, non-glandular hairs; perennial.
  2. Phyllaries usually distinctly purplish at least at the apices and commonly along the distal margins and midregion, hispid-pilose with thick-based, non-glandular trichomes ..... 7. ***Heterotheca inuloides***
  2. Phyllaries completely without purple coloration, villous with thin-based non-glandular trichomes ..... 8. ***Heterotheca viridis***
1. Outer phyllaries densely stipitate-glandular along the whole length, usually no or few non-glandular hairs or glabrous to strigose on the distal half with only fine and relatively thin-based glandular hairs; annual to biennial or perennial.
  3. Outer phyllaries completely glabrous to strigose along the distal midregion with appressed to ascending-appressed, fine and relatively thin-based, non-glandular hairs, eglandular to sparsely sessile-glandular distally or with short-stipitate glands near the phyllary apex, usually purple at the very apex ..... 6. ***Heterotheca leptoglossa***
  3. Outer phyllaries densely stipitate-glandular along the whole length, usually without non-glandular hairs or the non-glandular hairs few.
    4. Annual or biennial; phyllaries without purple tips, stipitate-glandular sometimes with non-glandular hairs sparsely intermixed on the distal third ..... 5. ***Heterotheca rosei***
    4. Perennial; phyllaries purple-tipped, stipitate-glandular and without non-glandular hairs ..... 4. ***Heterotheca mayoensis***

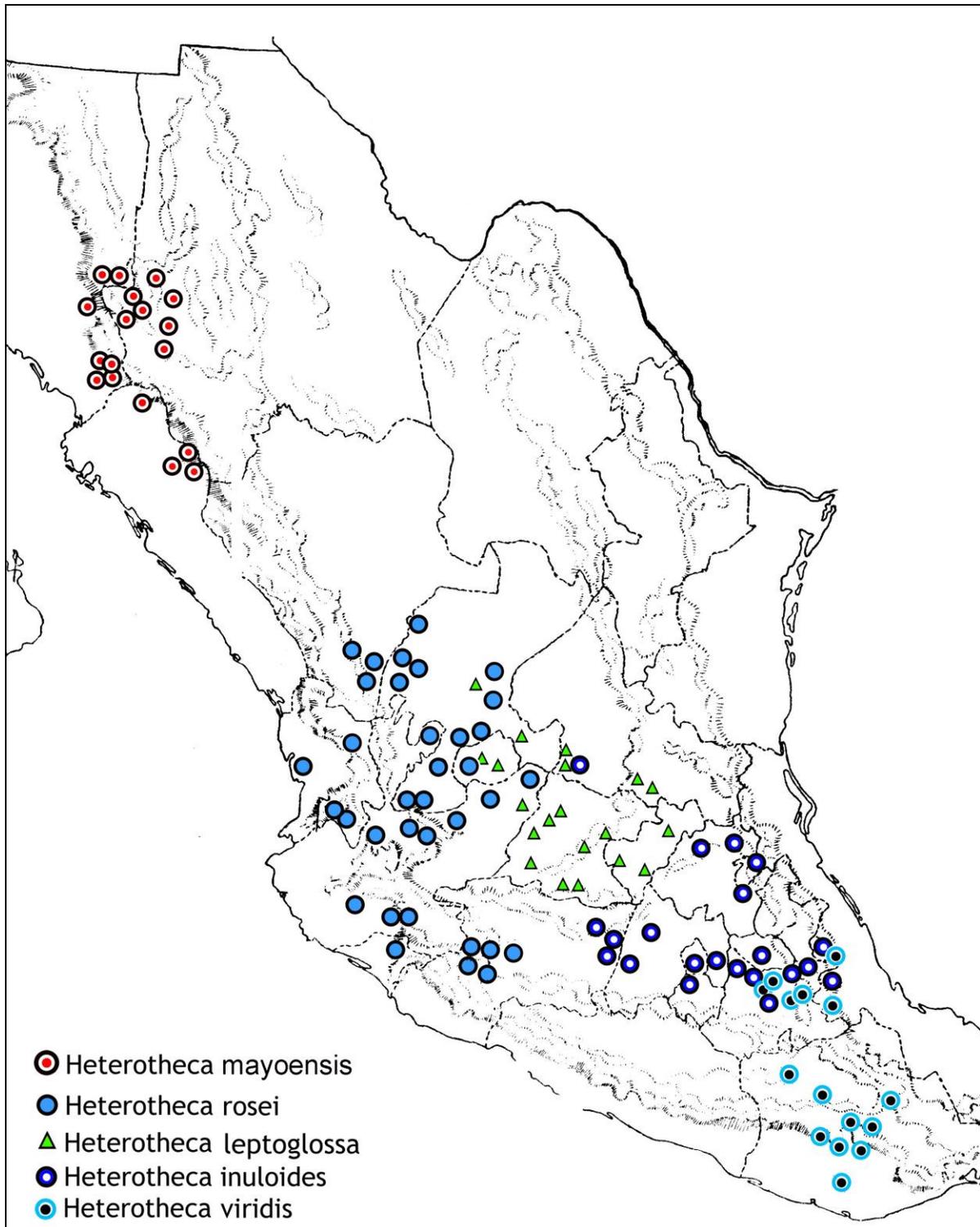


Figure 10. Distribution of Mexican endemics of sect. *Heterotheca* (the "*H. inuloides* group"): *H. mayoensis*, *H. rosei*, *H. leptoglossa*, *H. inuloides*, and *H. viridis*. *Heterotheca mayoensis* also is shown in Figure 5 with other species of northwestern Mexico.

**4. HETEROTHECA MAYOENSIS** Nesom, **sp. nov.** TYPE: MEXICO. Chihuahua. Mpio. Chinipas: Guicorichi, Rio Mayo, transition, slope of old milpa, 7 Oct 1935, *H.S. Gentry 1974* (holotype: MEXU 1356175 (Fig. 11); isotypes: MEXU 798554 (Fig. 12), MO (Fig. 13), PH!). The locality is at the western foot of Cerro Guicorichi, ca 9 km east of Loreto.

Distinct in its combination of oblanceolate to elliptic-oblanceolate leaves tapering to a narrow base, linear to filiform inflorescence bracts, stipitate-glandular phyllaries without non-glandular hairs, and its discrete, allopatric geographic range. Different from *H. subaxillaris* in its perennial duration, more elongate leaves, linear to filiform inflorescence bracts, smaller heads, and purple-tipped, stipitate-glandular phyllaries without non-glandular hairs. Different from *H. psammophila* in its perennial duration, mostly oblanceolate leaves tapering to a narrow base, and its discrete, allopatric geographic range. Most closely similar to *H. rosei* (see key and comments below).

**Plants** "perennial" (e.g., *Van Devender 93-1504, 93-1401; Sanders 14278; Reina 96-376*), a "colonial weed" (*Gentry 6170*), "rhizomatous" (*Vega & Torres 1527*), from a thick, woody taproot that often elongates and perhaps appears like a rhizome. **Stems** 0.2–1 m tall, sparsely hirsutulous with fine, even-length hairs 0.5–1 mm long, eglandular to sparsely minutely stipitate-glandular, in the inflorescence becoming mixed hirsutulous and stipitate-glandular, peduncles (distal 2–4 cm) densely stipitate-glandular without non-glandular hairs. **Leaves:** proximal and mid narrowly oblong-oblanceolate to elliptic-oblanceolate or narrowly elliptic-oblanceolate to elliptic-oblong, 3.5–9(–10) cm long, blades 8–20 mm wide, basally attenuate to a distinct petiole or petiolar region, clasping to subclasping, sometimes with an abruptly widened flange at the petiole base, distal cauline becoming narrowly oblong and petiolate, margins entire or subentire to serrate with 3–7 pairs of teeth, surfaces sparsely villous-hirsute, minutely short-stipitate-glandular with orange glands on both surfaces but more densely so adaxially, margins minutely ciliate or without distinctly differentiated cilia. **Inflorescence** a cymosely branched corymb, peduncles bracteate; bracts linear to filiform. **Heads** 8–10 mm wide, phyllaries in 3–4 graduate series, linear-lanceolate, 0.5 mm wide, not keeled, longest (inner) 6–9 mm long, consistently purple-tipped. **Ray flowers** 20–25, corollas 10–12 mm long. **Disc corollas** ca. 5 mm long. **Achenes:** ray glabrous, disc sparsely strigose-sericeous. **Chromosome number**,  $n = 9$  (count by D.J. Keil from *Lehto 19519*).

Flowering all year, perhaps most abundantly August-October. Tropical deciduous forest, oak, oak-pine, and pine forest, coniferous woods, clearings, roadsides, ruderal sites, fields, pastures, canyon bottoms; (400–) 700–1800 m.

Earlier (Nesom 1990) I noted that a population system in northwestern Mexico ("region a") might justifiably be formally regarded as a separate entity but treated the plants as part of the "psammophila" expression of *H. subaxillaris*. With formal recognition of *H. psammophila* as distinct and with a clearer definition of the geography (maps in Figs. 5 and 10) and morphology (Figs. 11-22) of the "region a" plants, they are here described as a distinct species.

In Chihuahua, where the range of *Heterotheca mayoensis* is nearly parapatric with that of *H. subaxillaris*, the two can be separate by the following couplet.

- a. Perennial; non-glandular stem hairs 0.5–1 mm long; phyllaries purple-tipped, innermost 6–8(–9) mm long, stipitate-glandular and lacking non-glandular hairs, mid to upper cauline leaves narrowly oblong; inflorescence bracts linear to filiform ..... ***Heterotheca mayoensis***
- a. Annual; non-glandular stem hairs 0.5–2 mm long; phyllaries without purple tips, innermost 5–6(–7) mm long, sessile- to stipitate-glandular and almost always hirsute with non-glandular hairs, mid and upper cauline leaves ovate-lanceolate to oblong-lanceolate, inflorescence bracts lanceolate to ovate-lanceolate ..... ***Heterotheca subaxillaris***

*Heterotheca mayoensis* is most closely similar to *H. rosei*, especially in its combination of vestiture and leaf morphology, and presumably part of the species group with geographic ranges restricted to Mexico. Compared to *H. mayoensis*, *H. rosei* has more slender taproots (presumably annual in duration), slightly larger heads, and distinctly larger stipitate glands. The two species are separated by more than 200 miles at their closest point.

***Heterotheca mayoensis*, additional collections. Chihuahua.** Mpio. Moris: Moris, Selva Baja Caducifolia, con encino, 700-1050 m, 29 Sep 1985, *Tenorio L. 10068* (MEXU); El Pilar, encino-pino alterado, 1400 m, 30 Sep 1985, *Tenorio 10079* (MEXU-2 sheets. Mpio. Temosachic: Nabogame, 1800 m, 5 Aug 1987, *Laferriere 674* (MEXU); Nabogame, 1800 m, 19 Aug 1987, *Laferriere 857* (MEXU); Nabogame, arroyo, 1800 m, 24 Oct 1988, *Laferriere 2187* (MEXU); Yepachic, abundant near stream, 1700 m, 18 Aug 1991, *Neff 8-18-91-8* (MEXU). Mpio. Urique: Sierra Tarahumara, Cuiteco, ruderal, 1732 m, Nov 2001, *Camou G. 516* (MEXU), *521* (MEXU). **Sinaloa.** Mpio. Badiraguato: Ocurahui, Sierra Surotato, pine forest area, ca. 6000-7000 ft, colonial weed about milpas, 27-30 Aug 1941, *Gentry 6170* (MEXU, NY, PH); Surutato a 5 km por la carretera a Santa Rita, Mesa del Fierro, bosque de coníferas, ca. 1800 m, Nov 28 1998, *Hernandez V. 1081* (MEXU); 1.4 mi NE El Cajon (11.3 mi NE Choix), dry sandy wash, 2100 ft, 25 Nov 1975, *Lehto 19519* [ $n=9$ , D.J. Keil 1975] (ASU); San Jose de los Hornos, 82 km NE de Mocorito camino a Surutato, bosque mixto de pino-encino, 1630 m, 2 Aug 1983, *Martínez 4191* (MEXU); 5 km SE de Surutato, 1650 m, bosque de encino, abundante, 22 Aug 1986, *Tenorio 11910* (MEXU, TEX); Surutato y alrededores, bosque de pino con presencia de *Acacia pennatula*, perturbado por actividades antrópicas, común, 1500 m, 9 Dec 2010, *Vega A. 11690* (MEXU); 11 km N de Surutato por la brecha Surutato-Santa Rita, llano entre claro de bosque, 2000 m, 9 Mar 1985, *Vega & Torres 1527* (MEXU). **Sonora.** Mpio. Alamos: Alamos, 17 Dec 1898, *Goldman 275* (NY); road N from Alamos to La Higuera, between Cerros El Cucurucho and El Aguaje, dry, short tree forest, with *Ipomea arborescens*, ca. 500 m, 29 Dec 1989, *Joyal 1345* (MEXU, TEX); Sierra Madre Occidental, Rancho Santa Barbara, Rio Cuchijaqui drainage, pastures and fields around ranch, ca. 1400 m, 17 Jul 1990, *Joyal 1490* (MEXU, TEX); San Bernardo, 26 Mar 1987, *López s.n.* (USON); El Caracol Trailer Park, ca. 10 mi W of Alamos on the road to Navajoa, flat weedy areas around the margins of the park, 400 m, 13 Dec 1988, *Sanders 8784* (TEX, UCR); 3 mi N of Rancho La Huerta (near the airstrip on the NW edge of Alamos) on the road to San Bernardo, tropical deciduous forest, uncommon, 2 Apr 1994, *Sanders 14278* (MEXU, UCR); 23 mi E of Navajoa on rd to Alamos, S side of road and roadcuts and on adjoining hills, 25 Feb 1967, *Sikes & Babcock 186* (TEX); 15 km E de Taymuco, 1400-1460 m, ecotono de selva baja caducifolia-encinar, 3 Oct 1985, *Tenorio 10169* (MEXU); Rancho La Sierrita (R. El Negrito), E slopes of the Sierra de Alamos, ca. 6 km (by air) SSW of Alamos, fallow field, 700 m, 26 Nov 1993, *Van Devender et al. 93-1401* (ASU, USON); ca. 1 km E of Mesa Colorada, disturbed roadside, 440 m, 12 Dec 1993, *Van Devender et al. 93-1504* (UCR, USON); 2 km WNW of Minas Nuevas on Alamos-Navajoa Road, N side of the Sierra de Alamos, roadside, 520 m, 27 Feb 1995, *Van Devender et al. 95-165* (USON); 5 km W of Las Chinacas on road from Las Tanques to Chinipas, cleared fields, originally pine-oak forest, 1500 m, 21 Aug 1991, *Yetman & Martin s.n.* (ARIZ). Mpio. Yécora: Yécora, Estanque del Arroyo de Yécora, entre el poblado de Yecora y las Cabañas Los Champiñones, bosque de pino y encino perturbado, frecuente en lugares arenosos, 1550 m, 4 Oct 1996, *Flores 4985* (USON); 5 km N of Tepustete, 1 Jan 1992, *Martin et al. s.n.* (ARIZ, MEXU); Yécora, abundant on flats near river, 17 Aug 1991, *Neff 8-17-91-1* (MEXU, TEX); Yécora, cerca del aserradero, 20 Aug 1991, *Reina s.n.* (USON); Yécora, a un lado de la pista, Yécora, 17 Sep 1991, *Reina s.n.* (USON); Yécora, near baseball field and cemetery, 1540 m, 6 Sep 1995, *Reina 96-376* (MEXU); Arroyo Hondo, 11.5 km E of El Kipur, 4 km W of Chihuahua border on Son 16, deep shady stream canyon with *Cupressus-Acer-Alnus* gallery forest, pine-oak forest on slopes, locally very common in rocky area in canyon bottom, 1460 m, 28 May 1996, *Reina 96-265* (MEXU); 8 km W of Yécora on Méx 16, Km 272 E of Cd. Obregón, 6 km E of Restaurant Puerto de la Cruz, 16 Aug 1997, *Trauba s.n.* (TEX); Yécora, arroyo in grassy field, 19 Aug 1997, *Trauba s.n.* (TEX); Yécora, 6 Oct 1995, *van Devender 95-731* (TEX); Arroyo El Otro Lado, Mesa El Otro Lado, 1-2 km NNE of Yécora on old road to Maycoba, pine-oak forest, edge of stream, 1520 m, 7 Sep 1995, *van Devender 95-811* (MEXU, TEX); Arroyo Hondo, 11.5 km E of El Kipur, 4 km W of Chihuahua border on Méx 16, shady canyon, 18 Jul 1997, *van Devender 97-882* (TEX).



Figure 11. *Heterotheca mayoensis*, Mpio. Chinipas, Chihuahua, holotype MEXU.



Figure 12. *Heterotheca mayoensis*, Mpio. Chinipas, Chihuahua, isotype MEXU.



Figure 13. *Heterotheca mayoensis*, Mpio. Chinipas, Chihuahua, isotype MO.



Figure 14. *Heterotheca mayoensis*, Mpio. Yécora, Chihuahua.

Figure 15. *Heterotheca mayoensis*, Mpio. Yécora, Chihuahua.



Figure 16. *Heterotheca mayoensis*, Mpio. Temosachi, Chihuahua.

Figure 17. *Heterotheca mayoensis*, Mpio. Urique, Chihuahua.

Figure 18. *Heterotheca mayoensis*, Mpio. Urique, Chihuahua.



Figure 19. *Heterotheca mayoensis*, Mpio. Badiraguato, Sinaloa.



Figure 20. *Heterotheca mayoensis*, Mpio. Badiraguato, Sinaloa. Nash et al. L19519 (ASU).



Figure 21. *Heterotheca mayoensis*, Mpio. Badiraguato, Sinaloa. Heads from Nash *et al.* L19519, Fig. 20. Involucres and distal portion of peduncles stipitate-glandular, without other hairs.



Figure 22. *Heterotheca mayoensis*, Mpio. Alamos, Sonora. Heads from *Van Devender 1401*.

**5. HETEROTHECA ROSEI** (Wagenk.) Nesom, **comb. et stat. nov.** *Heterotheca inuloides* var. *rosei* Wagenk., *Rhodora* 62: 69. 1960. **TYPE: MEXICO. Jalisco.** 30 mi E of Guadalajara, grassland and roadsides, sandy soil, 25 Jul 1956, *B.L. Wagenknecht 2846* (holotype: KANU!; isotypes: F digital image!, MIN digital image!, NCU digital image!, NY digital image!).

Annual or biennial? from a woody taproot ("perennial ... often flowering the first year, forming a short branched woody caudex" fide McVaugh 1984); phyllaries prominently stipitate-glandular and without non-glandular hairs or if present, the non-glandular hairs few and mostly on the distal third, usually with a prominent, raised keel on the proximal half.

In addition to a paucity or lack of non-glandular hairs, the phyllaries of *Heterotheca rosei* usually lack purple coloration or have only purplish margins, they are more densely stipitate-glandular than in typical *H. inuloides*, and the glands usually have thicker stipes. Judging from their more slender taproots, these plants are perhaps more short-lived than those of *H. inuloides*. These entities are morphologically distinct and geographically separate (non-overlapping).



Figure 23. *Heterotheca rosei*, heads from F isotype, Jalisco.



Figure 24. *Heterotheca rosei*, Jalisco.



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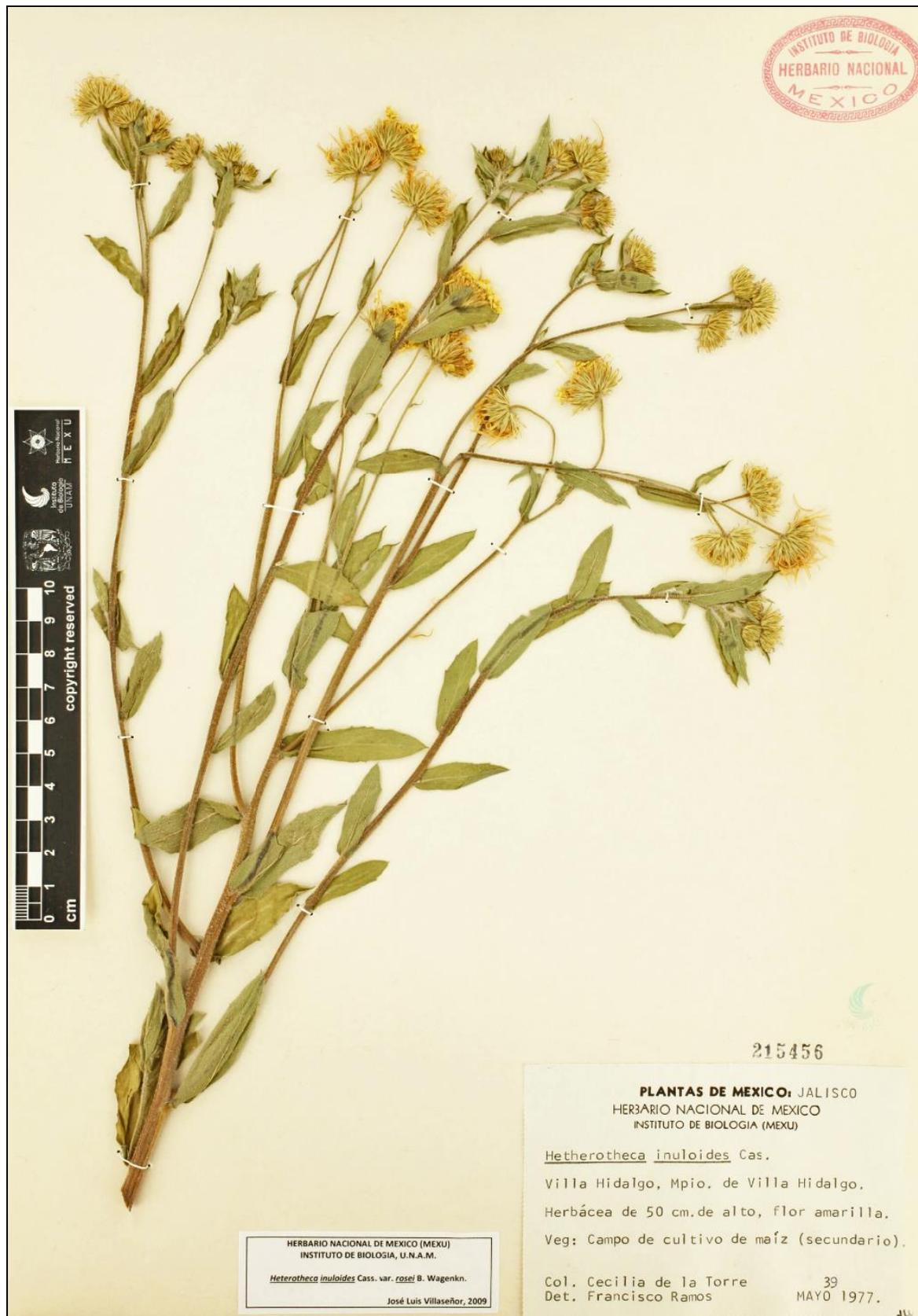
HERBARIO NACIONAL DE MEXICO (MEXU)  
INSTITUTO DE BIOLOGIA, U.N.A.M.  
*Heterotheca inuloides* Cass. var. *rosei* B. Wagenkn.  
José Luis Villaseñor, 2009

0 1 2 3 4 5 6 7 8 9 10  
cm  
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671449

HERBARIO DE LA UNIVERSIDAD DE GUADALAJARA  
INSTITUTO DE BOTANICA-JALISCO, MEXICO  
PLANTAS MEXICANAS  
Fam.  
*Heterotheca inuloides* Cass. var. *rosei* Wagenknecht  
COMPOSITAE  
LOC: Transecto entre El Rancho y el Arroyo Caliente, Bosque  
Escuela, La Primavera, Mpio. de Tala.  
HAB: Cañada húmeda en Bosque de Pino y Encino.  
EDU: JALISCO  
FECHA: 13 de Agosto de 1989 ALTITUD: 1450 m.  
OBS: hierba frecuente de 80 cm., lígulas y flores amaril-  
lilas.  
COL: AARON RODRIGUEZ C. & J.G. REYNOSO D.  
No. 1421  
DET: AARON RODRIGUEZ C.

Figure 25. *Heterotheca rosei*, Jalisco.

Figure 26. *Heterotheca rosei*, Jalisco.

- 6. HETEROTHECA LEPTOGLOSSA** DC., Prodr. 5: 317. 1836. *Heterotheca inuloides* var. *leptoglossa* (DC.) Cook & Semple, Botany (Ottawa) 86: 892. 2008. **LECTOTYPE** (Semple 2008, p. 892): **MEXICO. Guanajuato.** Mexique (Leon à l'ouest de Guanajuato), 1827, *J. Mendez s.n.* (G-DC G00455695 digital image!; isolectotypes: G-DC G00455696 digital image!, GH digital image!). Protologue: "in Mexico prov. Leonina ad occid. urbis Guanaxuato legit cl. Mendez."

Annual to biennial or short-lived perennial, from a slender, woody taproot; phyllaries (outer series) completely glabrous to strigose along the distal midregion with appressed to ascending-appressed, fine and relatively thin-based, non-glandular hairs, eglandular or the non-glandular hairs mixed with sparse sessile glands distally or the glands short-stipitate near the phyllary apex, usually purple at the very apex, phyllaries not keeled.  $2n = 18$ .

McVaugh (1984) included *Heterotheca leptoglossa* within his concept of *H. inuloides* var. *rosei*, but *H. leptoglossa* appears to be isolated from both *H. rosei* and typical *H. inuloides*. There is no unambiguous evidence of intergradation between *H. leptoglossa* and *H. inuloides* where their ranges are contiguous or slightly sympatric. *Heterotheca leptoglossa* and *H. rosei* are sympatric in Aguascalientes, Zacatecas, and northern Jalisco apparently without significant intergradation.

*Heterotheca rosei* differs from *H. leptoglossa* in its less strongly woody taproots (and presumably shorter duration) and in its phyllaries densely glandular with long, thick-stiped glands and without purple-tips. The non-glandular hairs of *H. rosei* (if present) are usually erect or ascending, in contrast to the appressed ones of *H. leptoglossa*.

- 7. HETEROTHECA INULOIDES** Cass., Dict. Sci. Nat. 51: 460. 1827. **TYPE: MEXICO.** No other data (probable holotype: FI, Herb. Webbianum ex Herb. Desfontaines, digital image!, photo-GH!).

"According to Cassini, this plant [the probable holotype] was said by Desfontaines to have originated in Mexico, sent by de Candolle from Geneva to the Jardin du Roi (presumably in Paris). The sheet at FI was annotated in Cassini's hand as 'Heterotheca inuloides, H. Cass.' There is in G-DC (fiche!) a very similar specimen noted as from 'J. de Paris 1828' that is possibly a duplicate of the type" (Nesom 1990).

Perennial; outer phyllaries densely stipitate-glandular in understory with thick, multicellular hairs, sparsely to moderately or densely villous-hirsute to hispid-pilose in overstory from base to tip with spreading to spreading-ascending, glassy, thick-based, non-glandular hairs.

- 8. HETEROTHECA VIRIDIS** (Nesom) Nesom, **comb. et stat. nov.** *Heterotheca inuloides* var. *viridis* Nesom, Phytologia 69: 286. 1990. **TYPE: MEXICO. Oaxaca.** Distr. del Centro, Monte Alban, 1850 m, 14 Oct 1832, *C. Conzatti 4794* (holotype: LL!; isotype: MEXU).

Short-lived perennial from a thick woody taproot; phyllaries usually without purple coloration, moderately to densely villous along whole length with long, whitish, thin-based, non-glandular trichomes, surface minutely glandular, inner phyllaries often prominently keeled. Apparent intermediates between *Heterotheca viridis* and typical *H. inuloides* occur in northern Puebla and along the adjacent border with Veracruz where they are sympatric, but the zone of contact is narrow and intermediates are relatively few, in contrast to the much broader ranges where *H. inuloides* and *H. viridis* are distinct and consistent in morphology. Villarreal and Estrada (2016) mapped only *H. viridis* for Veracruz.



Figure 27. *Heterotheca viridis*, Oaxaca, Kitchen 31 (ASU). Characteristic white-villous vestiture of involucre and peduncles.

**HETEROTHECA SECT. AMMODIA** (Nutt.) Harms, *Castanea* 39: 159. 1974. *Ammodia* Nutt., *Trans. Amer. Philos. Soc. n.s.* 7: 321. 1840. *Chrysopsis* sect. *Ammodia* (Nutt.) A. Gray, *Proc. Amer. Acad. Arts* 6: 543. 1866. **TYPE:** *Ammodia oregona* Nutt. = *Heterotheca oregona* (Nutt.) Shinnars.

Sect. *Ammodia* is characterized by a lack of ray flowers and an outer pappus of a few, very fine bristles 0.1–0.5 mm long (outer pappus in other sections is of relatively thick bristles or flattened scales, at least some of which are longer than 1 mm). All plants are perennial. The group is endemic to the Pacific coast region, occurring only in Washington, Oregon, and California. Semple et al. (1988) reported a diploid chromosome count for each of the four entities they recognized.

These taxa have generally been treated as varieties within a single species, beginning with Gray (1884), to Jepson (1901), Ferris (1960), Keck (1953), Munz and Keck (1959), and California treatments by Semple (1993 and subsequent). *Chrysopsis rudis* was described at specific rank by Greene (1894); it was treated at varietal rank without comment by Jepson (1901). Keck described var. *compacta* without any comment regarding its variability or interaction with other taxa.

Munz and Keck (1959) noted that the varieties "intergrade" but earlier botanists and contemporaries (e.g., Gray 1884; Jepson 1901; Ferris 1960) made no mention of their variability, nor can I find any such comment in regional California floras. Semple et al. (1988, p. 550, 551) observed that "Putative hybrids between pairs of the four varieties have been collected occasionally where sympatric. ... Intermediates collected represent about 10% of all herbarium specimens of the species

studied: 12 var. *oregona* x var. *rudis*, 2 var. *oregona* x var. *compacta*, 9 var. *rudis* x var. *compacta*, 5 var. *scaberrima* x var. *rudis*, and 9 var. *oregona* x var. *scaberrima*." Intergradation was not mentioned in the FNANM treatment of *Heterotheca* (Semple 2006).

In a multivariate analysis of the *Heterotheca oregona* complex, Semple et al. (1988) observed that "All four groups [taxa] were significantly different from one another ( $\alpha = 0.005$ )." Plots of 1st versus 2nd canonical variates (their Fig. 1) and 1st versus 3rd canonical variates (their Fig. 2) unambiguously separate the four taxa, except in Fig. 2, where var. *scaberrima* and var. *compacta* overlap. Following Semple's general concept of varietal taxa (see introductory comments above), Semple et al. treated each of the four at varietal rank. "The varietal differences are thought to have evolved as a consequence of geographic isolation" but "the ranges of the four races overlap to a great extent" and "the sympatric races now hybridize."

In the taxonomic summary here, *Heterotheca oregona*, *H. rudis*, and *H. scaberrima* are treated at specific rank. Plants identified as var. *compacta* by Semple and others appear to intergrade completely within more typical *O. rudis* and are not distinct from it in geography (see caveat below regarding the type of var. *compacta*).

1. Heads mostly scattered at ends of relatively long branches; leaves closely ascending, midcauline mostly 8–16 mm x 2–4(–5) mm, scabrous with only the multicellular trichome bases or hispid to hirsute or strigose-hirsute, rarely without eglandular hairs ..... **Heterotheca scaberrima**
1. Heads in a loose corymboid cluster; leaves spreading to loosely ascending, midcauline (8–)15–30(–35) mm x 3–10 mm, vestiture various.
2. Leaves completely without eglandular hairs, otherwise glandular to eglandular; stems minutely glandular, usually without eglandular hairs ..... **Heterotheca oregona**
2. Leaves sparsely hirsute to hirsute-villous or hirsute-strigose, eglandular to glandular; stems often minutely glandular, usually villous to villous-hirsute ..... **Heterotheca rudis**

**1. HETEROTHECA OREGONA** (Nutt.) Shinnery, Field & Lab. 29: 71. 1951. *Ammodia oregona* Nutt., Trans. Amer. Philos. Soc. n.s., 7: 321. 1840. *Chrysopsis oregona* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 6: 543. 1866. **LECTOTYPE** (Semple 1987, p. 381): **USA. Oregon.** "Gravel bars of the Columbia & other tributaries," 1834, *T. Nuttall s.n.* (BM digital image!; isolectotypes: GH digital image!, PH!).

Semple et al. (1988) mapped the range of var. *oregona* as extending from northwestern Washington continuously southward to San Luis Obispo Co., California — almost completely sympatric in its California range with var. *rudis* (var. *oregona* extending further south in California than var. *rudis*). Semple's map shows var. *rudis* as restricted to California (except for a locality in Josephine Co., Oregon, possibly *Howell s.n.* [ORE] from near Waldo in 1887, or *Peirson 7012* [RSA] from the Rogue River gorge in 1926, both of which have vestiture that tends toward *H. rudis*). *Heterotheca oregona* is recognized here as a morphologically consistent entity of Washington and Oregon, occurring in California sporadically southward in a narrow extension immediately along the coast as far as Marin County and apparently sympatric with *O. rudis* in most of its California distribution. *Heterotheca rudis* is essentially restricted to California, its distribution northward ending abruptly in Humboldt and Siskiyou counties (or possibly to southwestern Oregon — all specimens from ORE, OSU, and WILLU in the Oregon Flora Project database from Josephine, Curry, and Douglas counties are identified as *H. oregona* with *H. oregona* var. *rudis* as a synonym). I have not seen a record of *H. rudis* from Del Norte Co. California, where *O. oregona* has been abundantly collected.

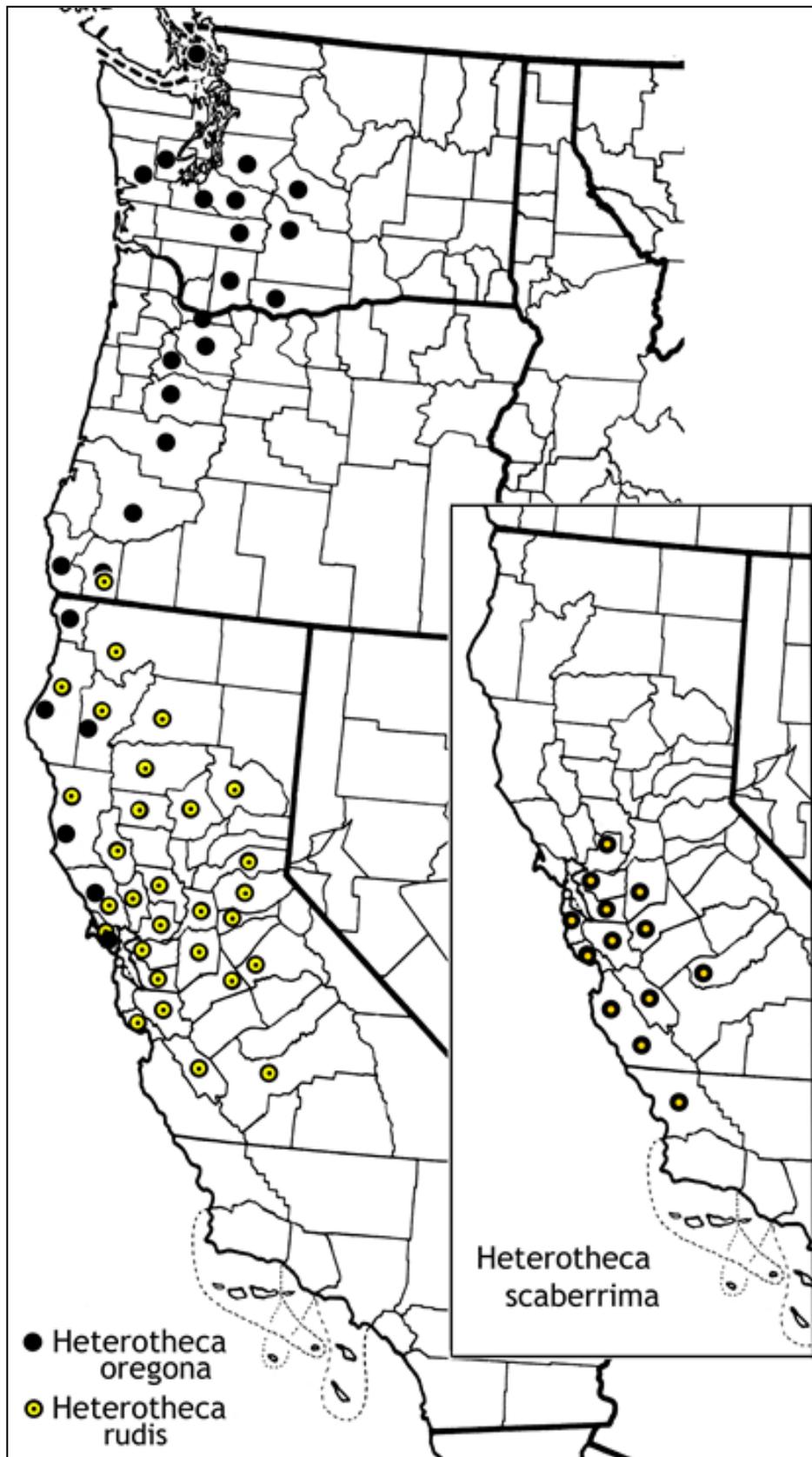


Figure 28. Distribution of *Heterotheca* sect. *Ammodia*: *H. oregona*, *H. rudis*, and *H. scaberrima*.



Figure 29. *Chrysopsis oregona* var. *compacta* holotype (identified here as *Heterotheca rudis*, see text).

**2. HETEROTHECA RUDIS** (Greene) Nesom, **comb. nov.** *Chrysopsis rudis* Greene, Man. Bay Reg., 174. 1894. *Chrysopsis oregona* var. *rudis* (Greene) Jepson, Fl. W. Mid. Calif., 558. 1901. *Heterotheca oregona* var. *rudis* (Greene) Semple, Brittonia 39: 382. 1987. **LECTOTYPE** (Semple 1987): **USA. California.** [Napa Co.]: Calistoga, 29 Aug 1888, *E.L. Greene s.n.* (NDG 53935 digital image!).

*Chrysopsis oregona* var. *compacta* Keck, Aliso 4: 102. 1953. *Heterotheca oregona* var. *compacta* (Keck) Semple, Brittonia 39: 382. 1987. **TYPE: USA. California.** Glenn Co.: Plentiful in dry gravelly stream bed near Newville, *Quercus douglasii* belt, 15 Oct 1922, *A.A. Heller 13736* (holotype: NY digital image!; isotypes: DS digital image!, MO digital image!, US digital image!, WTU!).

*Heterotheca rudis* characteristically has hairy (non-glandular) stems and leaves, and leaf size is more variable than in typical *H. oregona*. Most of the variability previously attributed to hybridization in the *H. oregona* complex instead appears to be infraspecific variation within *H. rudis*. The distinction between *H. rudis* and typical *H. oregona* is primarily in vestiture, but the discontinuity appears to be sharply delimited.

In 1988 (p. 556), Semple et al. observed that var. *compacta* is smaller in stature and has a relatively narrow capitulescence and smaller heads than the other taxa of sect. *Ammodia*. The type collection of var. *compacta* is a small plant and with relatively small leaves with densely strigose-villous to villous-hirsute vestiture (Fig. 5), but, as interpreted here, it appears to represent an extreme variant. In the present view, *compacta*-like variants intergrade with *Heterotheca rudis* sensu stricto in habit, leaf and inflorescence morphology, and vestiture. Semple et al. (1988) mapped var. *compacta*

and var. *compacta*-like variants as sympatric and almost perfectly congruent in geography with var. *rudis*. On the other hand, the striking appearance of the *H. compacta* type and the collector's description of it as "plentiful" suggests that the type locality should be reinvestigated, especially since serpentine is common in the Newville area.

**3. HETEROTHECA SCABERRIMA** (A. Gray) Nesom, **comb. et stat. nov.** *Chrysopsis oregona* var. *scaberrima* A. Gray, Synopt. Fl. N. Amer. 1(2): 124. 1884. *Heterotheca oregona* var. *scaberrima* (A. Gray) Semple, Brittonia 39: 383. 1987. **TYPE: USA. California.** Tulare Co.: Dry creek, Soledad, [no date], J.W. Congdon *s.n.* (holotype: GH digital image!).

*Heterotheca scaberrima* is distinct in morphology and has a relatively narrow geographical range, largely sympatric with *H. rudis* — few if any intermediates apparently are formed where the two occur together. *Heterotheca scaberrima* is treated here at specific rank, distinguished in the key above and as emphasized in the following comments by Semple et al. (1988, p. 557): "Variety *scaberrima* is the most distinctive of the species. The combination of small, coarsely scabrous, densely glandular leaves ... and densely glandular involucre with small outer phyllaries ... give the plants a readily recognizable appearance. The branches tend to be longer on average and the capitulescence is thus rather large and open compared to undamaged plants of the other varieties. Damage to the terminal meristem or procumbent orientation will result in elongation of the branches in all varieties giving a general appearance like undamaged plants of var. *scaberrima*. The leaves of secondary and tertiary branches are reduced in the species."