

**TAXONOMIC REVISION OF *HETEROTHECA* (ASTERACEAE: ASTEREA):  
SECT. *PHYLLOTHECA***

**GUY L. NESOM**

Research Associate

Academy of Natural Sciences of Drexel University

Philadelphia, Pennsylvania

guynesom@sbcglobal.net

**ABSTRACT**

A taxonomic revision of the primarily Californian *Heterotheca* sect. *Phyllothea* recognizes 10 species, including two new ones and several with modified circumscriptions and nomenclature. ***Heterotheca sandersii*** Nesom, **sp. nov.**, is endemic to a small region of Los Angeles and San Bernardino counties, along the western and southwestern base of the Santa Susana, San Gabriel, and San Bernardino Mountains. ***Heterotheca sanctarum*** Nesom, **sp. nov.**, is a tetraploid species endemic to Santa Clara, Santa Cruz, San Benito, San Mateo, Contra Costa, and Solano counties — for the most part, it was identified by Semple (1996) within his concept of *H. bolanderi* var. *bolanderioides*. ***Heterotheca arenaria*** (Elmer) Nesom, **comb. nov.**, has been identified as *H. bolanderi* but is a distinctive coastal strand endemic from Marin Co. northward to Humboldt Co.; *H. bolanderi* sensu stricto is endemic to the hills of Alameda, Contra Costa, Marin, San Mateo, Santa Cruz, and southern Sonoma counties. ***Heterotheca* [*Hectorea*] *villosissima*** (DC.) Nesom, **comb. nov.**, validates an earlier name for *H. echioides*. *Heterotheca sessiliflora* Nutt. comprises coastal strand populations from northern Baja California and southern San Diego Co., but the type collection was made in Santa Barbara Co. and the species is not currently known in the intervening area. *Heterotheca camphorata*, *H. fastigiata* (without varieties), *H. monarchensis*, and *H. thiniicola* are recognized with justification from morphology and geography.

The taxonomy of sect. *Phyllothea* follows earlier treatments for sect. *Heterotheca* and *Ammodia* (Phytoneuron 2019-64: 1–44) and sect. *Chrysanthe* (Phytoneuron 2020-68: 1–359). An introduction to the genus and Literature Cited are provided in the first.

***HETEROTHECA* SECT. *PHYLLOTHECA*** (Nutt.) Harms, Castanea 39: 158. 1974. *Chrysopsis* subg. *Phyllothea* Nutt., Trans. Amer. Philos. Soc. n.s., 7: 315. 1840. **TYPE:** *Chrysopsis sessiliflora* Nutt. = *Heterotheca sessiliflora* (Nutt.) Shinnars.

*Hectorea* DC., Prodr. 5: 95. 1836. **TYPE:** *Hectorea villosissima* DC. (*Heterotheca villosissima* (DC.) Nesom). See comments regarding *H. bolanderi* and *H. bolanderioides*.

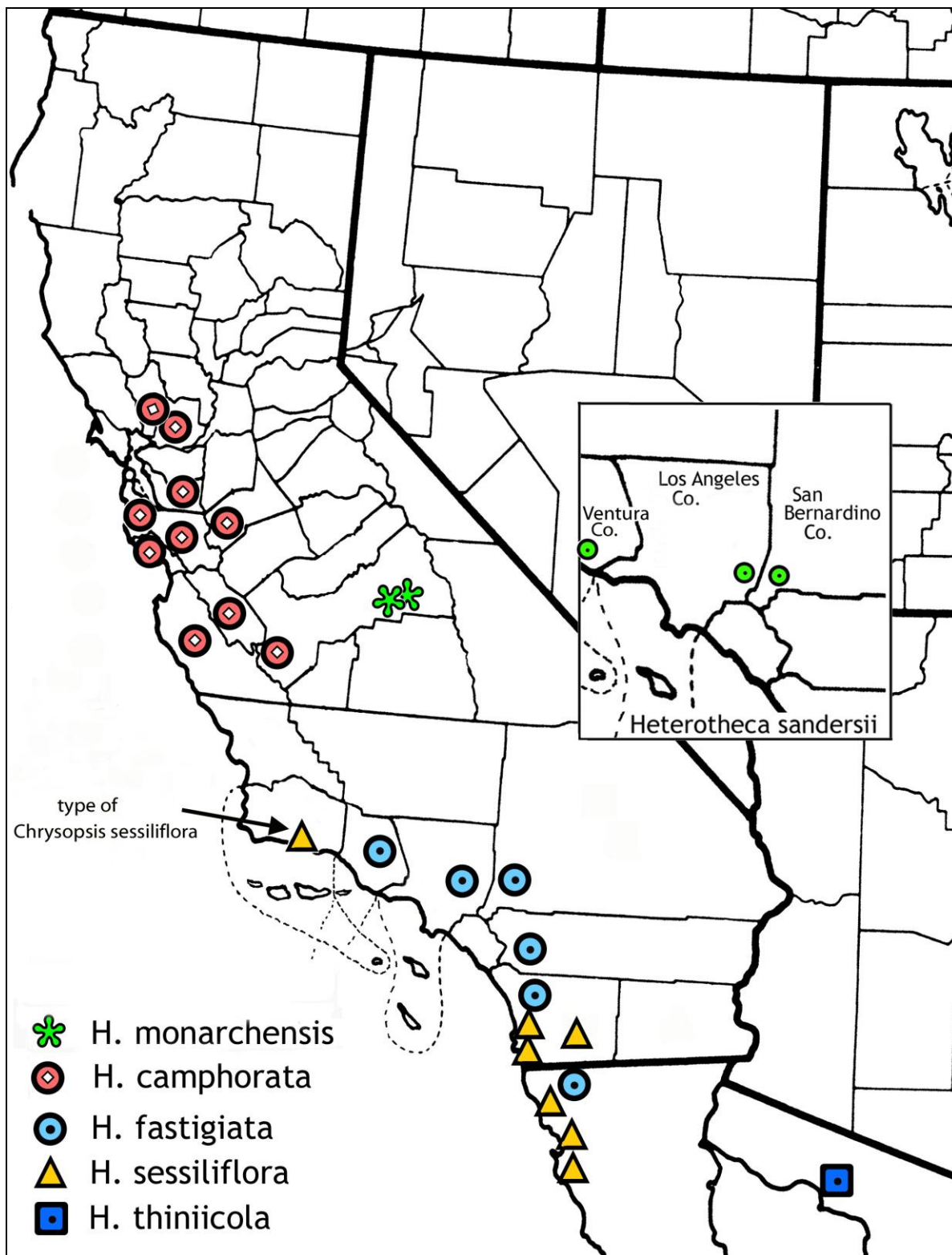
Plants of sect. *Phyllothea* are distinct in their disc corollas with lobes and often tubes prominently hairy with antrorsely oriented, filiform, multicellular-uniseriate hairs 0.5–2.0 mm long. Variation exists within species and the corolla hairs sometimes are reduced in density or essentially absent. These plants comprise a geographically coherent group of taxa restricted to coastal and near-coastal regions along the Pacific Ocean from Baja California north into central California, with one outlier (*H. thiniicola*) in northwestern Sonora and one (*H. monarchensis*) in the California Sierra. Sect. *Phyllothea* reasonably might include the species of sect. *Chrysanthe*, which is without clearly defined subgroups. Sects. *Heterotheca* and *Ammodia* each are strongly differentiated.

Apparently there has been little until studies by John Semple toward an explicit rationale for considering the entities of sect. *Phyllothea* as conspecific — original descriptions of most entities have been at specific rank. Gray (1884) treated the whole group as "var. *sessiliflora*" within a broadly encompassing concept of *Chrysopsis villosa* — along with all plants/taxa now treated as sect. *Chrysanthe* (i.e., Gray's *Chrysopsis villosa* vars. *canescens*, *echioides*, *foliosa*, *hispidia*, *rutteri*,

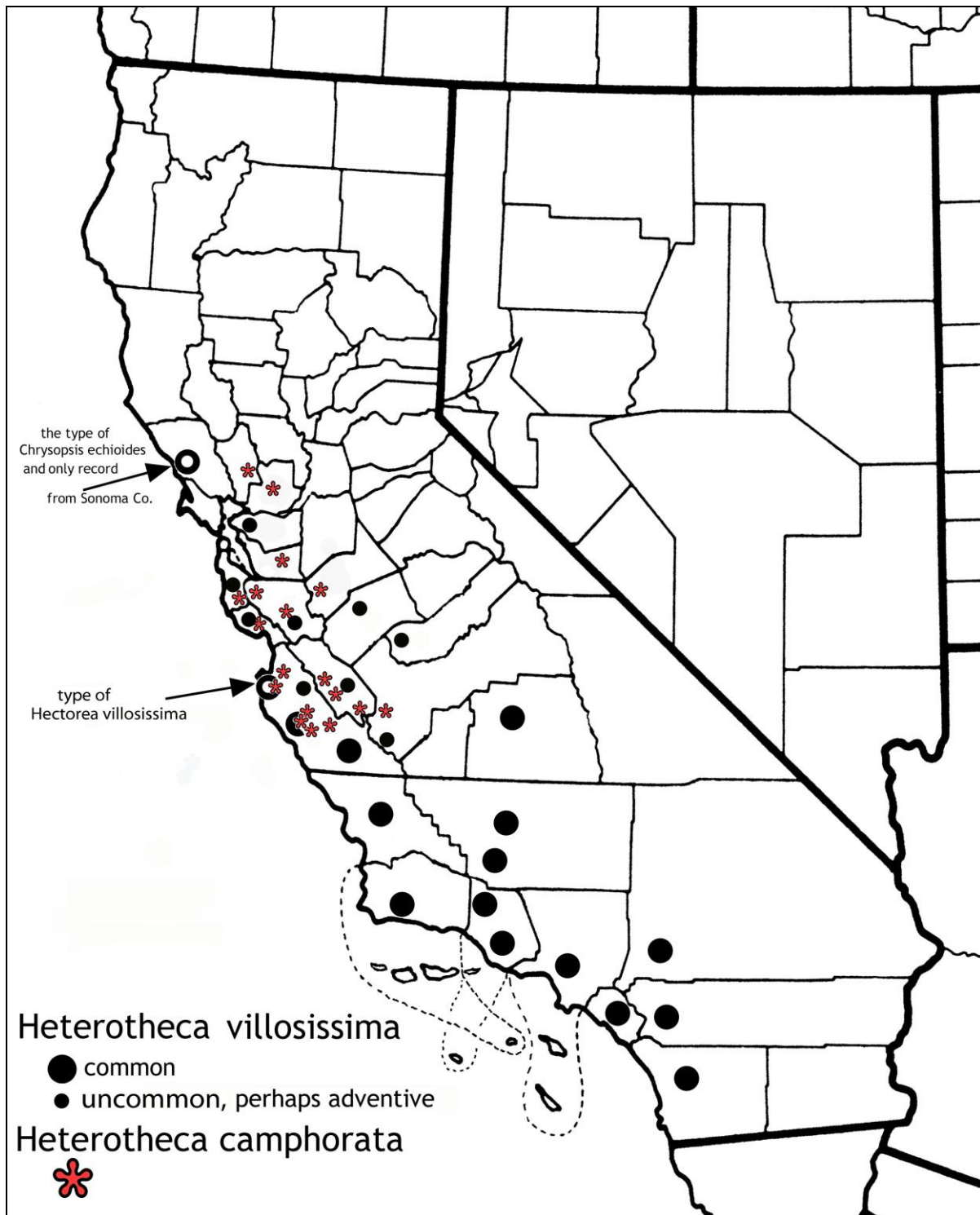
*stenophylla*, and *viscida*). Hall (1907) and other California botanists followed this course, with caveats: Howell et al. (1958), followed by Harms (1974), treated *Chrysopsis bolanderi* at specific rank; Shinnars (1951) recognized *H. echioides* and *H. sessiliflora*; Harms (1974) recognized *H. fastigiata*; Semple (1980) segregated *H. camphorata*. Semple (1992, 2001) consolidated nearly the whole group within the single species *Heterotheca sessiliflora*, keeping at specific rank the more recently described narrow endemics *H. thiniicola* and *H. monarchensis*. Semple's rationale appears to have been substantially based on his working concept of the varietal rank (i.e., treat entities as conspecific varieties if morphologically similar and sympatric). And in 2008 (p. 895) he noted that var. *echioides* functions within his *H. sessiliflora* as a "matrix" taxon by connecting, through hybridization, the entire complex into a single polymorphic species ... ."

Semple (1992, 1996) treated *Heterotheca sessiliflora* as comprising subspecies and varieties. *Hectorea villosissima* DC. (1836), however, proves to be the oldest name in sect. *Phyllotheca* and the system of infraspecific ranks set up by Semple within *Heterotheca sessiliflora* Benth. [1840] no longer can be considered correct, even if regarded as biologically appropriate. Semple (1996) cited *Hectorea* DC. as a synonym of *Heterotheca* Cass. but he apparently did not determine the identity of *Hectorea villosissima* (at least he did not cite the species name as a synonym of any other) or consider its nomenclatural significance.

Morphology and geography are interpreted here as supporting recognition of ten species, mostly resolving the biological dissonance of recognizing sympatric conspecific taxa. Morphological criteria for identifying these taxa are generally similar to those in Semple (1996) and other treatments, as discussed below. Nomenclature is significantly modified from previous taxonomy. As with the sect. *Chrysanthe* revision, identifications can be made using maps, illustrations, descriptions, and commentary; key couplets are provided to contrast species pairs, especially those that occur sympatrically.

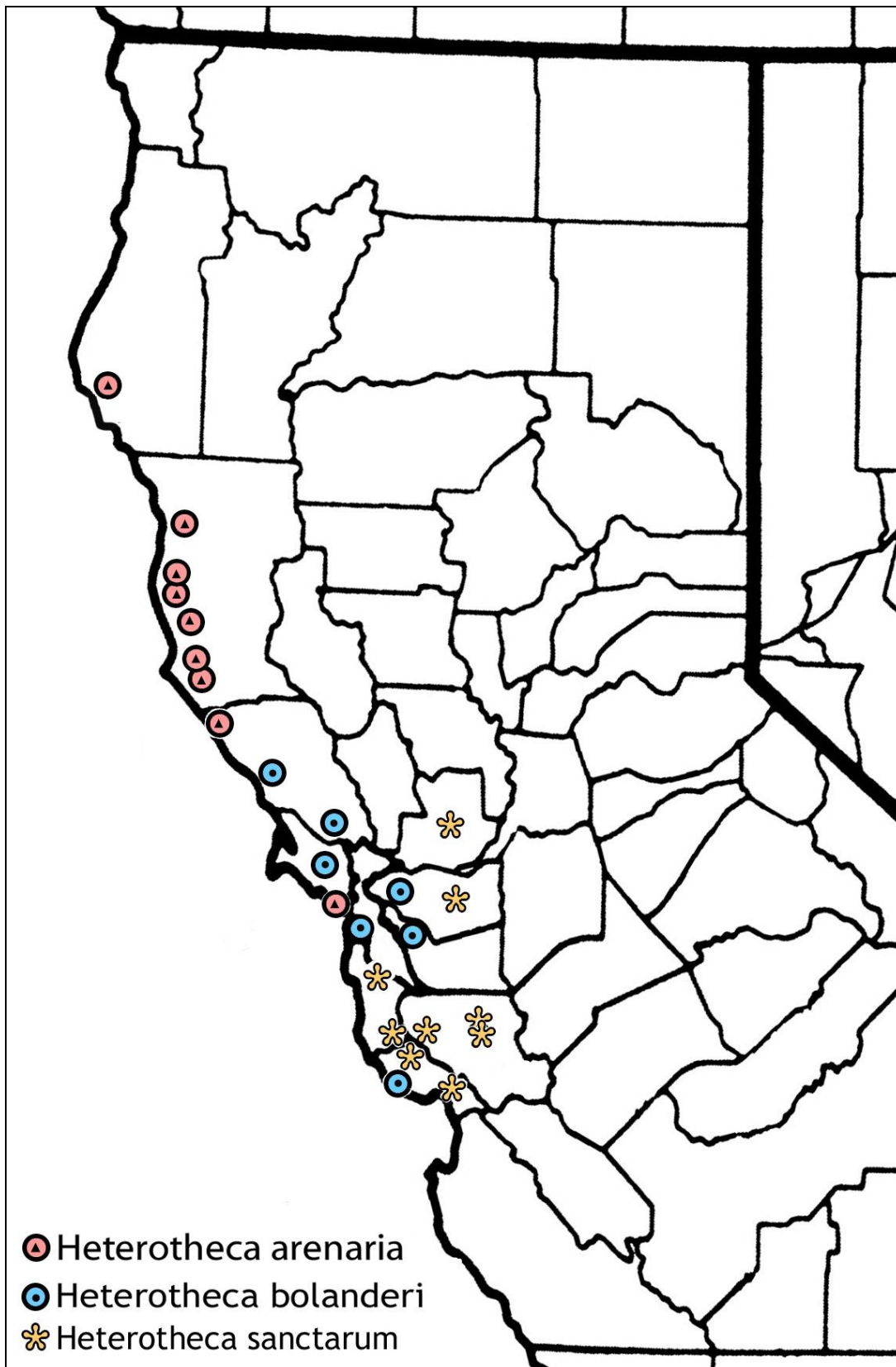


Map 1. Distribution of sect. *Phyllothea* species. See Figure 22 for details of the *H. sandersii* distribution.



Map 2. Distribution of *Heterotheca villosissima* and *H. camphorata*.





Map 3. Distribution of *Heterotheca bolanderi* and *H. sanctarum*. See Figure 53 for details of the *H. sanctarum* distribution.

1. **HETEROTHECA MONARCHENSIS** York, Shevock, & Semple in Semple, Rev. *Heterotheca Phyllotheca* 52, fig. 20. 1996. **TYPE: California.** Fresno Co.: Ca. 86 km E of Fresno, Sequoia National Forest, Monarch Wilderness, 2000 m NW of Boyden Cave on N side of Kings River canyon, rocky outcrops, 1800 m, 31 Jul 1995, *D.A. York & J.R. Shevock 109* (holotype: CAS; isotypes: FSC, JEPS, MO, RSA, US, WAT). Type distribution as cited by Semple (1996), neither specimens nor images seen during the present study.

*Heterotheca monarchensis* is known only from the Monarch Wilderness of Sequoia National Forest in Fresno County, where it occurs on limestone outcrops at about 6000 feet. It is distinct in its small stature (less than 20 cm tall), rhizomatous and mat-forming habit, densely villous-sericeous vestiture giving the plants a silvery green aspect, small, densely overlapping, oblanceolate cauline leaves with broadly undulate margins, and numerous, narrow capitular bracts. Semple (1996) placed it among the species of sect. *Phyllotheca* because of long hairs on the disc corolla lobes and presumably because of its locality in southern California. Leaf morphology has similarities with *H. fastigiata* and *H. villosissima*. Collection images and habit and habitat photos are available (see John Semple's 'Astereae Lab' web page and the USDA Forest Service web page) for the species.



Figure 1. *Heterotheca monarchensis*. Fresno Co. Photo by Dana York, 19 May 1996, from CalPhotos.

2. **HETEROTHECA THINIICOLA** (Rzed. & Ezc.) B.L. Turner, *Phytologia* 63: 128. 1987. *Haplopappus thiniicola* Rzed. & Ezc., *Cienc. Interamer.* 26: 16. 1986. *Heterotheca sessiliflora* var. *thiniicola* (Rzed. & Ezc.) Nesom, *Phytologia* 83: 17. 1997. **TYPE: MEXICO. Sonora.** Mpio. Puerto Penasco, Gran Desierto de Alta, 8 km NE de la Estacion Gustavo Sotelo, 17 Dec 1984, C. Ezcurra 84001 (holotype: MEXU; isotype: TEX!).

*Heterotheca thiniicola* is similar to *H. fasciculata* in its small, silver-sericeous leaves with wavy margins. Earlier I joined it at varietal rank with *H. sessiliflora* (Nesom 1997) toward consistency with Semple's inclusive taxonomy structure, but the long-disjunct geography of *H. thiniicola* (separated from closest *H. fasciculata* by about 200 miles) and its arid habitat and shrubby habit support its recognition at specific rank, especially in view of the overall taxonomic structure of sect. *Phyllotheca* outlined here.



Figure 2. *Heterotheca thiniicola*. Sonora, Felger 88-227 (DES).

3. **HETEROTHECA FASTIGIATA** (Greene) Harms, *Brittonia* 26: 61. 1974. *Chrysopsis fastigiata* Greene, *Pittonia* 3: 296. 1898. *Chrysopsis villosa* var. *fastigiata* (Greene) H.M. Hall, *Univ. Calif. Publ. Bot.* 3: 43. 1907. *Heterotheca sessiliflora* subsp. *fastigiata* (Greene) Semple, *Phytologia* 73: 451. 1992. *Heterotheca sessiliflora* var. *fastigiata* (Greene) Semple, *Rhodora* 103: 203. 2001. **TYPE: California.** [San Bernardino Co.]: San Bernadino Mts, 1000-1500 ft, 15 Oct 1895, *S.B. Parish 3815* (possible holotype: NDG 53796 image; isotypes: CAS image, GH image, UC not seen, US 652178-Fig. 3, US-2 sheets-Fig. 4).

Semple (1996) cited the NDG specimen as holotype — it has no annotation by Greene but is the only sheet in NDG that fits the protologue.

*Heterotheca sessiliflora* [subsp. *fastigiata*] var. *sanjacintensis* Semple, *Phytologia* 73: 452. 1992.

**TYPE: California.** Riverside Co.: Calif. Hwy 243 just S of Idyllwild Park at Manzanita Drive, 30 Sep 1987, *J.C. Semple 8982* (holotype: WAT; isotypes: CAS-Figs. 5 and 6, NY image, UC!). Semple (1996) also cited isotypes at MT and RSA. *Semple 8981* (OBI), from essentially the same locality, IDed by Semple as var. *sanjacintensis*, 2n = 9II.

*Heterotheca fastigiata* occurs in northern Baja California (Mpio. Tecate — e.g., Las Juntas, 1887, *Orcutt 9*, MO) and five California counties (San Diego, Riverside, San Bernadino, Los Angeles, Ventura). The plants are characterized by (a) small (5–20 mm long), relatively even-sized, densely overlapping and closely ascending to erect, silvery-sericeous, eglandular cauline leaves with undulate margins, truncate and often subclasping base, and appressed-strigose surfaces and (b) numerous small heads, without closely subtending capitular bracts, on bracteate peduncles (5–15(–30) mm long) in a paniculiform to loosely corymbiform arrangement. Stems are eglandular and puberulent to antrorsely short-strigose, often with a sparse overstory of long, villous hairs. All chromosome count vouchers seen are for diploids: Los Angeles Co.: *Semple 5592*, *Semple & Heard 8629*; Riverside Co.: *Semple & Chmielewski 8981*; San Bernadino Co.: *Semple & Heard 8632*, 8978. Flowering May through November.

Var. *sanjacintensis* as mapped by Semple is nearly congruent in geography with typical *Heterotheca fastigiata* and the specimens he annotated as var. *sanjacintensis* are heterogeneous in morphology. Semple noted that it has leaves "far less densely strigose" ... with "somewhat longer hairs," "the leaves are not nearly as densely pubescent and are more glandular giving them a light green appearance," and in the diagnosis it was compared to typical *E. fastigiata* — geography and apparent continuous variation in density of vestiture suggest that this is populational variation. Analogous variation exists in *H. villosissima* and even the type collection of *H. fastigiata* shows variation in density of vestiture (compare Figs. 3, 4, 5, and 6).

Hybrids are formed between *Heterotheca fastigiata* and *H. villosissima* (pers. observ. and see comment by Semple, 1996, p. 44) where they are sympatric. Much of this may correspond with the elimination of natural habitats and the widespread creation of hybrid ones.

1. Stems usually branching distally above a long, unbranched section, inflorescence usually compact; leaves small, densely overlapping, erect and appressed against the stem, margins wavy, eciliate or weakly so proximally, surfaces silvery- to gray-sericeous with closely set hairs; heads without capitular bracts; ray ligules mostly 3.5–6 mm long ..... **Heterotheca fastigiata**

1. Stems usually branching from midstem to distally, inflorescence looser and more elongate; leaves larger, slightly overlapping, usually distinctly spreading, margins wavy or not, long-ciliate proximally, surfaces greenish with reduced vestiture to loosely silvery-sericeous with denser vestiture; heads usually with short capitular bracts, sometimes without; ray ligules mostly 5.5–10 mm long ..... **Heterotheca villosissima**





Figure 3. *Heterotheca fastigiata*. Isotype (US 652178) of *Chrysopsis fastigiata*.

Specimen data entered  
By: J. J. W. [unclear]  
TYPE REGISTRY



ISOTYPE: *Chrysopsis fastigiata* Greene, *Pitcairnia* 3: 296, 1898.  
*Chrysopsis villosa* (Greene) H.M. Hall, Univ. Calif.  
 Publ. 3: 43, 1907. *Heterotheca fastigiata* (Greene) Harms,  
*Pitcairnia* 26: 61, 1924. *Heterotheca sessiliflora* (Nutt.) Shimmers sp.  
*fastigiata* (Greene) Semple, *Phytologia* 73: 451, 1992. TYPE: U.S.A.  
 California, San Bernardino Mts., 1000-1500' foot 10000-15000 as in  
 protologue, 15 Oct 1895, Parish 3815 (Holotype: NDG; isotypes:  
 CASI, GHI, UCI, USI)  
 = *Heterotheca sessiliflora* (Nutt.) Shimmers ssp. *fastigiata* (Reuth.)  
 Semple var. *fastigiata*  
 John C. Semple  
 19 May 1995  
 University of Waterloo, WAT

Isotype: *Chrysopsis fastigiata* Greene  
 = *Heterotheca fastigiata* (Greene) Harms  
 John C. Semple July 1995  
 Herbarium University of Waterloo

STUDIES IN CHRYSOPSIS  
*Chrysopsis fastigiata* Greene  
 ISOTYPE  
 William J. Dress  
 BALEY HERBARIUM  
 Sept. 26, 1965



PLANTS OF SOUTHERN CALIFORNIA.  
 SAN BERNARDINO CO.  
*Chrysopsis villosa*  
 var. *schoides* Gray  
 Vicinity of San Bernardino, alt. 1000-1500 ft.  
 No. 3815 Coll. S. B. PARISH, 15 Oct. 1895.

PRESENTED IN 1917 BY  
 MRS. GEORGE W. VANDERBILT

*C. fastigiata* Greene - type coll.

BILTMORE HERBARIUM.

*C. schoides* Parish.





Figure 4. *Heterotheca fastigiata*. Isotype (US 1682282) of *Chrysopsis fastigiata*.





Figure 5. *Heterotheca fastigiata*. Isotype of *H. sessiliflora* var. *sanjacintensis* (CAS).



Figure 6. *Heterotheca fastigiata*. Detail from isotype (NY) of *Heterotheca sessiliflora* var. *sanjacintensis*.



Figure 7. *Heterotheca fastigiata*. Ventura Co., Pollard s.n. (NO).





Figure 8. *Heterotheca fastigiata*. San Bernardino Co., *Semple & Heard* 8632 (GA).

4. **HETEROTHECA VILLOSISSIMA** (DC.) Nesom, **comb. nov.** *Hectorea villosissima* DC., Prodr. 5: 95. 1836. **TYPE: Protologue:** [MEXICO. Hidalgo]. "Prope Real del Monte legit cl. Haenke" but see comments below. **Probably: USA. California.** Monterey Co.: Vicinity of Monterey, 1793, *T. Haenke s.n.* (holotype: G-DC, Fig. 9).

Thaddäus Haenke was Naturalist-Botanist of the Malaspina Expedition of 1790-1793, which explored South America to Central America, California (the Monterey area), and Alaska and westward to the southwestern Pacific region (see Wikipedia for T. Haenke and the Malaspina Expedition). The type specimen of *Hectorea villosissima* clearly is a *Heterotheca* but there is no species like it in Hidalgo, Mexico, where the protologue indicates the collection was made, or even anywhere in Mexico. Instead, it is a plant of the species previously identified as *Heterotheca echioides*, which does occur in the area of Monterey, California, where the Malaspina Expedition stopped in 1793 (Monterey was its only stopping place in California). A packet affixed to the G-DC specimen notes "Mexiq. Haenke" but this and the protologue surely do not describe the actual collection locality. De Candolle's protologue description fits the Haenke specimen, and Asa Gray annotated the *Hectorea villosissima* type in 1887 as *Heterotheca echioides*.

- Chrysopsis echioides* Benth., Bot. Voy. Sulphur, 25. 1844. *Chrysopsis villosa* var. *echioides* (Benth.) A. Gray, Synopt. Fl. N. Amer. 23(1): 123. 1884. *Heterotheca echioides* (Benth.) Shinnery, Field & Lab. 19: 71. 1951. *Heterotheca sessiliflora* subsp. *echioides* (Shinnery) Semple, Phytologia 73: 450. 1992. *Heterotheca sessiliflora* var. *echioides* (Benth.) Semple, Rhodora 103: 203. 2001. **TYPE: California.** [Sonoma Co.]: Bodegas, 1841, *R.B. Hinds s.n.* (holotype: K-Fig. 10, fragment US! and specimen photo US!-mounted on the sheet with the fragment). Hinds was at Bodega Bay in Sep 1839, fide Raven (1964).

The type collection of *Heterotheca echioides* ("Bodegas," presumably Bodega Bay in Sonoma Co.; Map 2) was made north of the known range of the species (= *H. villosissima*). Only two specimens identified as *H. echioides* (or var. *echioides*, subsp. *echioides*) from Sonoma County have been included in the California Consortium database (as seen in 2015, 2016) — *Howell 5342*, 13 Jul 1930 (POM); *Rubtzoff 8329*, 16 Aug 1975 (CAS) — both collections, however, are correctly identified as *H. bolanderi* (pers. observ.). The only locality of *H. echioides* mapped by Semple (1996) in Sonoma County is Bodega Bay, presumably representing the type, as he cited no other collection from Sonoma County. The only species of sect. *Phyllotheca* currently known in Sonoma County are *H. arenaria* and *H. bolanderi*, and the Hinds collection is distinctly different from both species.

- Chrysopsis californica* Elmer, Bot. Gaz. 39: 48. 1905. **TYPE: California.** Santa Barbara Co.: Gaviota, [protologue: "sandy soil near beach"], May 1902, *A.D.E. Elmer 4148* (holotype: DS!; isotypes: MIN image, MO!, US-Fig. 13). The type is a silvery-sericeous plant with small capitular bracts — very similar in aspect to the type of *Hectorea villosissima*.

Leaves of *Heterotheca villosissima* sometimes are gray to silvery in aspect (like *H. fastigiata*) with densely villous to pilose-villous vestiture, but more characteristic vestiture is less dense and the surfaces more greenish, sometimes hirsute; proximal margins are long-ciliate; base usually narrowed, attenuate to rounded and usually subclasping. Stems eglandular and hirsute-pilose to hirsute-villous with thin, spreading to slightly deflexed hairs; phyllaries are glandular and villous with fine hairs. Cauline leaves usually are not densely overlapping and axillary tufts of small leaves are characteristic, these often lengthening into lateral branches. Capitular bracts usually are present, commonly about 1/3–1/2 the involucre length; they sometimes are absent or even more reduced in size, perhaps reflecting gene flow from *H. fastigiata* (where sympatric). Numerous chromosome counts by Semple (fide label data) document only diploids in *H. villosissima* — from Kern, Fresno, Monterey, San Bernardino, San Luis Obispo, Santa Barbara, and Ventura counties.

A collection from southern Oregon, far out of range and perhaps a waif, is tentatively identified here as *Heterotheca villosissima*: Jackson Co.: Dead Indian Mem. Road, 2 mi E of Emigrant Creek bridge, gravelly, grassy disturbed roadside, 2150 ft, 23 Jul 2005, *Duncan 3026* (SOC, Fig. 21).

Contrasts of *Heterotheca villosissima* with *H. fastigiata*, *H. bolanderi*, and *H. sessiliflora* are given in key couplets following each of the latter species.



Figure 9. *Heterotheca villosissima* DC., holotype (G-DC), probably from the vicinity of Monterey, California (see text). Small capitular bracts present.





Figure 10. *Chrysopsis echioides*, the type collection (K) from Sonoma Co., California, placed here as a synonym of *Heterotheca villosissima*. Collected north of the currently known range of the species but the morphology is that of *H. villosissima* — see comments in text. Small capitular bracts present.



Figure 11. *Heterotheca villosissima*. Monterey Co., Elmer 3393 (US). Capitular bracts present.





Figure 12. *Heterotheca villosissima*. Monterey Co., Ewan 9171 (NO). Capitular bracts present. Vestiture similar to that of the *Heterotheca villosissima* type (Fig. 9). Unusually long peduncles with reduced bracts, perhaps resulting from proximal stem damage.

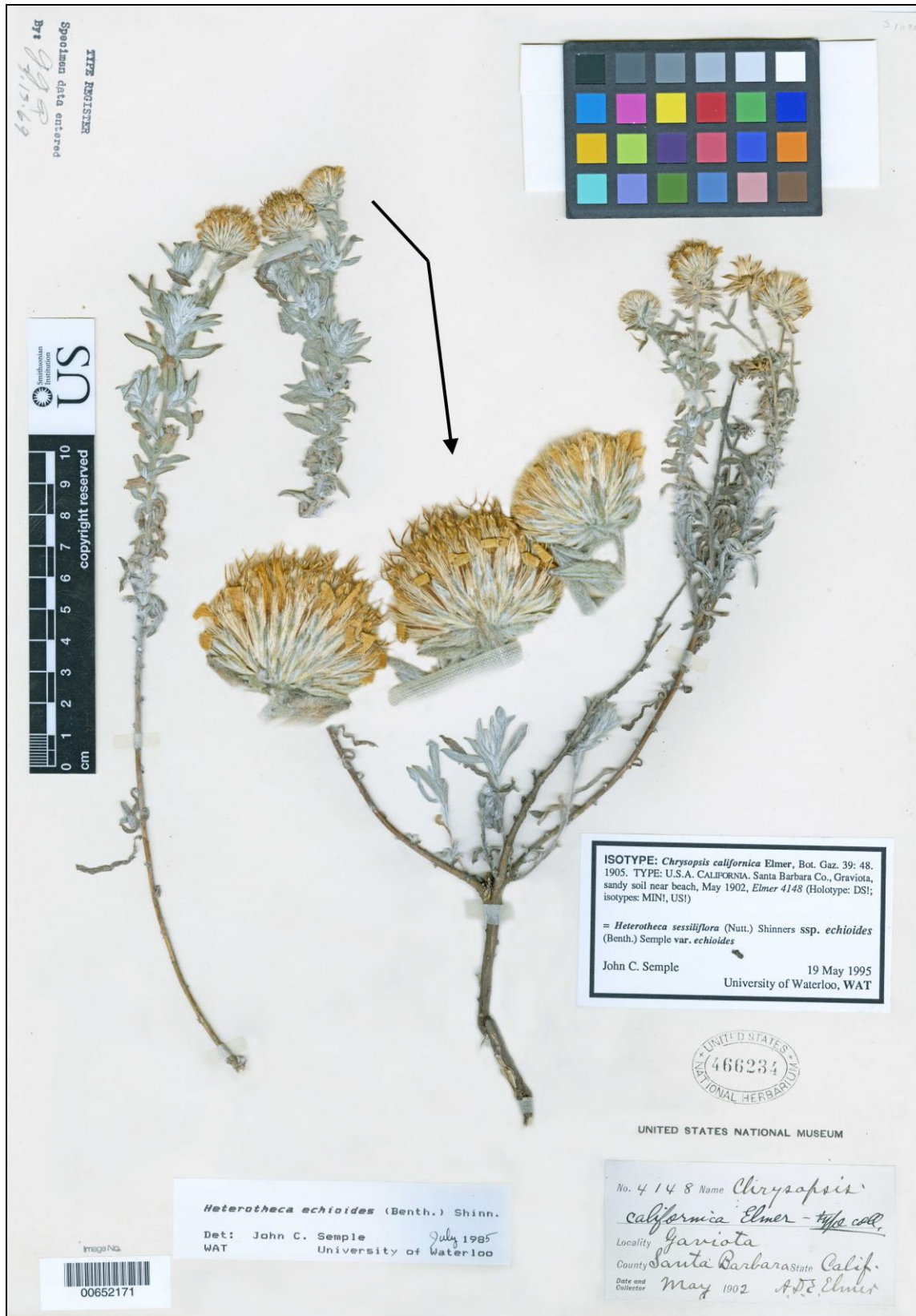


Figure 13. *Heterotheca villosissima*. Santa Barbara Co., isotype of *Chrysopsis californica* (US). Capitular bracts present.





Figure 14. *Heterotheca villosissima*. Los Angeles Co., Sanders 25600 (KANU). Capitular bracts present.



Figure 15. *Heterotheca villosissima*. Los Angeles Co., Cromwell s.n. (APSC). Capitular bracts apparently absent or few.





Figure 16. *Heterotheca villosissima*, perhaps with genetic influence of *H. fastigiata*. Los Angeles Co., Braunton 706 (US). Capitular bracts apparently absent.



Figure 17. *Heterotheca villosissima*. Riverside Co., Roos s.n. (GSW). Small capitular bracts variably present.





Figure 18. *Heterotheca villosissima*. Riverside Co., Sanders 35,894 (BRY). Capitular bracts present.



Figure 19. *Heterotheca villosissima*. San Diego Co., Lauri 371 (SDSU). Capitular bracts present.





Figure 20. *Heterotheca villosissima*. San Bernardino Co., Bell 11,190 (RSA). Capitular bracts present.





**5. HETEROTHECA SANDERSII** Nesom, **sp. nov.** **TYPE: California.** Los Angeles Co.: San Gabriel Mts, mouth of Burro Canyon near the confluence of the E and W Forks of the San Gabriel River, ca. 1460 ft (stream bottom) to 1530 ft (slopes), locally common biennial/short-lived perennial on disturbed flats, 20 Jun 1990, *T. Ross 3589* with Fritsch (holotype: RSA!; isotype: UC-Fig. 23).

Distinctive in its heads without capitular bracts, on long, naked or few-bracteate peduncles in loosely paniculate clusters, strongly keeled phyllaries, dark green, hirsute to hirsute-villous leaf and stem surfaces not obscured by vestiture, herbage drying with a dark cast, and stems densely and evenly stipitate-glandular, without eglandular hairs or also sparsely hirsute to villous with spreading hairs. Different from *H. fastigiata* in its dark green, hirsute to hirsute-villous stems and leaves, glandular stems, and keeled phyllaries. Different from *H. villosissima* in its densely stipitate-glandular stems, essentially eciliate leaf and bract margins, longer peduncles, lack of capitular bracts, and prominently keeled phyllaries.

Short-lived perennial herbs from a woody taproot. **Stems** erect, mostly 20–60 cm tall, densely and evenly stipitate-glandular, without eglandular hairs or also sparsely hirsute to villous with spreading hairs. **Leaves** densely arranged and overlapping proximally, more widely spaced distally, mostly oblong to oblong-lanceolate, (10–)15–30(–40) mm long, 3–8(–10) mm wide, bases of proximal subclasping, becoming non-clasping distally, margins eciliate or sometimes with a few weak cilia proximally, not undulate, surfaces hirsute to hirsute-villous, eglandular or minutely and inconspicuously glandular. **Heads** in loosely paniculate clusters, more or less solitary on long (2.5–9 cm), naked or few-bracteate peduncles, peduncular bracts 15–40(–55) mm long, flowering branches from proximal to distal nodes; involucre campanulate, 8–15 mm wide, 7–10 mm long; phyllaries linear-lanceolate, in 4–5 series strongly graduate in length, inner 7–10 mm long, outermost ca. 1/3–1/5 the inner length, inner to outer strongly keeled with a narrow, raised, indurate midregion, distal 1/3–1/2 green except for indurate margins. **Ray flowers** 12–16. **Disc corollas** minutely strigose-villous with fragile hairs near the tube-throat junction and a few longer hairs from near the base of the lobes. **Achenes** 3–4 mm long, densely strigose; pappus bristles longer than the disc corollas.

Alluvial slopes and benches, sandy flats, roadsides, 450–1550 ft; flowering Mar–Aug. *Heterotheca sandersii* is named for Dr. Andrew Sanders, Curator of the UCR Herbarium and a long-time student of the Californian flora.

**Additional collections examined. California.** Los Angeles Co.: San Gabriel Canyon, 1 mi above dam, from 0.5 mi below dam to 1.0 mi above, 1300–1600 ft, 18 May 1936, *Clokey & Templeton 5666* (JEPS, RENO image, RSA, SMU, UC, UCR; and as cited by Semple, CAN, KANU, NY-2, WTU); Claremont, roadside, 1200 ft, 22 Apr 1921, *Cowles 4482* (POM; San Gabriel Valley, S of Santa Fe Dam along E side of Live Oak Lane, 0.6 km SE of intersct I-605 and Arrow Hwy, 128 m, rare, disturbed roadside among weedy species and grasses, 4 May 2010, *Parikh and Gale 3144* (UCR); Lady Bug Canyon, Angeles Crest Hwy, 2 Sep 1937, *Ramsey 163* (POM); NE end of Santa Susana Mts, Newhall Ranch, Santa Clara River bed, below confluence of Castaic Creek, E of Del Valle, 920 ft, riparian forest and open sandy areas below bluffs on S side of river, scarce perennial in dry sand on open flats, 6 Aug 2003, *Sanders 27138* (RSA, UCR); San Gabriel Valley, San Gabriel River channel between Ramona Blvd and Lower Azusa Rd, SW lobe of Irwindale between Baldwin Park and El Monte, under SCE powerlines, channelized river between rock berms, vegetation periodically cut and thinned, fairly common perennial on open, sandy flats in channel, 28 May 2009, *Sanders 37011* (UCR); San Gabriel Valley, W edge of I-605 and ca. 1 mi W of the center of the Santa Fe Flood Control Basin, N of Arrow Hwy and S of Duarte, 460 ft, alluvial slope with remnant patch of brushy sage scrub with chaparral elements, scarce perennial in open, disturbed area, 1 Jun 2009, *Sanders 37081B* (UCR); Pasadena, Arroyo Seco, 30 Aug 2003, *Wilcox s.n.* (UCR). **San Bernardino Co.:** San Bernardino Natl Forest, 1.6 air mi NNE of Cajon Jct, localized population in open area beside Cajon Pass railway tracks, post-fire surveys on the Blue Cut Fire of 2016, 27 Jun 2017, *Bell 11,109* (RSA); Ontario, Etiwanda Wash [E. Etiwanda Creek], SW corner of Etiwanda Ave and 4th St/San Bernardino Rd, 1030 ft, dry sandy wash with sparsely distributed "islands" of vegetation, 12 Mar 1998, *Provance 182* (UCR); Santa Ana River wash, W side of the Riverside Drive/Main St. bridge, from under the bridge to ca. 0.25 mi W of it, 800–820 ft, uncommon perennial, open areas on sandy benches, 5 Aug 2000, *Provance 2180* (UCR); Colton, Santa Ana River from

Riverside Ave. (N. Main St.) bridge downstream to Riverside County line, disturbed riparian zone in sandy river bottom, with *Salix*, *Baccharis salicifolia*, etc., 820 ft, 28 Jul 1994, *Sanders 15189* (RSA, UCR, UTEP, not seen); Agua Mansa area, N side of the Santa Ana River just E of Riverside Ave, 850 ft, disturbed riparian forest at site of old horse show facility, scarce perennial on sandy bench near the river, 28 May 1998, *Sanders 21877* (TEX); San Bernardino Valley, Santa Ana River floodplain SE of East Highlands, pipeline route from Cone Camp Rd toward Mentone, between Greenspot Rd and the main channel, 1550 ft, coarse sandy and gravelly soil with stones and boulders, sage scrub with chaparral elements, uncommon perennial in dry open sites, 5 Jun 2006, *Sanders 33098* (UCR). **Ventura Co.:** Donton property (Nature Conservancy) along Santa Clara River from E of the 101 freeway, bridge between Ventura and Oxnard, open wash, 54-60 ft, 31 Mar 2015, *Gross et al. 6910a* (RSA).

1. Heads on long, ebracteate or bracteate peduncles, without capitular bracts; stems densely and evenly stipitate-glandular stems and leaves often drying with a distinctly dark cast; all phyllaries (inner to outer) prominently keeled ..... ***Heterotheca sandersii***  
 1. Heads on sparsely to densely leafy stems, usually with small capitular bracts; stems usually eglandular or minutely glandular; stems and leaves drying greenish to silvery-gray, without a dark cast; phyllaries not keeled or just the inner proximally ..... ***Heterotheca villosissima***

The geographic range of *Heterotheca sandersii* is small and most of the known localities are essentially in urban areas (three are in the Angeles National Forest, in San Gabriel and Lady Bug canyons) — all are along the western and southwestern base of the Santa Susana, San Gabriel, and San Bernardino Mountains (Fig. 22). The habitats are mostly alluvial and associated with (from west to east) Arroyo Seco, the Santa Clara River, San Gabriel River, East Etiwanda Creek, and Santa Ana River.

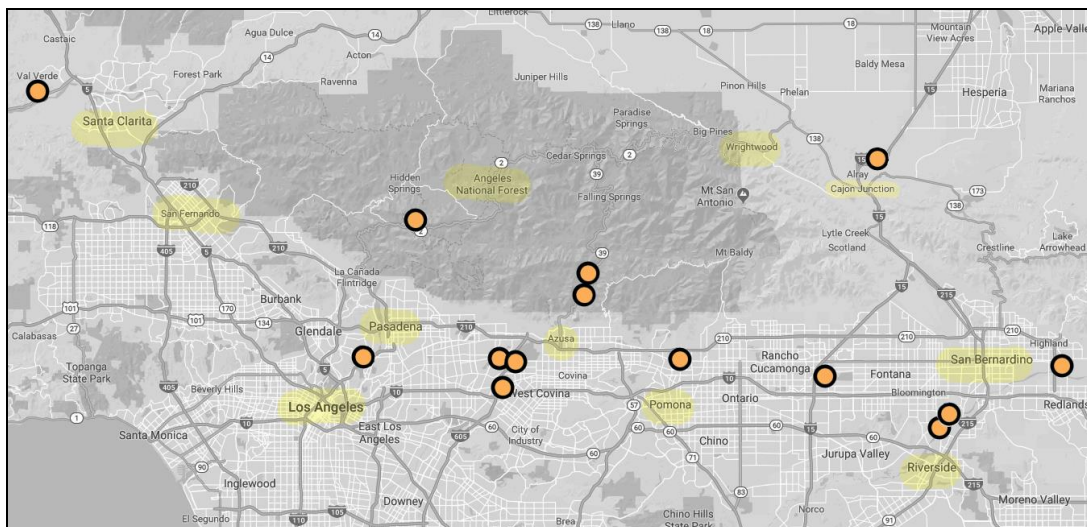


Figure 22. Distribution of *Heterotheca sandersii*. Localities mapped here are in Los Angeles and San Bernardino counties. The collection from Ventura Co. (see Map 1) is not shown at the smaller scale here, perhaps a waif transported downstream along the Santa Clara River.

*Heterotheca sandersii* is unusual enough in appearance that collectors have speculated that the plants might be hybrids between *H. grandiflora* and *H. sessiliflora* (sensu lato) (see labels for *Sanders 37011*, *37081B*; *Provance 2180*), perhaps because of the dark-drying herbage and the relatively large heads with distinctly keeled phyllaries. The achenes, however, are not dimorphic (as in *H. grandiflora*) and the numerous collections with coherent geography suggest that *H. sandersii* is a stable entity. A chromosome count has not been made.

*Heterotheca sandersii* has been collected in close proximity to *H. fastigiata* at the northeastern end of the Santa Susana Mountains, in San Gabriel Canyon and at lower elevations along the San Gabriel and Santa Ana rivers, and along the Etiwanda Creek Wash.



Figure 23. *Heterotheca sandersii*. Los Angeles Co., isotype (UC).





Figure 24. *Heterotheca sandersii*. Los Angeles Co., Sanders 37081B (UCR).



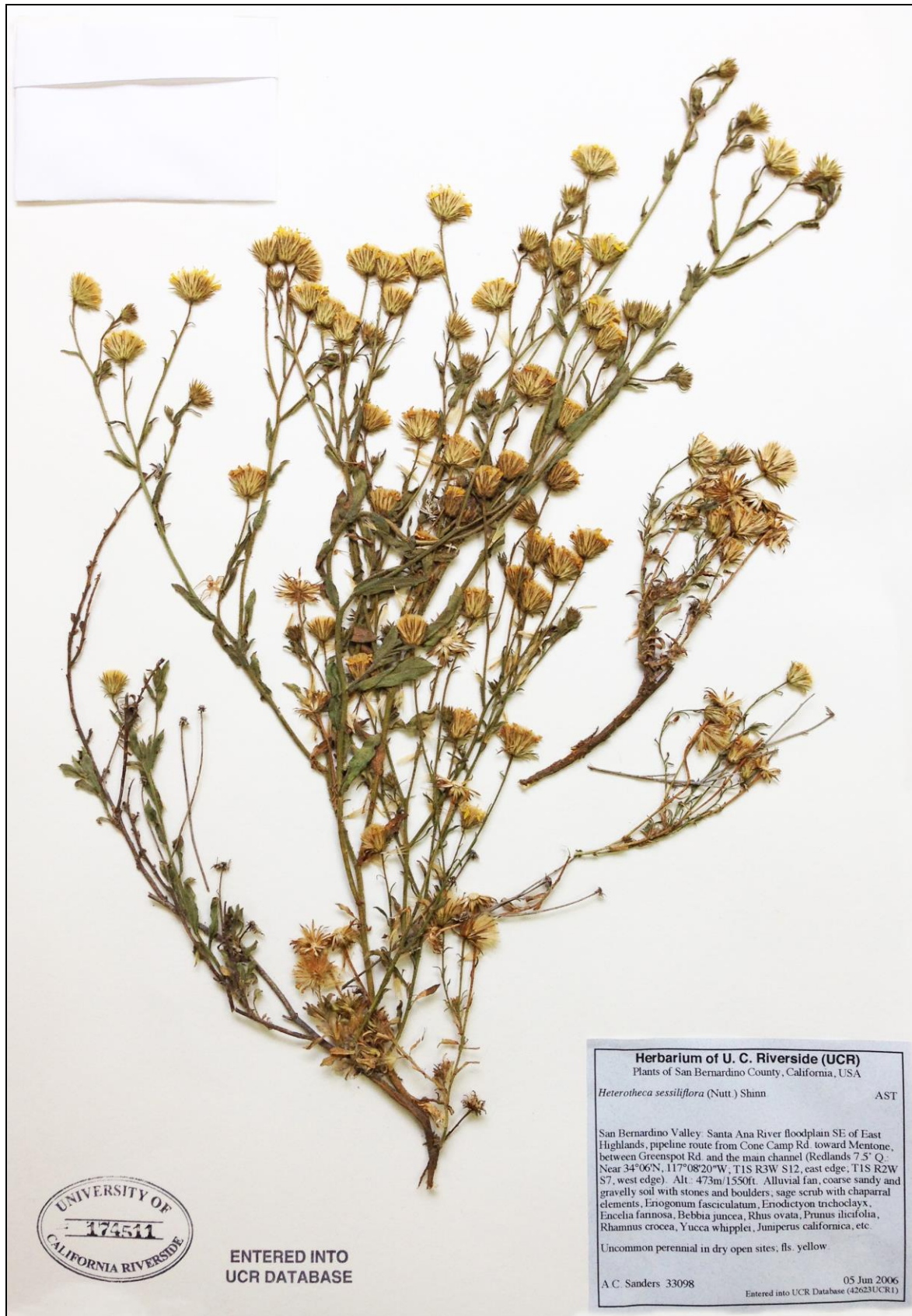


Figure 25. *Heterotheca sandersii*. San Bernardino Co., Sanders 33098 (UCR).



Figure 26. *Heterotheca sandersii*. San Bernardino Co., Bell 11,109 (RSA).



Figure 27. *Heterotheca sandersii*. Los Angeles Co., Clokey & Templeton 5666 (RENO). Middle two heads are at anthesis, others pre-anthesis with still lengthening peduncles.



**6. HETEROTHECA SESSILIFLORA** (Nutt.) Shinnery, Field & Lab. 19: 71. 1951. *Chrysopsis sessiliflora* Nutt., Trans. Amer. Philos. Soc. n.s., 7: 317. 1840. *Chrysopsis villosa* var. *sessiliflora* (Nutt.) A. Gray, Synopt. Fl. N. Amer. 1(2): 123. 1884. **TYPE: California.** [Santa Barbara Co.]: **Protologue:** "St. Barbara, Upper California. Flowering in April," 1836, *T. Nuttall s.n.* (holotype: BM, Fig. 28; isotype: GH image, detail Fig. 29).

Handwritten labels by Nuttall on the holotype and the isotype specify Santa Barbara as the collection locality (the BM sheet has 3 labels, each apparently separately written by Nuttall).

**Plants** often subshrubby, forming colonies from rhizomes or rooting caudices. **Stems** ascending, up to 100(–130) cm high, sessile-glandular, moderately to densely villous to hirsute-villous or pilose-hirsute, less commonly hirsutulous, hairs spreading to loosely antrorsely appressed. **Leaves** basal and cauline; basal usually shed by flowering; cauline usually closely overlapping, broadly oblong to oblong-ovate, base truncate and sessile to truncate-rounded and subclasping, apex rounded to acute, margins straight or undulate, surfaces densely and evenly minutely sessile-glandular (orange), the glands mostly obscured by the dense, loosely villous-strigose to hirsutulous vestiture. **Heads** relatively few in a corymbiform arrangement, with narrow capitular bracts equalling or longer than the involucre and with spreading-ciliate margins; involucre 13–22 mm wide; phyllaries glandular and moderately strigose, at least distally. **Ray flowers** ca. 15–30. Chromosome number,  $2n = 18$  (*Semple & Chmielewski 8991*). Figures 28–36.

**Representative collections examined. MEXICO. Baja California.** Descanso, dunes, 5 Apr 1949, *Higgins & Harbison s.n.* (DS); Playas De Rosarito, just S of El Descanso, common on inner slope of dunes, some with *Het. grandiflora*, bushy, ca. 1 m high, 8 May 1977, *Moran 24002* (ARIZ, DES, RSA, UCR); near mouth of Rio San Miguel, W of La Mision, local in dunes, 29 Apr 1972, *Moran 19118* (ASU, CAS); Ensenada, sand dunes, 16 Oct 1936, *Rose 36758* (CAS); Tia Juana, 1912, *Smith 5203* (US); 2 mi N of Rosarito Beach, landward margin of sand dunes, 7 Sep 1929, *Wiggins & Gillespie 3877* (CAS, DS, US); ca. 13 mi S of Tijuana near road to Ensenada, 27 Jun 1962, *Wiggins & Thomas 342* (DS). **USA. California. San Diego Co.** (native range): Ocean Beach near San Diego, Oct 1906, *K. Brandegee s.n.* (RENO, RSA); S San Diego, 3 Oct 1903, *Chandler 4117* (DS); Silver Strand Beach State Park, stabilized sand dunes, 30 Aug 1932, *Demaree 9308* (US); Tijuana River, 8 Aug 1902, *Herre s.n.* (DS); near National Monument, SW corner of U.S., 11 Jun 1928, *Johnson s.n.* (CAS); Silver Strand, partially stabilized areas on the sand dunes, 19 Sep 1933, *Purer 5565* (DS); Del Mar, hills S of racetrack near Torrey Pines Woodland, N-facing slope at mouth of steep drainage, 2 Jul 1988, *Reiser s.n.* (SD); Torrey Pines beach, dry sandy flats behind beach, with [*Isocoma*], 15 ft, 19 Aug 1950, *Roos 4938[a]* (DS, GH, UC); Torrey Pines Park, matted perennial at edge of salt marsh with *Baccharis viminea* 19 Aug 1950, *Roos 4938[b]* (RSA); San Diego, CA-75, Imperial Beach and Silver Strand State Beach, just N of S entrance to CA-75, 1 Oct 1987, *Semple & Chmielewski 8991*, voucher for  $2n = 18$  (GH, NY, RSA); vicinity of San Diego, 1 m high, dry slopes, 200 ft, 8 Sep 1916, *Spencer 77* (US); Crown Pt., near Pacific Beach, 24 Aug 1933, *Youngberg 2844* SDSU-2 sheets). **San Diego Co.** (probably a waif): Pine Valley, [ca. 3700 ft], 12 Aug 1894, *Mearns 3976* (US, Fig. 36).

*Heterotheca sessiliflora* is distinct in its colonial habit, tall stems, broadly oblong, usually closely overlapping cauline leaves with glandular surfaces obscured or not by non-glandular hairs of variable density, and relatively large heads consistently subtended by capitular bracts equalling or longer than the involucre. It is endemic to coastal strand habitats in the southern half of San Diego Co. and a roughly equivalent area along the coast of northwestern Baja California. The type of *H. sessiliflora*, however, was collected in Santa Barbara Co., north of the currently known range of the species.

The inland plant collected by Edgar Mearns at Pine Valley in 1894 (Fig. 36) probably was a waif there or was perhaps even established from a garden planting. At the time, there was gold mining in Pine Valley and presumably an active connection between there and the San Diego area.



Over the course of the present study, I identified collections of typical *Heterotheca sessiliflora* using the epithet "litorea" in attempt to account for the geographical discrepancy of the type collection, but that solution proved to be no less problematic.



Figure 28. *Heterotheca sessiliflora*, the type from BM, Nuttall *s.n.* from Santa Barbara in 1836.



Figure 29. *Heterotheca sessiliflora*, detail from GH isotype.





Figure 30. *Heterotheca sessiliflora*, from dunes just south of of El Descanso, Baja California. Details from Moran 24002 (DES).





Figure 31. *Heterotheca sessiliflora*, near Torrey Pines, San Diego Co. Reiser s.n. (SD).



Figure 32. *Heterotheca sessiliflora*, Crown Point, San Diego Co. Youngberg s.n. (SDSU).





Figure 33. *Heterotheca sessiliflora*, Silver Strand Beach, San Diego Co. Demaree 9308 (US).





Figure 34. *Heterotheca sessiliflora*, Ocean Beach, San Diego Co. K. Brandegee s.n. (RENO).



Figure 35. *Heterotheca sessiliflora*, Baja California. Moran 1918 (ASU). Nonglandular vestiture unusually dense.





Figure 36. *Heterotheca sessiliflora*, Pine Valley in 1894, San Diego County. Mearns 3976 (US). Probably a waif at this locality (see text, p. 35).



Apparently because of its seaside habitat, typical *Heterotheca sessiliflora* apparently is not sympatric with other species of the section. *Heterotheca villosissima* is distinct from *H. sessiliflora* in its smaller and solitary/caespitose habit, narrower, less congested cauline leaves, characteristically less dense vestiture and reduced glandularity of the leaf surfaces, more elongate capitulescence, and smaller and fewer capitular bracts (if present).

**7. HETEROTHECA CAMPHORATA** (Eastw.) Semple, *Canad. J. Bot.* 58: 148. 1980. *Chrysopsis camphorata* Eastw., *Zöe* 5: 81. 1900. *Chrysopsis villosa* var. *camphorata* (Eastw.) Jeps., *Man. Fl. Pl. Calif.*, 1036. 1925. *Heterotheca sessiliflora* var. *camphorata* (Eastw.) Semple, *Phytologia* 73: 451. 1992. **TYPE: California.** Santa Cruz Co.: Glenwood, Jul 1900, *H. Davis s.n.* (holotype: CAS; isotypes: DS, GH, NY, RM-3 sheets! images, UC, US-Fig. 37).

*Chrysopsis vestita* Greene in Baker, *W. Amer. Pl.* 1: 8. 1902. **TYPE: USA. California.** Santa Clara Co.: Palo Alto, occasional near the marshes, 15 Sep 1902, *C.F. Baker 1670* (holotype: US, Fig. 38; isotypes: GH image, K image, LL! image, MO!, POM, NY, UC). POM, NY, and UC as cited by Semple.

Semple's isotype annotation labels say "Holotype at NDG, not seen" but (fide Barbara Hellenthal, pers. comm. 2016) there is no specimen of this in NDG.

*Heterotheca camphorata* is characterized by its minutely but prominently sessile-glandular to short-stipitate-glandular and otherwise sparsely hispid-pilose to hirsute-villous upper stems, leaves, and capitulescence, or the stems may lack non-glandular hairs. Heads are on bracteate peduncles; capitular bracts are absent or small and inconsistently present. The species is known from a cluster of 9 counties (Maps 1, 2; uncommon in Napa and Solano cos.) and is abundantly represented by collections — it is not often misidentified. It is sympatric with *H. sanctarum* (tetraploid; unambiguous hybrids not seen but possibly present, see below) and *H. villosissima* (diploid; apparent hybrids and introgressants occur).

Semple (1996, p. 46) noted that diploids and tetraploids occur within *Heterotheca camphorata* and that ploidy level does not appear to be correlated with variation in head size. The only vouchers I have seen, however, are for diploid counts: Fresno Co.: *Semple 8944*; Monterey Co.: *Semple 8932, 8933, 8934, 8937, 8938, Semple 8603, 8606*; Santa Clara Co.: *Semple 8922, 8923*; Santa Cruz Co.: *Semple 5668, Semple 8920, Semple 8597*. Semple's tetraploid counts (see Semple 2008: *Semple 8924, Semple 8926*) are from the Mt. Hamilton area in Santa Clara Co., involving plants identified here as *H. sanctarum* (4x) and apparent hybrids between it and *H. camphorata*.

*Heterotheca camphorata* was treated as *H. sessiliflora* var. *camphorata* by Semple in 1996, but subsequent treatments (Semple in FNANM 2006 and in the Jepson Flora 2012) recognized it less formally. In 2006, Semple listed var. *camphorata* only as a synonym of subsp. *echioides* but referred to it as distinct in his subsequent comments. Similarly, he noted in 2012 that "densely glandular plants [of *H. sessiliflora* subsp. *echioides*] from southern SnFrB, northern SCo with ± glabrous disk corolla lobes may be treated as *Heterotheca sessiliflora* var. *camphorata* (Eastw.) Semple."



Figure 37. *Heterotheca camphorata*, Santa Cruz County. Isotype of *Chrysopsis camphorata* (US). Stems sessile- to short-stipitate-glandular, without non-glandular hairs.



Figure 38. *Heterotheca camphorata*, Santa Clara County. Isotype of *Chrysopsis vestita* (US). Stems sparsely hirsute with non-glandular hairs, perhaps reflecting gene flow from *H. villosissima*.



**8. HETEROTHECA BOLANDERI** (A. Gray) Harms, Brittonia 26: 61. 1974. *Chrysopsis bolanderi* A. Gray, Proc. Amer. Acad. Arts 6: 543. 1866. *Chrysopsis villosa* var. *bolanderi* (A. Gray) A. Gray, Synopt. Fl. N. Amer. 1(2): 123. 1884. *Heterotheca echioides* var. *bolanderi* (A. Gray) Nesom, Phytologia 83: 17. 1997. **TYPE: California.** [Alameda Co.]: Oakland Hills, near San Francisco, 1863, *H.N. Bolander* 2466 (holotype: GH image; isotypes: K, US image, YU image).

*Heterotheca sessiliflora* var. *bolanderioides* Semple, Phytologia 73: 450. 1992. *Heterotheca echioides* var. *bolanderioides* (Semple) Nesom, Phytologia 83: 17. 1997. **TYPE: California.** Contra Costa Co.: Charles Tilden Regional Park, Vollmer Peak, scattered population along ridge top, in rocks and loose gravel in grassy area between shrubs, 16 Aug 1990, *J.C. Semple et al.* 9339, voucher for 2n = 18II (holotype: UC, Fig. 42; isotypes: CAN, CAS image, MO image, NY image, RSA!, WAT).

*Heterotheca bolanderi* has been recognized (e.g., Ferris, Munz, Jepson) as a distinct entity of west-central California characterized by its taprooted, caespitose habit, relatively large and generally few heads subtended by foliaceous capitular bracts that at least partly obscure the involucre. Leaves are greenish with sessile-glandular surfaces and relatively dense non-glandular vestiture (loosely strigose with long, fine hairs to strigose-villous or strigose-hirsute). Proximal cauline leaves are spatulate and petiolate, often withered by flowering; the distal are oblanceolate and epetiolate. Uppermost cauline leaves (peduncular bracts) and capitular bracts are as long or longer than the involucre.

*Heterotheca bolanderi* as most recently treated by Semple is viewed here as comprising three morpho-geographic elements: (1) the southernmost element is segregated as the previously undescribed species *H. sanctarum*; (2) the geographically central element, typical *H. bolanderi*, occurs from Santa Cruz, San Mateo, and Alameda counties into Sonoma Co.; and (3) the northern element, here recognized as *H. arenaria*, includes coastal strand/sandy-habitat populations from Marin Co. to Sonoma Co., Mendocino Co., and into southern Humboldt Co.

Semple (1992) found that inland populations of *Heterotheca bolanderi* are tetraploid, compared to the coastal diploids (here as *H. arenaria*). He observed that the diploid is restricted mostly to sandy, coastal strand habitats (sometimes on near-beach clay slopes and bluffs) while the tetraploid occurs on "mostly serpentine soils on hill and mountain tops surrounding San Francisco Bay" (Semple 1996). Tetraploid habitats are recorded as ridge tops, slopes, roadsides, in rocky and gravelly soil.

Although Semple noted in 1992 that most collections of var. *bolanderioides* had been previously identified as subsp. *bolanderi* (hence, presumably, the newly coined "-oides" epithet), the protologue diagnosis contrasted var. *bolanderioides* with [*H. sessiliflora*] var. *echioides*. Var. *bolanderioides* was distinguished in 1996 by a key couplet (p. 27) again contrasting it with var. *echioides*. Semple observed (1996, p. 49) that "individuals of var. *bolanderioides* can be similar in indument ..... to diploids of var. *echioides*, which usually has a leaf indument of dense spreading to appressed hairs obscuring the underlying glands and smaller involucre. It is uncertain whether var. *bolanderioides* is a tetraploid derivative of var. *echioides* or whether it may be an allopolyploid involving ssp. *echioides* and ssp. *bolanderi*." His hypothesis that var. *echioides* might be involved in the ancestry of var. *bolanderioides* apparently was based also on his observations (via keys and descriptions) that

the tetraploids (vs. diploids) range greater in height and ray ligule length and have a greater density of long hairs on the disc corolla lobes and tube.

In the present study it appears that Semple's concept of the *Heterotheca bolanderi* tetraploids included two elements: (1) a series of populations treated here as the separate species *Heterotheca sanctarum*, which is more similar to *H. echioides* (= *H. villosissima*) than to *H. bolanderi*, and (2) plants recognized as *H. bolanderi* sensu stricto.

The type of *Chrysopsis bolanderi* was collected from an inland area — the Berkeley Hills (including the "Oakland Hills" as noted by Bolander for the type collection, see Wikipedia entry for "Berkeley Hills"), with western slopes in Alameda County, eastern slopes in Contra Costa County — where apparently only the tetraploid occurs, and I find no morphological difference between the type of *C. bolanderi* and plants from the same area recorded by Semple as tetraploid. Semple (1996) mapped and cited only collections of var. *bolanderioides* and "aff. *bolanderioides*" from the Berkeley Hills of Alameda County as well as from Contra Costa County (including Vollmer Peak, the type locality of var. *bolanderioides*, in the Berkeley Hills) just outside Berkeley's eastern limit. His map shows diploids (*H. arenaria*) only along the immediate coastal strand.

**Southernmost collections of typical *Heterotheca bolanderi*.** Santa Cruz Co.: coastal terrace E of Calif Hwy 1 (Cabrillo Hwy) and across from Greyhound Rock parking lot, ca. 6 mi NW of Davenport, coastal prairie, 15 Aug 1982, *Buck 110* (JEPS) — *Buck 110* is typical in morphology but *Buck 111* (JEPS) from the same locality is unusual, with narrow leaves and heads lacking capitular bracts; San Vicente Rd, 3 mi from coastal hwy, ca. 500 ft, *Hesse 1379* (JEPS); San Vicente Rd, 2.5 mi from coast hwy, 475 ft, 26 Aug 1954, *Hesse 1380* (JEPS); Santa Cruz Terrace, coastal prairie, Swanton Pacific Ranch, 100-150 m, 13 Jul 2017, *Richardson 101* (OBI).

The only collection of typical *Heterotheca bolanderi* from Solano Co.: Mare Island, S end of island, 30 m, 18 Jun 2003, *Kelch & Murdoch AGM94* (JEPS).



Figure 39. *Heterotheca bolanderi*. Marin Co., Novato; photos by Jacob Martin, 17 Jun 2020. iNaturalist.





Figure 40. *Heterotheca bolanderi*. Marin Co., Mt. Tamalpais Watershed; photo by "kercado\_eli," 14 Jun 2014. iNaturalist.





Figure 41. *Heterotheca bolanderi*. San Mateo Co., San Bruno Mountain Park; photo by Scott Loarie, 10 Jun 2012. iNaturalist.



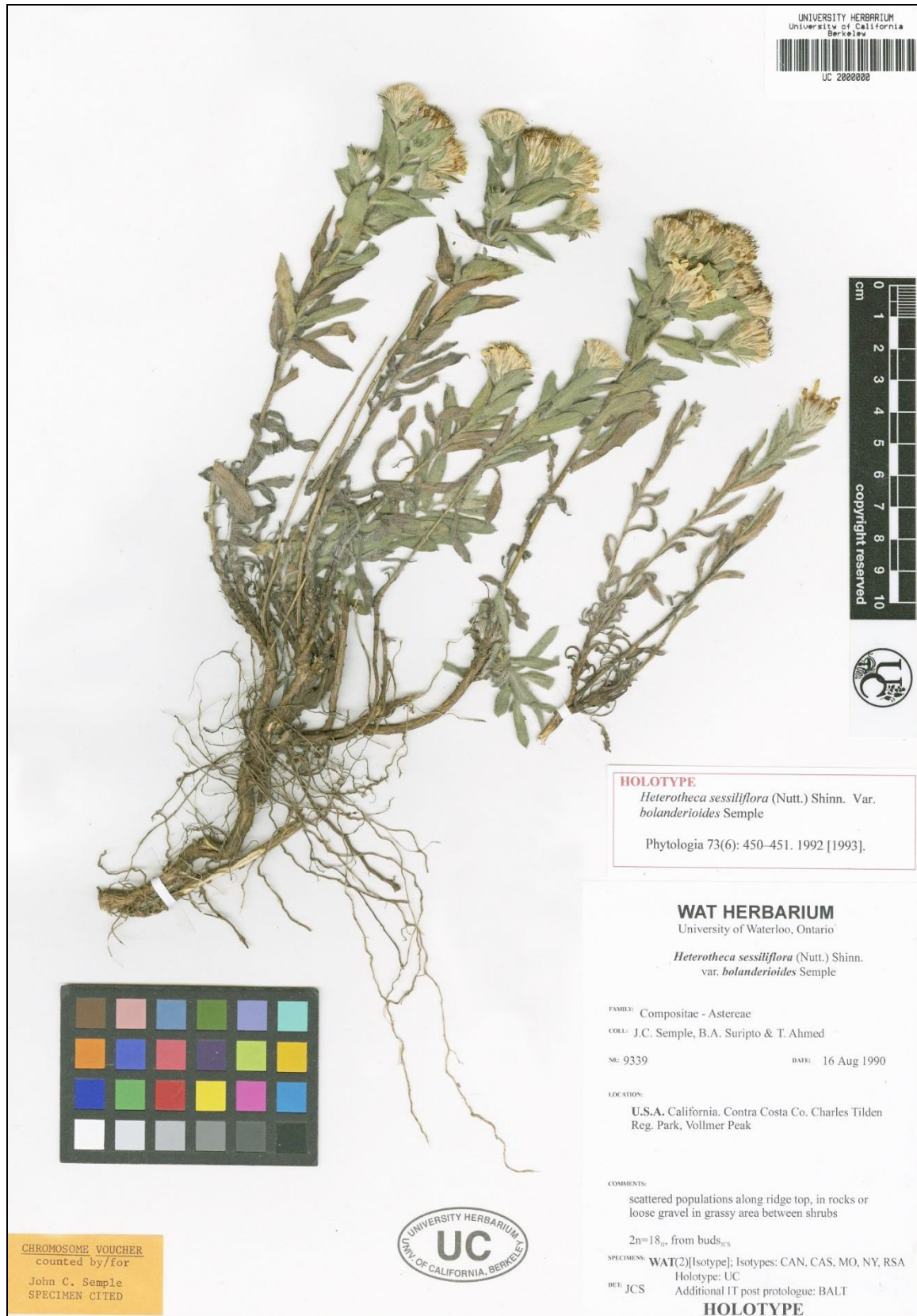


Figure 42. *Heterotheca bolanderi*. Holotype (UC) of *H. sessiliflora* var. *bolanderioides*.



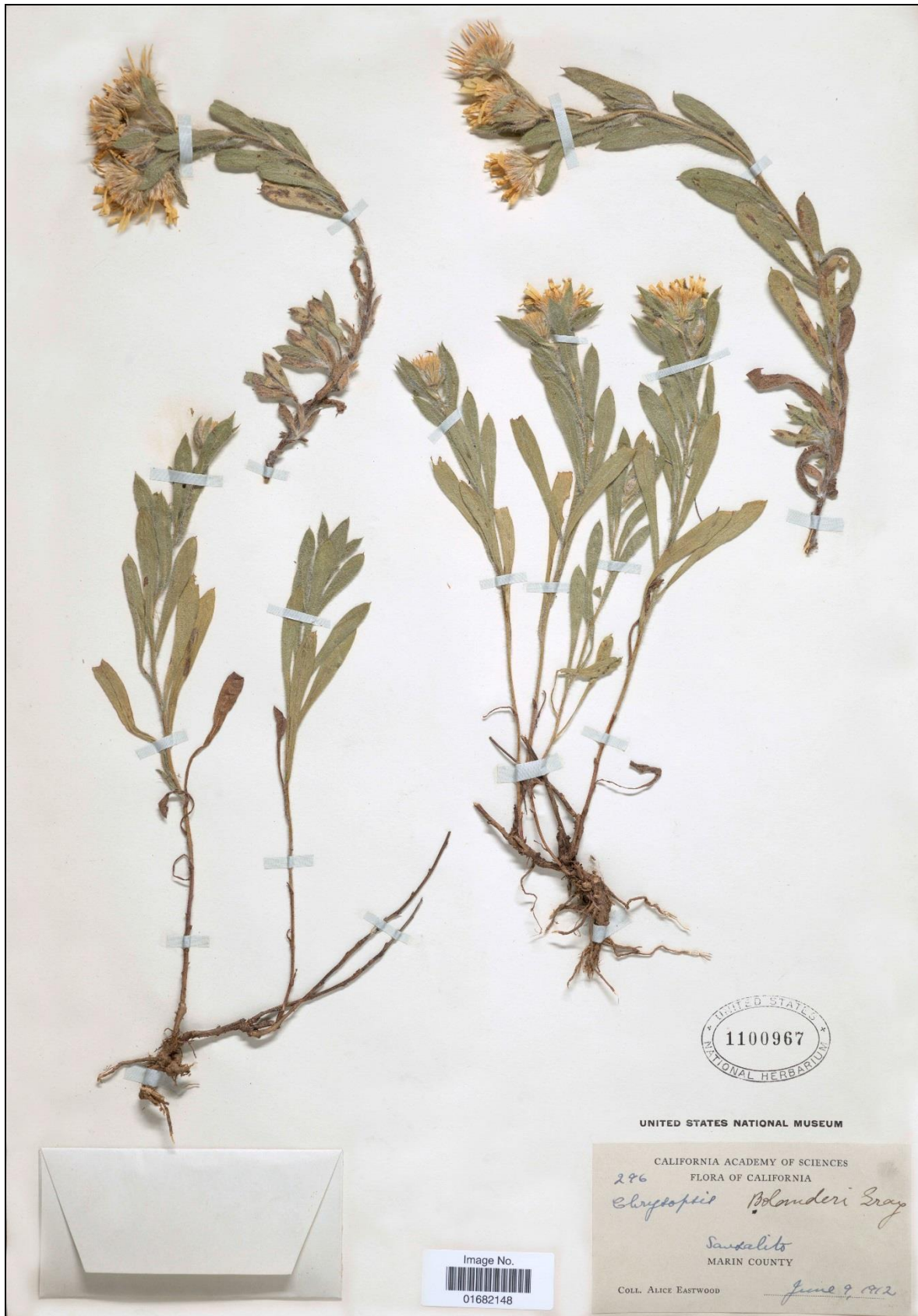


Figure 43. *Heterotheca bolanderi*, Marin County. Eastwood 296 (US).



Figure 44. *Heterotheca bolanderi*, Marin County. Rose 46270 (US).





Figure 45. *Heterotheca bolanderi*, Alameda County. Erter 14965 (BRY).



**9. HETEROTHECA ARENARIA** (Elmer) Nesom, **comb. nov.** *Chrysopsis arenaria* Elmer, Bot. Gaz. 41: 321. 1906. **TYPE: California.** Marin Co.: Point Reyes post office, [from the protologue: "dense prostrate mats on the windward side of the drifting sand dunes"], Jul 1903, *A.D.E. Elmer 4556* (holotype: A?; isotypes: CAS!, COLO image, DS!, GH image, NY-Fig. 50, RM, RSA!, US image).

The type of *Heterotheca arenaria* is from Marin County but the species becomes abundant in southern Mendocino County (around Anchor Bay) and northernmost Sonoma County, continuing northward to the apparent limit of its natural distribution in the Fort Bragg area (e.g., Noyo, Pudding Creek, 10-Mile River) and an extended record from Humboldt County. Disjunct plants in Washington state (cited below) apparently are adventive. During one part of this study, before realizing the major distinctions from typical *H. bolanderi*, I annotated collections of *H. arenaria* as "*H. bolanderi* var. *mendocinoensis*."

*Heterotheca arenaria* is distinct in its sandy habitats along the coastal strand. Label notes with *Jepson 17739* (JEPS), from near Fort Bragg, describe "Stems many, radiating from the root-crown and prostrate, with only ascending end, thus forming a densely close mat, quite thick and unbroken, an almost perfect circle 4 feet across." The spreading "stems" might be thought of as thin, elongate caudex branches or as scale-leaved rhizomes — Figures 46–52 show the rhizomes and colonial habit. Cauline leaves are densely clustered on the short stems, spatulate to oblong-ob lanceolate or oblong-obovate, not clasping, the basal and proximal smaller and usually withered by flowering. Heads solitary on short branches, on distinct peduncles with reduced bracts; capitular bracts absent. Chromosome number,  $n=9$  (Mendocino Co.: S of Westport, *Semple & Heard 8535* (MO!); Mendocino Co.: S of Mendocino, *Semple & Semple 5681* (BRIT!, MO!, NY-Fig. 51).

Vestiture of *Heterotheca arenaria* is similar to that of *H. bolanderi*, perhaps accounting for the two entities being treated as conspecific. Surfaces are sessile-glandular and loosely strigose to strigose-villous with long hairs; margins are ciliate with hairs quickly elongating into long, villous, filiform-flexuous distal portions.

**Southernmost collections of *Heterotheca arenaria*:** Sonoma Co.: Sea Ranch, near State Hwy 1, below S end of Yardarm Drive, Unit 15 Owners' Map, 16 Sep 1976, *Heknter 269* (UCD, not seen); Black Point Road, 13 Jul 1930, *Howell 5342* (CAS); 2 mi S of Anchor Cove, 2 Sep 1927, *Wolf 1345* (DS).

**Northernmost collection of *Heterotheca arenaria*:** Humboldt Co.: 2 mi S of Petrolia on Mattole River near where road crosses river, 30 Aug 1927, *Wolf s.n.* (SBBG 455062, as cited in Consortium of California Herbaria). Perhaps not part of the natural range.

**Representative collections of *Heterotheca arenaria* from Washington state (adventive):** Clallam Co.: E shore of Washington Harbor, steep sand bank above beach, 14 Sep 1921, *St. John 5869* (UC!, WS!) — annotated by Semple 1993 as "Probably adventive from Calif." Semple (1996) cited three other collections of *Heterotheca bolanderi* from Washington (all from Island Co.): *Gardner s.n.*, *Gardner 153*, and *Naas & Naas 5579*).

A collection identified here as *Heterotheca arenaria* is labeled as from Nevada Co., California, but is out of range and the label probably is in error: Nevada City, 19 Jul 1932, *McMinn 3025* (RSA).



Figure 46. *Heterotheca arenaria*. Top: Mendocino Co., Point Arena area; photo by 'avocat', 3 Aug 2019, iNaturalist. Bottom: Mendocino Co., north of Elk; photo by Asa Spade, 9 Aug 2019, iNaturalist.





Figure 47. *Heterotheca arenaria*. Mendocino Co., Mendocino Headlands State Park; photo by Karlyn H. Lewis, 7 Aug 2016, iNaturalist.





Figure 48. *Heterotheca arenaria*. Mendocino Co., MacKerricher State Marine Conservation Area; photo by Asa Spade 14 Aug 2019, iNaturalist.





Figure 49. *Heterotheca arenaria*. Mendocino Co., Point Arena-Stornetta Public Lands. Photos by Morgan Stickrod, 23 Nov 2020, iNaturalist.



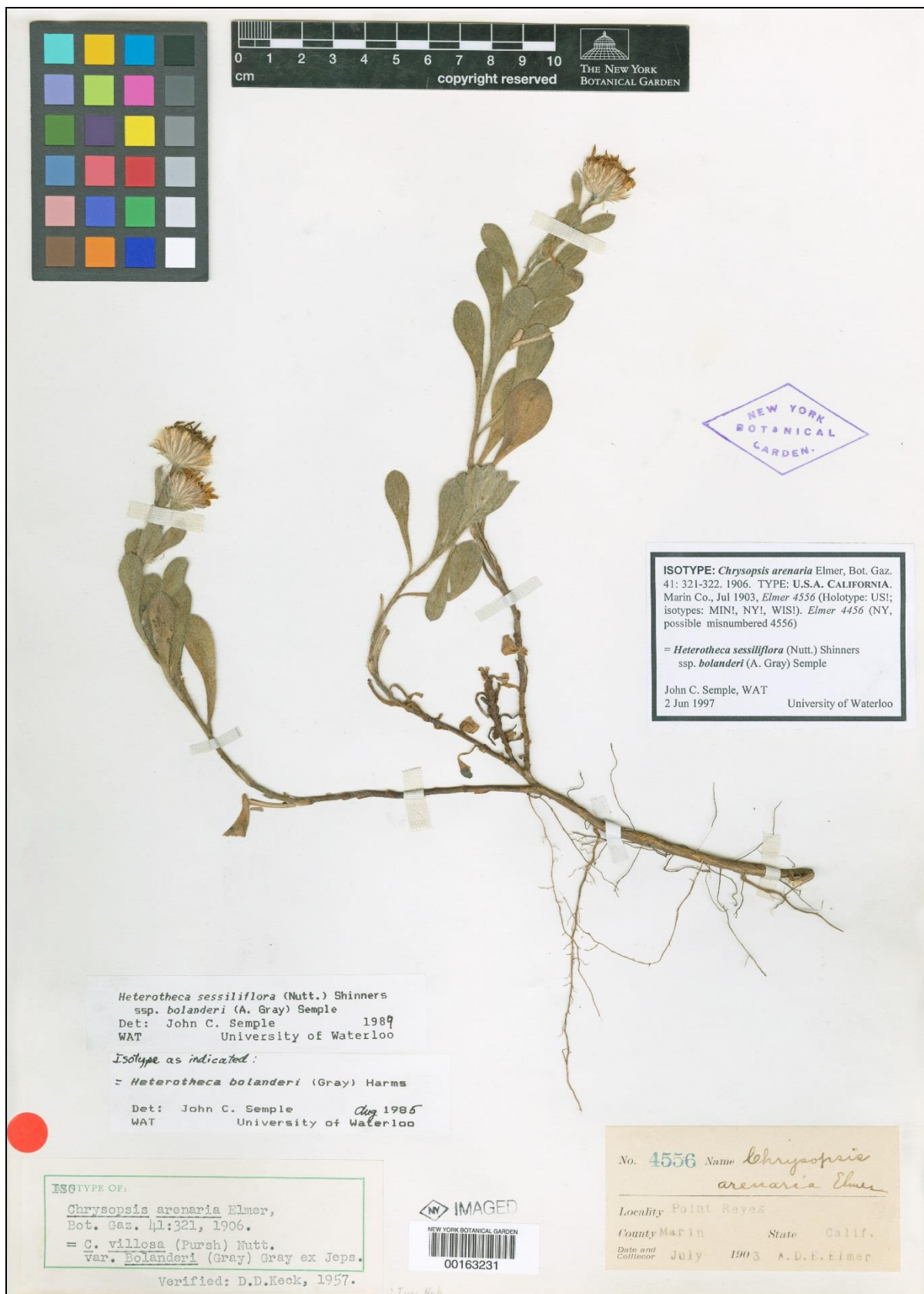
Figure 50. *Heterotheca arenaria*. Marin Co. Isotype of *Chrysopsis arenaria* (NY).



Figure 51. *Heterotheca arenaria*. Mendocino Co., *Semple 5681* (NY). Voucher for diploid chromosome count of  $2n=18$ . "Large population, plants forming low mats."





Figure 52. *Heterotheca arenaria*. Mendocino Co., Howe 3581 (SDSU).

**10. HETEROTHECA SANCTARUM** Nesom, **sp. nov.** **TYPE: California.** Santa Clara Co.: Saratoga Summit (jct of Saratoga Road and Skyline Blvd), dry open hills, 750 m, 23 Sep 1941, L.S. Rose 41459 (holotype: POM!; isotypes: BRU image, BRY!, CAS!, COLO image, DS!, GA image, LL!, MISSA image, MO-2 sheets!, PH-2 sheets!, RM!, SMU!, TEX-2!, UC!-Fig. 56, US-2 sheets images, Fig. 54). Semple (1996, p. 49) cited additional duplicates of *Rose 41459* at CAN, GH, NDG, NY, UBC, UNCC, and WIS.

Distinct in its densely overlapping, silvery-sericeous leaves without undulate margins, the basal and proximal early-withering, lack of axillary leaf clusters, heads in a closely corymboid cluster on short peduncles, capitular and subcapitular bracts mostly oblong to oblong-ob lanceolate, 1/4–1/2 as long as the involucre and not at all obscuring it, bract margins densely long-ciliate. Different from *Heterotheca bolanderi* in its smaller, silvery-sericeous leaves and smaller capitular bracts. Different from *Heterotheca villosissima* in its villous stems, more densely overlapping leaves, and larger heads in a corymboid cluster (shorter peduncles). See key couplets below.

Perennials, apparently from woody rhizome or rhizome-like caudex branches (*Fosberg 43225*: "small clumps, erect, usually of a few stems"). **Stems** strictly erect, 20–40 cm tall, stems vestiture 1-storied, sparsely villous with long, irregularly spreading hairs, minutely and inconspicuously glandular, especially distally. **Leaves**: basal and lower cauline (proximal half of stem) withered and shed by flowering, persistent cauline usually densely overlapping, ascending, sessile, often subclasping, mostly oblong-ob lanceolate to oblong-lanceolate, 10–25(–40) x 2–8 mm, densely but loosely silvery sericeous to silvery gray on both surfaces, surfaces minutely and obscurely glandular, mostly obscured by the non-glandular vestiture of fine, thin-based hairs, base truncate, apex rounded-apiculate to acute-apiculate, margins not undulate; axillary clusters of small leaves usually absent. **Heads** in a loose to closely corymboid arrangement, peduncles relatively short (mostly 10–25 mm), longer on proximal branches. **Involucres** 12–17 mm wide (pressed), inner phyllaries 6–9 mm long, oblong-lanceolate to linear-lanceolate; phyllaries sparsely to moderately strigose-sericeous, minutely glandular; capitular and subcapitular bracts mostly oblong to oblong-ob lanceolate, 1/4–1/2 as long as the involucre, not at all obscuring the involucre, bract margins densely long-ciliate. **Ray florets** 10–15.

Flowering (May-)Aug-Oct; sandstone, rocky slopes, grassland, chaparral openings, blue oak woodland, 500–2800(–3800) ft.

Tetraploid counts of *Heterotheca sanctarum* have been made from Santa Clara and Santa Cruz counties (*Semple 5670*, *Semple & Chmielewski 8915*, *8916* [ $2n = 18\text{II} + 14\text{II} + 2\text{IV}$ ], *8918*, *8924* [diploids, triploids, tetraploids present, fide *Semple 2008*] and *8926*). A count by *Semple* (fide label data, *Semple & Chmielewski 8919*) suggests that diploids occur in Santa Cruz Co. but this collection is a mix of *H. sanctarum* and *H. camphorata* (identified in *Semple 2008* as "aff. var. *echioides*") and the diploid count needs to be verified, since all counts of *H. camphorata* have been diploid. It seems likely that *H. sanctarum* is consistently tetraploid.

*Heterotheca sanctarum* is sympatric with *H. camphorata* in Santa Clara, Santa Cruz, and San Benito counties and hybrids apparently are formed in Santa Clara Co., although the two species remain distinct for the most part. Possible evidence of gene flow shows in glandular involucre of *H. sanctarum* otherwise of characteristic morphology.

*Heterotheca sanctarum*, for the most part, was identified by *Semple* (by citation in 1996 and by annotation) within his concept of *H. bolanderi* var. *bolanderioides*. Plants of *H. sanctarum*, however, are distinct from both varieties of *H. bolanderi* in their silvery-sericeous leaf vestiture, which often more resembles that of *H. villosissima* and *H. fastigiata*. Treatment of *H. sanctarum* at specific rank allows that this entity may be as closely related (or more closely) to *H. villosissima* as to *H. bolanderi*. This similarity may underlie *Semple's* diagnostic comparison of his var. *bolanderioides* [emphasizing the *H. sanctarum* populations] to var. *echioides* (= *H. villosissima*).



1a. Leaves silvery to silvery-gray, 10–25(–40) x 2–8 mm; heads with capitular bracts 1/4–1/2 as long as the involucre, not at all obscuring the involucre ..... ***Heterotheca sanctarum***

1a. Leaves gray-green, mostly 20–45(–55) x 3–10 mm; heads (in var. *bolanderi*) with capitular bracts mostly as long or longer than the involucre, obscuring the involucre ..... ***Heterotheca bolanderi***

1b. Capitular bract margins densely long-ciliate; involucre 12–17 mm wide (pressed); axillary clusters of small leaves mostly absent; stems villous; inflorescence characteristically corymboid; tetraploid ..... ***Heterotheca sanctarum***

1b. Capitular bract margins ciliate but not prominently long-ciliate; involucre (8–)10–14 mm wide (pressed); axillary clusters of small leaves consistently present; stems hirsute; inflorescence characteristically subcorymboid to elongate-paniculate; diploid ..... ***Heterotheca villosissima***

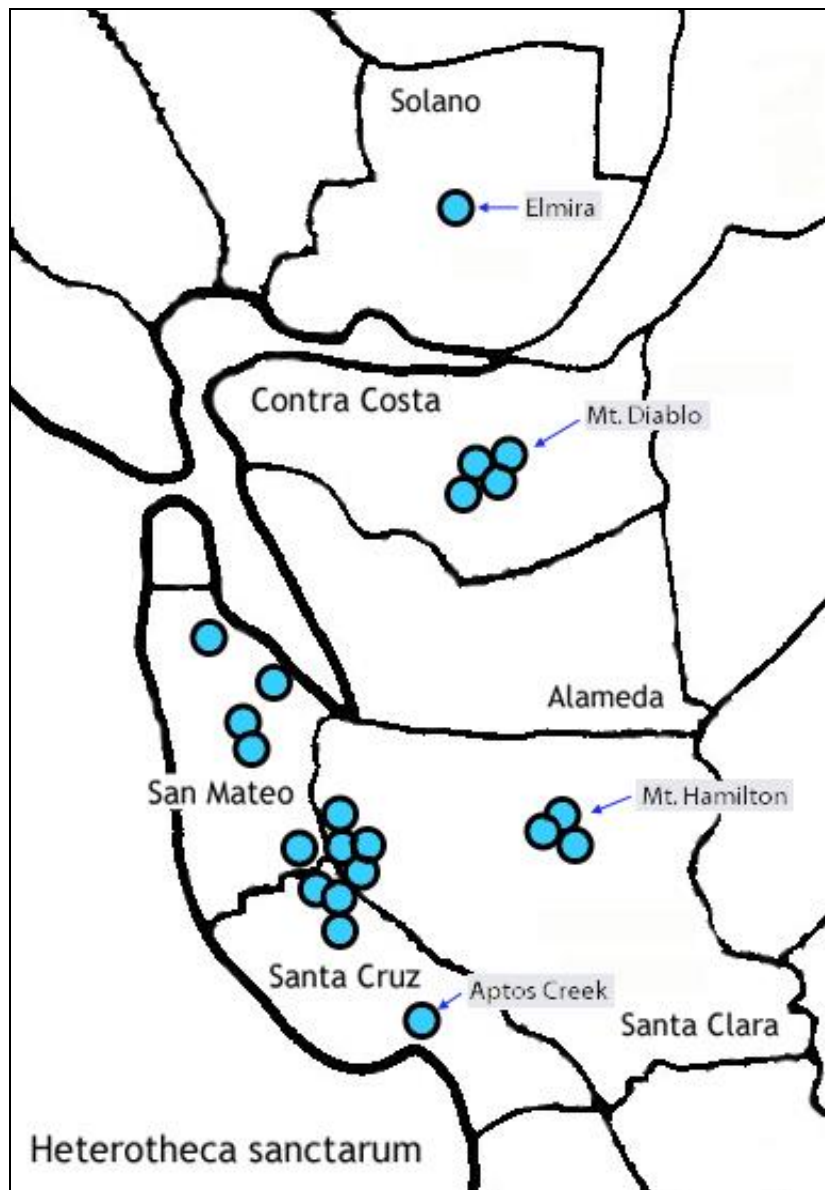


Figure 53. Distribution of *Heterotheca sanctarum*. Outlying localities are in Solano Co. (Elmira), Contra Costa Co. (Mt. Diablo), Santa Clara Co. (Mt. Hamilton), and Santa Cruz Co. (Aptos Creek). See Map 3 for broader context.

**Additional collections examined. California.** Contra Costa Co.: Mt. Diablo, Mt. Zion near base, open grassy hillside, 2 Dec 1930, *Bowerman 501* (UC); Black Diamond Mines Regional Preserve S of Pittsburgh, steep S-facing side of Rose Hill above cemetery near sandstone outcrops, ca. 1200 ft, 5 May 1991, *Ertter 9770* (UC); S side of Mt. Diablo, W end of Black Hawk Ridge, above chaparral on S slope, 2000 ft, 2 Sep 1996, *Ertter 15275* (BRIT, UC); SW side of Mt. Diablo, Wall Point Rd across Pine Ridge ca. 1/2 air mi ENE of Macedo Ranch, blue oak woodland on sandstone, 24 Nov 1996, *Ertter 15415* (UC); W flank of Mt. Diablo, Shell Ridge Open Space, exposed sandstone on main ridgeline, 16 Feb 1997, *Ertter 15458* (UC); SW side of Mt. Diablo, Secret Trail at head of Pine Canyon, oak woodland on sandstone, 14 Sep 1997, *Ertter 15812* (UC); Mt. Diablo, dry hillside, 5 Oct 1933, *Schreiber 940* (UC); Mt. Diablo State Park, Wall Point, grassland, 1450 ft, 29 Jun 2015, *Slakey 134* (UC). San Mateo Co.: ridge between Slate and Oil Creek, 2200 ft, 21 Jun 1935, *Carlson 77* (UC); Corte de Madera, 23 Sep 1906, *McGregor s.n.* (CAS); San Bruno Mtn., open slopes, ca. 1200 ft, 20 Aug 1966, *Rose 66087* (BRY, OBI, UC); Coal Mine Ridge, near Stanford University, 22 Sep 1906, *Rust 6* (DS). Santa Clara Co.: Saratoga, dry exposed slopes, 6 Oct 1906, *Abrams s.n.* [x *H. camphorata?*] (CAS, UC, WTU); Castle Rock Ridge, 7 Oct 1906, *Abrams s.n.* (DS); Black Mtn, occasional on open, grassy slopes, 20 Oct 1901, *Baker 56* (MO, POM); Black Mtn on Palo Alto Rd, *Baker 2418* (LL); Page Mill Rd, E slope of Santa Cruz Mts, dry bank, ca. 500 ft, 24 Jun 1934, *Blake 11759* (LL); W slope of Mt. Hamilton, dry gravelly slope, blue oak, 3800 ft, Sep 1934, *Ewan 8939* (UC); 8 mi from San Jose on road to Mt. Hamilton, 13 Aug 1933, *Howell 11511* [x *H. camphorata?*] (CAS); Castle Rock Ridge, 3 mi S of jct of Skyline Blvd and Saratoga Rd, dry open slopes, 2200 ft, 21 Sep 1937, *Rose 37666* (CAS, PH, RSA, UC); Page Mill Rd, NE of Calif Hwy 35, serpentine roadside, 85 road embankment, 21 Sep 1987, *Semple & Chmielewski 8915* (MO, RSA); Palo Alto on Page Mill Rd, 9.0 km NE of Calif Hwy 35, Foothills Park area, roadside embankment, 21 Sep 1987, *Semple & Chmielewski 8916* (MO); W of Palo Alto on Calif Hwy 35, 17.5 km SE of Hwy 84, Santa Clara MilePost 17.5, 22 Sep 1987, *Semple & Chmielewski 8918* (RSA-the 2 stems on left, larger stem on right is *H. camphorata*); Mt. Hamilton Rd to Lick Observatory, ca. milepost 18.53 at sharp corner in road, open roadside embankment, 23 Sep 1987, *Semple & Chmielewski 8924* (MO); Mt. Hamilton Rd to Lick Observatory, ca. milepost 14.62 at sharp corner in road, exposed rock, 23 Sep 1987, *Semple & Chmielewski 8926* (MO); W slope of Mt. Hamilton dry rocky exposed slopes, 2750 ft, 1 Sep 1934, *Sharsmith 1354* (TEX, UC); W slope of Mt. Hamilton, 1/2 mi by road above Hall's Valley, dry rocky exposed slopes on upper slopes of mountain, 2150 ft, 21 Oct 1934, *Sharsmith 1411* (UC); W side of Mt. Hamilton near summit, grassy slope in *Pinus sabiniana* belt, 4300 ft, 13 Sep 1936, *Sharsmith 3889* (UC); Mt. Hamilton, Sep 1904, *Smith s.n.* (UC); Mt. Hamilton foothills, 9 Sep 1908, *Smith s.n.* [x *H. camphorata?*] (JEPS); Monte Bello Ridge, ca. 8.5 mi S from Palo Alto, between summit of Black Mtn and Page Mill Rd, open grassland, ca. 2400 ft, 3 Oct 1965, *Thomas 11454* (RSA). Santa Cruz Co.: head of Aptos Creek, 12 Oct 1902, *Abrams 3073* (RM); 4 mi SE of Saratoga Gap on Summit Rd, Santa Cruz Mts, common in chaparral opening, 900 m, 3 Sep 1962, *Fosberg 43225* (POM); near Saratoga summit, ca. 2500 ft, 2 Sep 1954, *Hesse 1211* (UC), *1388* (UC), *1389* (UC); 7 mi WSW of Saratoga, 2000 ft, 29 Apr 1935 [old stems], *Johannsen 605* (UC); Castle Rock Ridge, 3 mi S of the jct of Skyline Blvd. and Saratoga Rd, 670 m, 21 Sep 1937, *Rose 37666* (UC); Calif Hwy 35 NW of Saratoga, high elevation, 20 Aug 1981, *Semple 5670* (JEPS, MO); Calif Hwy 35, 5.6 km S of Calif Hwy 9, near rock exposure along roadside, 22 Sep 1987, *Semple & Chmielewski 8919* (MO); ca. 1 mi S of Saratoga Summit, 3 Oct 1953, *Thomas 3590* (CAS, RSA); Castle Rock Ridge, 2500 ft, 29 Jul 1934, *Yates s.n.* (RM). Solano Co.: Fields near Elmira, 11 Jun 1910, *Toy s.n.* (DS).





Figure 54. *Heterotheca sanctarum*, Santa Clara Co. Isotyp (US).



Figure 55. *Heterotheca sanctarum*. Detail from US isotype shown in Figure 54.



Figure 56. *Heterotheca sanctarum*, Santa Clara Co. Isotype (UC).



Figure 57. *Heterotheca sanctarum*, Santa Cruz Co. Yates 4954 (UC).





Figure 58. *Heterotheca sanctarum*, Santa Cruz Co. Hesse 1211 (UC).





Figure 59. *Heterotheca sanctarum*. San Mateo Co., Russian Ridge Open Space Preserve. Photo by Will Ferguson, 18 Nov 2018. iNaturalist.





Figure 60. *Heterotheca sanctarum*. Detail from Figure 58.



Figure 61. *Heterotheca sanctarum*. Santa Clara Co., Sierra Azul Open Space. Photo by Edward Rooks, 5 Oct 2018. iNaturalist.