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PLANT PORTRAIT

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1163. *Heterotheca camporum* (Greene) Shinners

Compositae

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Summary

Heterotheca camporum (Greene) Shinners (Compositae: Astereae: Chrysopsidinae) is described and illustrated. Notes are provided for the species' cultivation, propagation, likely pests and diseases, and availability. A full synonymy is given, along with type citations and known presence of type material, together with relevant notes. Selected illustrations of the species are cited, and statements of the species' distribution, habitat and ecology, phenology, etymology, conservation status and vernacular names provided. The Wakehurst plants vary considerably in capitulum size, but critical morphological characters are identical, placing the material in *Heterotheca camporum* var. *camporum*, one of the Western Goldenasters. There are currently two concepts of the infrageneric division of *Heterotheca* Cass. Semple's, used in the *Flora of North America*, would place our material in *Heterotheca* sect. *Phyllotheca* (Nutt.) Harms. In contrast, Nesom's more recent sectional concept restricts sect. *Phyllotheca* to the western seaboard of the United States; more specifically he considered the section essentially Californian. Nesom placed our species, one of 49, in sect. *Chrysanthe* G.L. Nesom; our species belongs in the *Heterotheca villosa* group or complex. *Heterotheca camporum* is easily confused with *Chrysopsis mariana* (L.) Elliott, the name on the accession of this material in the North American Prairie plantings at Wakehurst; it has historically been confused with this species in Illinois, and probably elsewhere.

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INTRODUCTION

When the authors first came across the subject of this plate, *Heterotheca camporum* (Greene) Shinners (Compositae: Astereae: Chrysopsidinae) (Lemonyellow false Goldenaster, Prairie Golden Aster, Western Golden Aster, Golden Aster), it had been accessioned and identified as the variable and widespread *Chrysopsis mariana* (L.) Elliott (Maryland Goldenaster, Golden Aster). The main planting was in the Atlantic Coastal Plain Prairies community bed of the North American Prairie plantings at Royal Botanic Gardens, Kew at Wakehurst Place, Ardingly, West Sussex. However, it was after it started flowering in mid-2024, and subsequent collections made in September of the same year, that the first author questioned its identity. On both occasions, the second author had collected representative material that included flowering stems with small- to medium- (c. 25 mm across rays) and relatively large-sized capitula (c. 45 mm across the rays, with the rays to c. 20 mm long × 4.5 mm wide). The selected material was from different plants, and the aim was to illustrate the plant and produce the colour plate (plate 1163) and text figure (figure 1) that accompany this article. Both authors had noted that the ray limbs were far, far larger than those described in the *Flora North America* account for *Chrysopsis mariana* (Semple, 2006b), and other accounts by Semple (1996) and Nesom (2020b: 129) effectively concurred. A thorough re-examination of the material, and a reappraisal of the literature, provided the answer as to the identity of the material growing at Wakehurst; it was *Heterotheca camporum* var. *camporum*.

A synoptical short history of the two allied genera, *Heterotheca* Cass. and *Chrysopsis* (Nutt.) Elliott is worth providing, as it provides an excellent modern example of the classical 'lumpers versus splitters' approach to the taxonomy of the two genera (see Semple, 2025).

Heterotheca Cass.

The genus *Heterotheca*, known as the Goldenasters, or sometimes Camphorweed or Telegraph Weed, was described based upon one species possessing heteromorphic achenes – those of the ray florets triquetrous to cylindrical, and of the disc florets obcompressed (Cassini, 1817: 137). The lack of a biseriate pappus on the ray achenes of the generitype is not considered diagnostic for the genus. Based originally on *Inula subaxillaris* Lam., the formal transfer of this species to *Heterotheca* occurred some seventy years later, courtesy of Britton & Rusby (1887).

Species have routinely been added through to 1951 when Shinners (1951) merged the by now larger genus *Chrysopsis* (see Gray, 1884 –12 spp. in 2 formal sections) with *Heterotheca*. This was also supported by Harms (1965) in a cytogenetic study that included several crossing experiments and examination of the F1 progeny. Shinners considered that the diagnostic difference (of the epappose ray achenes) of no consequence. Working towards a Flora of an area of North-Central Texas (Shinners, 1958), all the required combinations were made, including many of taxa from other States.

Harms (1968: 12) followed Shinners' broad concept of *Heterotheca*, with four sections, and in providing a conspectus of *Heterotheca* sect. *Chrysopsis* (Nutt.) V.L. Harms (Harms, 1974: 158), considered that Nuttall had recognised *Chrysopsis* as a section of *Inula* L. A while later, and in dispensing with any formal infrageneric taxa, Semple (1981: 324) mentioned nothing in the generic synonymy, but incorrectly stated in his Historical Review … that Nuttall's name appeared as a 'sectional name under the genus *Inula* L.' It seems likely that both authors (Harms and Semple) had possibly not read enough of Nuttall's account. Nuttall had very clearly (in his second paragraph of the protologue) noted 'Herbaceous; flowers fastigiate, subcorymbose, stem simple or paniculately branched; radial florets rarely ever more numerous than in *Aster*, to which this subgenus is very closely related. …'.



PLATE 1163 *Heterotheca camporum* var. *camporum* CHRISTABEL KING

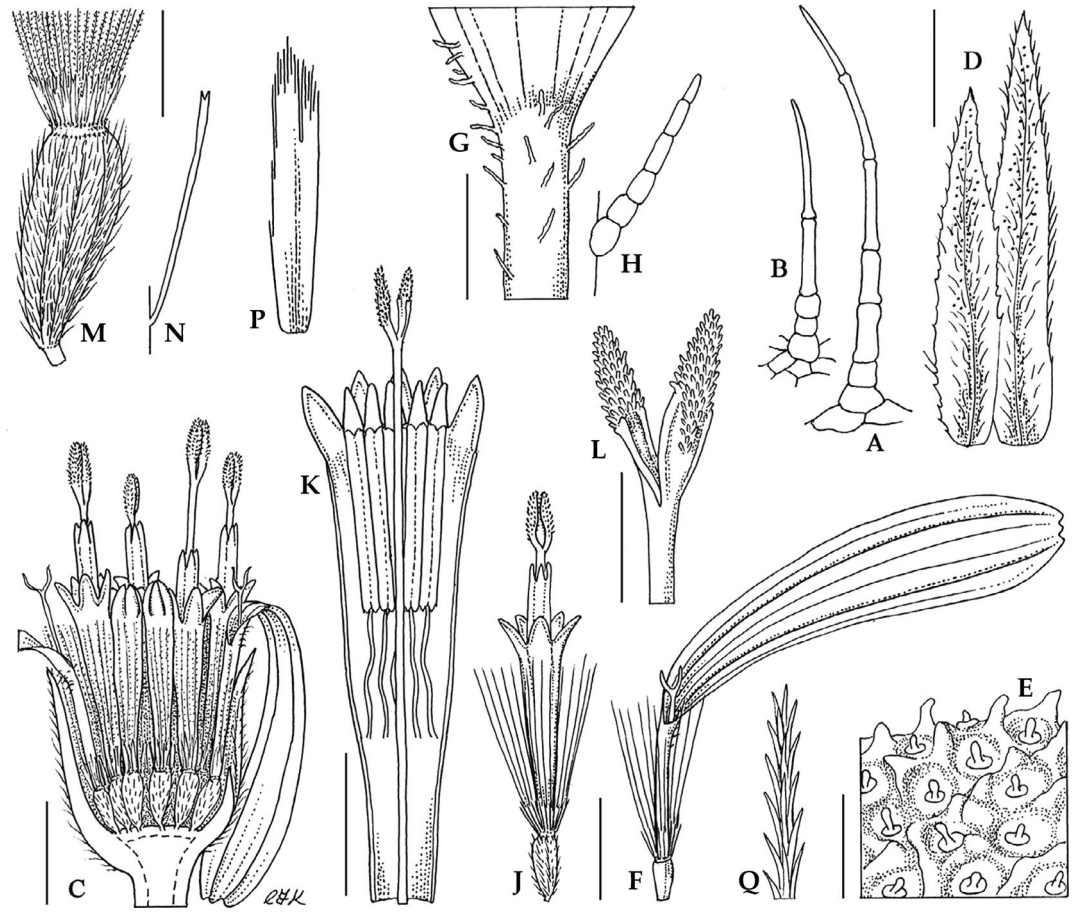


FIGURE 1 *Heterotheca camporum*. A, osteolate hair from leaf margin, highly magnified; B, osteolate hair from abaxial leaf surface, highly magnified; C, l.s. flowering capitulum; D, phyllaries – showing outer (l) to inner (r); E, receptacle surface post achene dispersal; F, ray floret; G, detail of abaxial surface of base of ray limb and ray corolla tube; H, detail of uniseriate, septate hair from ray floret; J, disc floret; K, disc floret corolla, opened out to show attachment point of anther filaments; L, style arms of disc floret; M. disc floret achene with base of pappus; N, setula from disc floret achene with highly magnified detail of apex of setula; P, scale-like outer pappus setae, highly magnified; Q, detail of apex of disc floret inner pappus seta. Scale bars: E, G, L, M = 1 mm; D, K = 2 mm; C, F, J = 4 mm. Drawn by Christabel King from material (Accession No. 2020–761*1) growing in the Atlantic Coastal Prairies section of the North American Prairie plantings at Royal Botanic Gardens, Kew at Wakehurst Place.

Semple's generic concept of *Heterotheca* is still that of a genus of 28 spp., in three sections: the type, sect. *Heterotheca* (7 spp., essentially across the southern States from the Pacific through to the Atlantic and Mexico; see Wagenknecht, 1960; Semple, 1996, 2025), sect. *Ammodia* (Nutt.) V.L. Harms (1 sp., coastal North America from the Pacific States; Semple et al., 1988; Semple, 1996, 2025), and sect. *Phyllotheca* (Nutt.) V.L. Harms (20 spp., albeit with 24 varieties, the most widespread section in the genus; Semple, 1996, 2025). Semple's generic concept (Semple, 2006c) is that provided in the *Flora of North America*, but this account lacks his infrageneric treatment – this has been provided separately (Semple, 2025). In contrast, Nesom's concept of *Heterotheca* is of 70 spp. (raising many of Semple's varieties to species level), in four sections, sect. *Heterotheca* (8 spp.) and sect. *Ammodia* (3 spp.) (both sections treated in Nesom, 2019), sect. *Phyllotheca* (10 spp., primarily Californian; Nesom, 2021), and the largest, sect. *Chrysanthe* G.L. Nesom (49 spp.; Nesom, 2020b), formed from dividing Semple's concept of sect. *Phyllotheca*.

Chrysopsis (Nutt.) Elliott

Eleven species, known widely as the Goldenasters, Golden-Asters or Camphor weeds, now form the genus *Chrysopsis* (Nutt.) Elliott, nom. cons. (Nesom, 1991a, 2000; Semple, 1981, 2006b). *Chrysopsis* is based on Nuttall's *Inula* L. subgen. *Chrysopsis* Nutt. (Nuttall, 1818b: 150) of which *Inula mariana* L. (= *Chrysopsis mariana*) is the conserved type. Incidentally, this has doubtless led some authors to cite the species as '*Chrysopsis mariana* Nutt.' (e.g. Kuntze, 1891: 334, who considered Rafinesque's *Diplogon* had priority). Elliott's combination was conserved (see Briquet in Wettstein et al., 1906: 254 [= 92]), against *Diplogon* Raf. (Rafinesque, 1819: 195), even though it dates from 1823 (Elliott, 1823: 335), with Elliott removing all of the non-Inuloid taxa, but continuing to maintain the yellow ray limb colour as characteristic of his genus. The name *Diplogon* dated from 1818, although at that time the name was invalid, it was simply a *nomen nudum* in Rafinesque's lengthy critique of Pursh's *Flora of North America* (see Rafinesque, 1818) under his 'observation' 118 (of 137!): 'And also *Inula mariana* with some other species, which must form the genus *Diplogon*, Raf. N.G.' Valid publication came a year later (in yet another of Rafinesque's critiques, this time of Nuttall's *The Genera of North American Plants*… – see Nuttall, 1818a, b), although the generic name was finally rejected against Elliott's. Rafinesque's comments are perhaps relevant: 'The sub-genus *Chrysopsis*, N., (*Inula*, L. and *Aster*, L.) was named *Diplogon* in Fl. Missurica, and adopted by us as a N. G.; that name is preferable, since some of the species have white flowers!' (Rafinesque, 1819: 195). Perhaps somewhat interestingly, *Chrysopsis* has been conserved twice, the second time it was against *Diplopappus* Cass. (Cassini, 1817: 137) (see Greuter & Flann, 2010: 1285–1285; and the acceptance of this proposal in Brummitt, 2011: 1209 – a unanimous vote for recommendation).

Small (1933) was less inhibited than Gray, recognizing four [unranked] groups within *Chrysopsis*, a genus he considered contained 20 species, some 13 present in the southeastern States. Semple (1985: 429) clearly recognised Small's groups as 'sp. groups') in commenting under '*Pityopsis* sect. *Graminifolia*', although Small himself declared only that 'Complex genera have been divided into more natural groups, both for convenience of study and also in order to make the genera, as far as possible, correspond in rank to the great majority of groups of species now recognized as genera by most present-day botanists.' (Small, 1933: Preface p. v). An overview of both *Chrysopsis* and *Heterotheca* were given by Nesom (2000).

Subtribal placement of *Heterotheca* and *Chrysopsis*

Nesom (2020a) summarized his revised thinking on the subtribal classification of the tribe Astereae (see Nesom, 1994) and, having noted the overview provided by Brouillet et al. (2009), confirmed his placement of both *Heterotheca* and *Chrysopsis* in the subtribe Chrysopsidinae – along with *Bradburia* Torr. & A. Gray, *Croptilon* Raf., *Noticastrum* DC., *Osbertia* Greene, *Pityopsis* Nutt. and *Tomentaurum* G.L. Nesom. Nesom (1991a) had reunited *Bradburia* with *Chrysopsis* earlier in his work on the group, but later (Nesom, 2020a) decided to re-separate the species and re-recognize *Bradburia*, as had Semple (1996: 7) when beginning to revise *Heterotheca*.

In an earlier cladistic analysis, Nesom (1991b) had proposed a phylogeny of the eight genera he considered constituted the Goldenasters, based on three lineages. In one, the South American *Noticastrum* appeared with *Osbertia* and *Chrysopsis*; *Tomentaurum*, *Croptilon* and *Pityopsis* formed a second lineage, and; *Heterotheca* sect. *Ammodia*, *Heterotheca stenophylla* (A. Gray) Shinners, *H. mexicana* V.L. Harms & B.L. Turner and the remainder of *Heterotheca* in the third.

Semple's (2025) only critique of this arrangement was based on Brouillet et al. (2009). He noted that *Pityopsis* appeared as a 'polytomy at the base of the Chrysopsidinae Clade' (in Brouillet et al., 2009), '*Chrysopsis* grouped with *Bradburia'* and *Noticastrum* grouped with the majority of *Heterotheca*, *Croptilon* and *Noticastrum*. His final comment 'Further work is needed' may simply refine the picture, but not necessarily suggest abandoning the concept of Nesom's subtribe.

Inadvertently, the first author did not include *Heterotheca camporum* in the 'One hundred and six interesting North American Prairie Compositae …' (Hind, 2023 [2024]: Appendix1, p. 390); but its basionym, *Chrysopsis camporum* Greene had been. Other than this taxonomic faux pas, the number of species listed remains unchanged, as does the number of genera. However, it is clear that a number of equally useful and attractive Prairie Compositae can be added from *Heterotheca* (e.g. *H. canescens* (DC.) Shinners (Hoary Goldenaster), *H. hirsuta* (Greene) G.L. Nesom (Spokane False Goldenaster), *H. hirsutissima* (Greene) G.L. Nesom (Harsh False Goldenaster), *H. villosa* (Pursh) Shinners (Hairy Goldenaster)), in addition to *Pityopsis graminifolia* (Michx.) Nutt. (Grass-leaved Goldenaster or Narrowleaf Silkgrass), and the related *Croptilon* (Stiff-leaf Scratchdaisy, e.g. *Croptilon rigidifolium* (E.M. Smith) E.B. Smith) providing that seed supplies can be found.

CULTIVATION

The Wakehurst accession of the plant covered in this plate is Accession No. 2020–761 but, regrettably, there is no source data available for the collection, other than it was originally supplied as *Chrysopsis mariana*.

Heterotheca camporum still remains poorly known in cultivation, and was not listed in Cullen et al. (2000), Diboll & Cox (2023) or Cubey et al. (2024). However, in what was clearly a broad-concept *Heterotheca*, it may have been included within *H. villosa* (Pursh) Shinners listed by King (2000: 564) and Sutton (2001: 57 – albeit alongside *H. mariana* (L.) Shinners). It had been mentioned previously by Jeffrey (1992: 619 – as *Chrysopsis camporum*) who considered it a useful 'late summer and autumn-flower perennial for the border, wild garden and native plant collections.' As an excellent butterfly plant, it is a good plant for dry prairie plantings, rock gardens, and in a collection of meadow plants, but can also be useful in general borders and in cottage gardens.

It is an easily grown species that will tolerate a wide range of soils, but prefers a well-drained situation in full sun (but will tolerate very light shade) and, when established, is particularly drought tolerant. It is an adaptable plant and, once established, ideal for hot, dry and sunny banks on sandy soils. It certainly does not tolerate having its roots in water. Plants can flower in their first year from seed sown in the early spring – see Propagation below.

It is usefully hardy, and was listed as Z5 (−20°F to −10°F; −28.8°C to −23.4°C) by Jeffrey (1992: 619), is listed from USDA hardiness zones 4–8 (−30°F to −25°F to 10°F – 25°F; −34.4°C to −28.9°C to −12.2°C to −6.7°C), and can be expected to flower for well over four months, at least until stopped by the first hard frost.

As one of the many homochromous yellow-flowered species listed in Hind (2023 [2024]) it can be planted with like-coloured species and contrasted in its leaf form (e.g. *Coreopsis lanceolata* L. – Hind et al., 2023 [2024]; *Rudbeckia hirta* L. – Hind & Lambkin 2023d [2024d], albeit with the characteristic dark cone; *Solidago nemoralis* Aiton – Hind & Lambkin, 2023b [2024b]), or planted with other contrasting-coloured prairie plants (e.g. *Echinacea purpurea* (L.) Moench – Hind et al. 2025 [2026]; *E. tennesseensis* (Beadle) Small – Hind, 2018; *Eurybia spectabilis* (Aiton) G.L. Nesom – Hind & Lambkin, 2023a [2024a]; *Liatris aspera* Michx. – Hind & Lambkin, 2023e [2024e]; *Parthenium integrifolium* L. – Hind & King, 2023 [2024]; *Ratibida columnifera* (Nutt.) Wooton & Standley var. *pulcherrima* (DC.) D.J.N. Hind –

Hind, 2006; *Symphyotrichum laeve* (L.) G.L. Nesom – Hind & Lambkin, 2023c [2024c]; *Vernonia missurica* Raf. – Hind & Langhorne, 2023 [2024]). Clearly some forethought will have to be taken in terms of balancing the heights of associated species.

Propagation. Three straightforward methods are available for the species that the first author has outlined before (Hind, 2023 [2024]): By far and away the easiest method of propagation of the North American Prairie Compositae, and the one certainly to provide the highest yield, is by sowing achenes (seeds). Other than sowing achenes direct (as soon as they ripen in late summer or early autumn), two main treatments are generally used, even in the Compositae, and these are covered below – mature, clean achenes are needed for sowing.

Dry stratification. Ripe achenes can be pre-treated by subjecting them to cold (of c. 0°C) for a month or more (typically between 30 and 60 days). Dry achenes can be stored in zip-locking bags in a fridge, or in a rodent-proof container (typically a storage tin) in an unheated building (outhouse, shed, etc.) over winter depending upon the species. The achenes can then be sown directly into prepared ground in their final growing position/s or, for those species that don't mind disturbance, the achene/sand mix can be sown in 8 cm pots and seedlings pricked out when they're large enough to handle.

Cold moist stratification. Ripe achenes require 4–6 weeks treatment to break their dormancy and improve germination; this method effectively mimics overwintered achenes under a layer of soil or snow. The achenes should be sown (in the autumn or early winter) onto the surface of a damp (but not soaking wet) proprietary seed compost mix in pots or trays, and covered with a thin layer of grit or vermiculite. The pots can be bagged and placed in a fridge for between four and six weeks, or placed in a frame or cold greenhouse. If the achenes begin to germinate, remove the pots from the fridge and, bag-free, maintain them in warm bright conditions. When the seedlings are large enough to handle, they can be potted on, keeping them moist all the time. Alternatively, the achenes can be sown in the spring, provided they have been stratified. The achenes can be mixed with moist sand and stored in the fridge for about 60 days before sowing. The achene/sand mix could also be spread into the plants' final growing positions.

Cuttings & Division. One option for vegetative propagation is the use of stem cuttings, which should be taken from early- to mid- season growth; the use of rooting hormone powder is optional, but may provide higher success rates. On the whole it is far better to use relatively nutrient poor composts to root prairie plant cuttings in, and a proprietary seed compost will suffice, ideally not peat-based. One word of caution, cuttings taken in the summer, or from new growth, have a low success rate, compared with those taken from early- to mid- season growth. Leafy stems wilt very rapidly, so the aim should be to take cuttings early in the morning, and keep them in the shade, or enclosed in plastic bag or propagator. Other options for vegetative propagation include rhizome cuttings in addition to division. Reasonably long segments of the rhizome (ideally with a terminal bud) can be planted horizontally and covered with soil or horticultural grit (c. 2.5 cm deep) in their final position (not forgetting to mark where they are to avoid unwarranted disturbance before they start growing in the spring), or in pots to be planted out later when established. Extra protection of autumn-divided rhizomatous plants, with a good mulch, may be advisable in areas prone to very cold winters. Once the rhizomatous rootstock has well-established there is scope for dividing the plants by splitting the rhizomes, with pieces possessing actively growing shoots likely to provide the best material. Rhizomatous species can be divided at almost any time during the year.

Pests & Diseases. The Goldenasters are all of relatively low maintenance, and not prone to any pests or diseases, and apparently usually ignored by deer. Other than snail damage as the new season's grown appears, no other real pests are known. Mildew may be an issue, especially on poorly drained soils which is remedied by either moving the plantings to a better-drained position, or planning the planting only in well-drained soils in full sun.

Availability. In the current *RHS Plant Finder* (Cubey et al., 2024) the species is apparently unavailable in the UK, although clearly available from some suppliers in the United States; it is a plant that would be well-worth sourcing seed for a mixed prairie planting, or especially for drier borders.

NOMENCLATURE & DESCRIPTION

Heterotheca camporum (Greene) Shinners, Field & Lab. 19: 71 (1951).

Chrysopsis camporum Greene, Pittonia 3 (14): 88 (1896). Type: 'A most distinct prairie species, of apparently limited range in the middle Mississippi Valley, in southern Illinois and perhaps adjacent Missouri, also extending thence southeastward; apparently first collected by *Short*, and confused with *C. villosa*.' Holotype (according to Semple, 1996: 152, and Nesom, 2020b: 129): NDG (53779 – 'Prairies of Illinois', dist. 1842); isotypes: GH (00055849 – 'Prairies of Illinois'), NY (00163161 – 'Prairies of Illinois', dist. 1837; 00163226 – 'The branched specimens are from the open prairies./ The single from the woods of Illinois', dist. 1837, considered an isotype by), PH (00004318 – 'Open prairies of Illinois, Septr.', dist. 1837, det. as isotype by Shinners), US (00652172 – 'Prairies of Illinois'). Note: Harms (July 1963) clearly selected the NDG material as the lectotype, but it is unclear if this was formerly published, especially since Semple (1996: 152) considered this collection the holotype of the name.

Chrysopsis villosa (Pursh) Nutt. ex DC. var. *camporum* (Greene) Cronquist, Bull. Torrey Bot. Club 74 (2): 150 (1947).

Heterotheca villosa (Pursh) Shinners var. *camporum* (Greene) Wunderlin, Ann. Missouri Bot. Gard. 59 (3): 471 (1973). Note: IPNI (2012) indicates '1973' yet the cover of 59 (3) suggests '1972'; confirmation of the date is from a footnote at the end of 59 (3) indicating that 59 (2) was published in 'March 1973'.

Illustrations (selected). Britton & Brown, Ill. Fl. N. States & Canada 3: 324, Fig. 3656 (1898) (b&w); Britton & Brown, Ill. Fl. N. States & Canada, Ed. 2, 3: 373 (1913) (b&w); Semple, Univ. Waterloo Biol. Ser. 37: 157 (1996) (b&w of both vars., and dist. map); Yatskievych, Steyermark's Fl. Missouri, Rev. Ed., 2: 241, Plate 236 (2006) (b&w); Mohlenbrock Ill. Fl. Illinois Pt. 1: 101 (2015); Nesom, Phytoneuron 2020–68: 130, Fig. 81; 131, Fig. 82 (2020b) (col. images of herbarium material). Note: the thumbnail drawings in both editions of Britton & Brown are somewhat stylized and scarcely critical enough to identify the species.

Perennial herb, 20–75 (– 90) cm tall (var. *glandulissima* can grow up to 140 cm), plants about 30–60 cm across, often odoriferous (and somewhat smelling of camphor); usually taprooted and with stout (c. 14 mm diam.), moderately short lateral rhizomes (in our material) with new rosettes borne at ends of short lateral rhizomes, rhizome hollow (at least in our material), surface appearing braided. *Stems* erect or ascending (often purplish or reddish-brown at base), usually simple, predominant indumentum strigose, of sparse to sub-dense eglandular, multicellular, uniseriate osteolate hairs (these denser on young stems and both leaf surfaces, indumentum eventually spreading and sparse on older basal portions of stems), and sparsely to

moderately short-stipitate-glandular amongst strigose hairs. *Leaves* moderately pubescent, hairs mostly restricted to veins and veinlets (although occasionally few in areolae), scabrid or strigose, all pointing to leaf apex and appressed to leaf surfaces, basal cell distinctive, smooth-surfaced and curved towards leaf apex, main portion of hair 2–3 celled, uniseriate, septate, often swollen at each septum and surface appearing textured (often described as, apical cell long-acute, both surfaces also short- to medium- stipitate-glandular, usually restricted to areolae, *basal leaves* spathulate to oblanceolate, 38–73 mm long × 6–15 (−18) mm wide, bases attenuate, margins obscurely dentate apically or entire, apices acute to obtuse, surfaces initially moderately-dense to densely strigose, *cauline leaves* sessile, blades lanceolate to elliptic-oblong, 20–45 × 2–7 mm, smaller distally, margins entire or obscurely dentate or serrate, long-ciliate (especially along basal narrowed portion/ pseudopetiole), cilia c. 2.5 mm long, all osteolate, apices acute. Inflorescences of solitary capitula, or few- to many-headed (1–24), lax to somewhat congested cymes to corymbs, capitula pedicellate, *pedicels* (from axils of uppermost cauline leaves or bracteoles) 0.5–3.5 cm long, moderately-densely stipitate-glandular (glands yellow to brown); bracteoles on pedicels 0–3, linear, stipitate-glandular, usually with many subtending involucre and almost appearing as subinvolucral bracts (or even calycular bracts), 5–7 mm long × 0.7–1 mm wide, margins conspicuously (under a lens) spreading-long-ciliate towards base, cilia c. 1–2.5 mm long, uniseriate, septate, osteolate, but more robust than hairs on leaf lamina and stems. *Capitula* heterogamous and radiate, homochromous, 2.5–4.5 cm diam. (across spreading rays); *involucres* campanulate, 7–10 mm tall × 10 mm diam., appearing turbinate when dry; *phyllaries* 4–5-seriate, erect, linear (middle and innermost) or narrowly triangular (outermost), gradate, imbricate, sparsely strigose abaxially, margins finely or very narrowly hyaline, area above midrib narrowly or broadly green with a central orangish vein (visible when dry), apices acute but adaxially with a tuft of several eglandular hairs, abaxial faces sparsely- to moderately- short-stipitate-glandular, outer phyllaries 5–7 mm long × 0.5–1.0 mm wide, innermost phyllaries c. 12 mm long × 1.5 mm wide; receptacle at first concave, becoming convex at achene loss, alveolate (although sometimes described as foveolate, but clearly incorrect in our species as surface usually with short scales on margins of alveolae between achene insertion points), epaleaceous, glabrous. *Ray florets* 16–24 [−38], female, ray limbs 10–17 (−20) mm long × (1–)2–4.5 mm wide, concolorous and uniform in colour throughout length, Aureolin 3 to Lemon Yellow *60*4 (RHS, 1938), Yellow Group 12A (RHS, 1995), ray limbs at first erect in bud, markedly rolled lengthwise, and eventually expanding as rays begin spreading, then becoming coiled and tending to darken slightly as they age and senesce, eventually falling when brown-coloured, corolla tube 6–8 mm × c. 1 mm diam., very sparsely pubescent and hairs relatively few in band at base of abaxial surface of ray limb, eglandular, uniseriate, septate, with rounded apical cell; style arms scarcely exserted. *Disc florets* hermaphrodite, fertile, 25–40 (−66); corollas 5–7 mm long × c. 1 mm diam., duller yellow than in ray limbs, lobes 0.5–1 mm long, acute, tube glabrous; anther cylinders completely exserted, yellow, apical anther appendages long-triangular, c. 0.5 mm long, translucent, apex obtuse to rounded, basal anther appendages shortly tailed, entire, acute; style long-exserted from corolla throat, yellow, style arms c. 1 mm long, spear-shaped, at first adnate at apices, eventually spreading, abaxially long-papillate in upper half of arm. *Achenes* monomorphic, obcompressed, 2–3.9 (−6) mm long, obcompressed, often with 2 darker, or almost concolorous, marginal veins with few shallow ribs on faces, or smooth, body straw-coloured (or almost an olive-green in fresh immature achenes), sparsely to moderately-densely or densely setuliferous, setulae of long twin-hairs, usually twisted/contorted throughout length, apical cells scarcely subequal, and barely separate, finely acute; *carpopodium* a narrow, glabrous annulus, sometimes scarcely asymmetrical; *pappus setae* biseriate, outer setae scale-like, 0.2–1 mm long, apices acute, margins laciniate, inner 4–6 (−8) mm long, somewhat flattened and bristle-like, sub-densely finely barbellate, off-white to fawn-coloured, persistent (see also Semple, 2006a). An entirely tetraploid species: $2n = 36$ (Semple, 1996: 145). Figure 1.

DISTRIBUTION. United States of America (Arkansas, North Carolina, Illinois (see note referring to Mohlenbrock below), Indiana, Iowa, Missouri (Yatskievych, 2006), Tennessee, Virginia (Weakley et al., 2012) – ephemeral introductions of the species have occurred in Alabama, Georgia, Kentucky (Jones, 2005), Michigan, New Jersey and possibly other eastern States, although apparently excluding the SE US coastal plain. Note: Mohlenbrock (2015) commented that several records for *Chrysopsis mariana* for Illinois were misidentifications for '*C. camporum* Greene' (= *Heterotheca camporum* (Greene) Shinners). He also cited the species (as *Chrysopsis camporum*) from Manitoba to British Colombia, south to New Mexico and Alabama, but provided no additional evidence for such a wide distribution which is unsupported by either Semple (1996) or Nesom (2020b). NOTE: Nesom (2020b: 10 – Map 9 & in dupl. 132 – Map 83) provided an up-to-date distribution map for the species' two varieties, suggesting a more obvious geographical separation of the two.

HABITAT & ECOLOGY. Prairies, especially on sandy plains, sandy barrens, limestone glades, cracks in limestone bluffs and pavements, open oak woodlands (especially in the central Oak-Hickory vegetation zone), and in disturbed areas such as roadsides, fields, railroads, rights-of-way, especially on sandy soils. (30)–100–300 (−800) m (Semple, 1996: 152).

PHENOLOGY. Flowering (mid-June–) July–October (–December), depending on the severity of the first frosts.

ETYMOLOGY. The generic name is from the Greek *Heteros* (Ετερος) = different, and *theke* (θηκη) = container, alluding to the difference in shape of the ray and disc floret achenes of the generitype. The Latin specific epithet *camporum* = 'of the fields'. Note: In Semple's infrageneric key (Semple, 1996: 25), only his concept of *Heterotheca* sect. *Heterotheca* possessed heteromorphic achenes. Section *Ammodia*, and the more widespread sect. *Phyllotheca*, both possessed homomorphic achenes; Nesom's narrower concept of sect. *Phyllotheca* (Neson, 2021) and his concept of sect. *Chrysanthe* (Nesom, 2020b), both possessed homomorphic achenes.

CONSERVATION STATUS. A widespread species (with one variety, var. *glandulissima*, clearly expanding its distribution) without any obvious threats, and capable of spreading in several disturbed habitats; LC (Least Concern) – for either of the varieties.

VERNACULAR NAMES. PRAIRIE GOLDEN ASTER (Britton & Brown, 1898: 324); GOLDEN ASTER (or GOLDEN-ASTER) (usually referring to the whole genus *Chrysopsis*, and often to species of *Heterotheca*), LEMONYELLOW FALSE GOLDENASTER. Britton & Brown (1913: 374) cited *Chrysopsis camporum* in the synonymy of *Chrysopsis villosa* (Pursh) Nutt., providing the vernacular name of HAIRY GOLDEN ASTER for the latter.

DISCUSSIONS

When both authors had started working on the material growing at Wakehurst, it became evident that several aspects of the plants did not agree with the descriptions available in the literature (e.g., Britton, 1901: 930; Semple, 1981: 349–350; 2006b: 215), specifically the size of the ray limbs. Whilst certainly a GOLDENASTER, the larger capitula amongst the Wakehurst material possessed ray limbs of up to 20 mm long × 4.5 mm wide, significantly larger than those recorded in *Chrysopsis mariana*, or any other species in the genus. Verification of the material was mandatory and began with the general key to the Astereae in *Flora of North America* (FNAA, 2006), since the plant was being illustrated for *Curtis's Botanical Magazine*, and a comparison with the generic

descriptions and keys to both *Chrysopsis* (Semple, 2006b) and *Heterotheca* (Semple, 2006c). Semple et al.'s comparative paper on aspects of the morphology, anatomy, habit and habitat amongst the GOLDENASTERS (Semple et al., 1980: Figs 15–17 & 20) proved invaluable, and provided a diagnostic character allowing confirmation of the genus to which the Wakehurst material belonged – *Heterotheca*, and not *Chrysopsis*. The possession of osteolate hairs on the stems, leaves, bracts and bracteoles confirmed it did not belong in *Chrysopsis*.

Hair types – and how to solve a taxonomic problem

Stimulated by their studies into *Senecio* L., and the profusion of literature on anatomy, palynology and cytology in the Compositae, Drury & Watson (1966) diverted their studies into a brief survey of the whole family. The apparent lack of a critical review of generic classification of the family since Bentham's account of the family (Bentham, 1873), led them to look more critically into the major groupings of genera which had 'been overlooked by taxonomists.', e.g. the 'Inuloideae' = Inuleae *sensu lato*. Their summary results provided observations on crystals in achene cuticles, leaf indumentum and stem anatomy, and these were illustrated and tabulated, dividing the Inuleae into two groups of the eight subtribes following Bentham's synopsis.

Drury & Watson segregated the eglandular leaf hairs into two distinctive groups, 'Type A' and Type B'. 'Type A' were those 'where the cells are relatively large and thick-walled, often striated or slightly granular in surface view and dilated at the junctions …'. 'Type B' hairs were those with 'one to three short, thin-walled basal cells are attached to a greatly elongated and often thick-walled, tapering terminal cell …'; no formal naming of these hair types was provided.

Payne (1978), in an attempt to provide a dictionary of hair terms (of both hair types and descriptive of the indumentum), appears to have provided amongst the earliest formal terms for the hairs seen by Drury & Watson: 'Type A' hairs were termed osteolate (or osteoform), and 'Type B', flagelliform, terms successively used by Semple et al. (1980), etc. Within the GOLDENASTERS, flagelliform hairs were found in *Chrysopsis* but not in *Heterotheca*, but osteolate hairs only in *Heterotheca*. In our material, osteolate hairs were very much in evidence on the stems, leaves, bracts and bracteoles, confirming that our material belonged in *Heterotheca*.

Nuttall's generic confusion

Torrey & Gray (1842: 252) were clearly under the impression that Nuttall's rank of *Chrysopsis* was '§ of Inula', but 'excl. spec.'; this is interpreted as a Section, overlooking Nuttall's comments. The species entry in Torrey & Gray (1842: 254) had a slightly confusing entry in *Chrysopsis* under '§2 *EUCHRYSOPSIS*' of '*C*[*hrysopsis*] *Mariana* (Nutt.)'. A check in Nuttall's *Genera* … suggested the reason why. Nuttall (1818b: 149–153) divided *Inula* into two unranked groups of species based on corolla colour. Within the first group, after 'Species. 1 I[nula] *Helenium*', and under a subheading of '*CHRYSOPSIS.†' accounts are provided of 'Species 2′ through to '10.', although Nuttall quite clearly referred to it as a subgenus 'very closely related' to *Aster* L.; '[an apparently unranked infrageneric group] II. Flowers not yellow' accounted for [Species 11.] *Inula linariifolia* (L.) Nutt. (a name not currently in IPNI – IPNI, 2012) [= *Ionactis linariifolia* (L.) Greene] to 'Species 15' *Inula humilis* (Willd.) Nutt. (also not currently in IPNI) [= *Doellingeria infirma* (Michx.) Greene] and 'Species 16' *Inula amygdalina* (Lam.) Nutt. [= *Doellingeria umbellata* (Mill.) Nees]. It is clear that Nuttall's generic concept was wanting; his Preface (Nuttall, 1818a: vii) indicated that 'To the names of species or genera proposed by the author, will be found an asterisk (*) prefixed.', yet his discussion (Nuttall, 1818b: 150), only

'Species 1′, *Inula helenium* [L.] actually belongs to *Inula* L. in the Inuleae, the remainder in [his subgenus] *Chrysopsis*, *Croptilon* Raf., or *Heterotheca* to the Astereae.

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