

TAXONOMIC REVIEW OF *CHRYSOGONUM* (ASTERACEAE: HELIANTHEAE)

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ABSTRACT

Three allopatric varieties are recognized within *Chrysogonum virginianum*: the northern var. *virginianum*, with non-stoloniferous plants and mostly leafy aerial stems; the southern (Gulf coastal plain) var. *australe*, with flagellate stolons and only leafless aerial stems; and the geographically intermediate var. ***brevistolon***, var. nov., with stolons of intermediate length and mostly leafy aerial stems. These three taxa are separated by other minor and overlapping differences. Intermediates apparently occur, but uncommonly, between var. *virginianum* and var. *brevistolon*. Variety *australe* is more strongly separated in geographic range and more distinct in morphology.

RESUMEN

Se reconocen tres variedades alopátricas en *Chrysogonum virginianum*: la norteña var. *virginianum*, con ejemplares no estoloníferos y la mayoría de los tallos aéreos con hojas; la sureña (llanura costera del Golfo) var. *australe*, con estolones flagelados y únicamente tallos aéreos sin hojas; y la intermedia geográficamente var. ***brevistolon***, var. nov., con estolones de longitud intermedia y con la mayoría de los tallos aéreos con hojas. Estos tres taxa se separan por otras diferencias menores que se solapan. Se encuentran intermedios aparentemente, pero raramente, entre var. *virginianum* y var. *brevistolon*. La variedad *australe* se separa más en el rango geográfico y tiene una morfología más distinta.

Chrysogonum L. is a monotypic genus represented by *C. virginianum* L. ("Green-and-gold") of the eastern United States, ranging from Mississippi, Alabama, and Florida north to Ohio and Pennsylvania. It has mainly been treated as a single species with two varieties (e.g., Ahles 1968; Stuessy 1977; Cronquist 1980). *Chrysogonum australe* Alexander ex Small was originally published as a separate species (Small 1933) but reduced in rank by Ahles (1964), without comment, to *C. virginianum* var. *australe* (Alexander ex Small) Ahles. In an unpublished treatment of the flora of "the Carolinas and Virginia," Weakley (in manuscript) recognizes *C. australe* as a separate species but provides no rationale for the taxonomic judgement.

Stuessy (1977) distinguished two varieties (var. *virginianum* vs. var. *australe*) based on plant height (15–35 cm vs. 3–14 cm), stem orientation (erect vs. often decumbent), and disposal of leaves (primarily cauline vs. nearly all basal). Stuessy mapped intermediates, not only in the area of North Carolina and South Carolina where the ranges of the two taxa (in his concept) meet, but also nearly throughout the geographic range of the whole complex. Ahles' (1968) distinction of the two taxa in North Carolina and South Carolina was based primarily

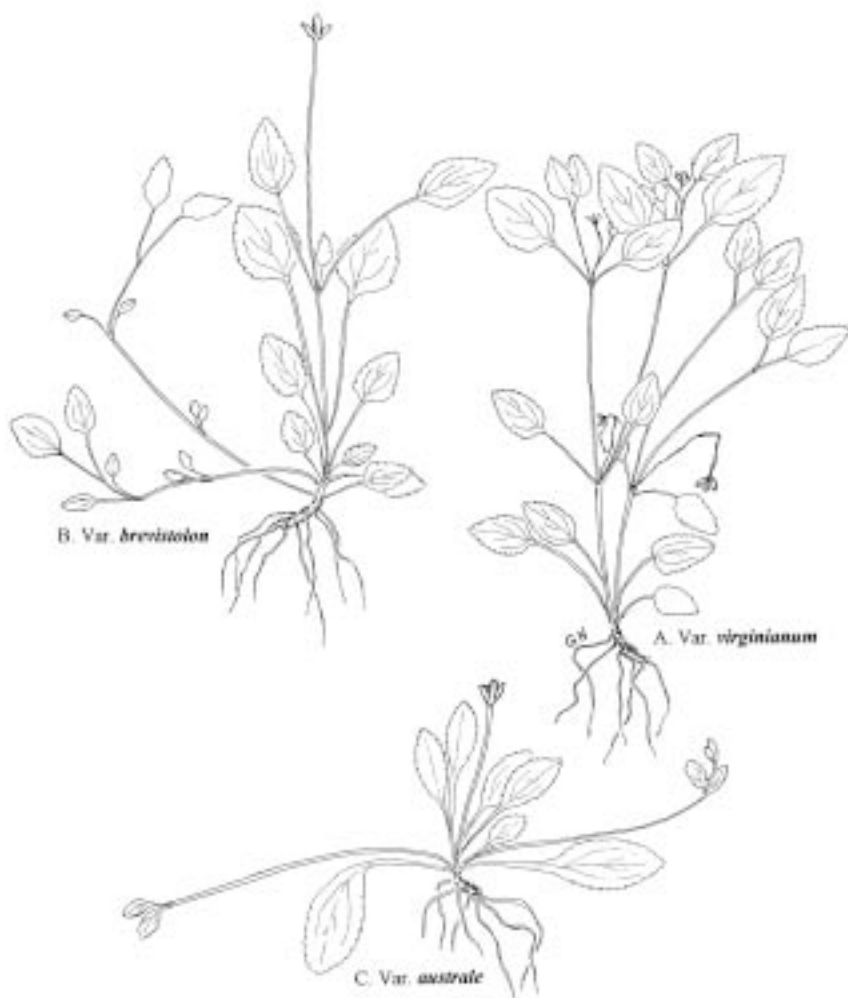


FIG. 1. Growth form of the three varieties of *Chrysogonum virginianum*. A. Var. *virginianum*. B. Var. *brevistolon*. C. Var. *australe*.

on stolon production and his concepts and mapping are closer to what is presented here.

In the present study, variation patterns within the *Chrysogonum virginianum* complex are reviewed and three morpho-geographic entities are recognized (Fig. 1; Fig. 3). Their morphological distinction is based primarily on production (or not) of stolons, length of stolon internodes, whether or not the flowering stems are leafy, and height of flowering stems. Variation in other features (vestiture,

leaf morphology, capitular and floral morphology, and cypselae and elaiosome morphology) is overlapping and/or parallel among the three taxa.

Data for the present study are from the field and from herbarium specimens. Map records are from BRIT, MO, NCU, OS, SMU, TEX-LL, USCH, and VDB, with some distribution points added from various references (Strausbaugh & Core 1977; Harvill et al. 1981; Fisher 1988; Brown & Brown 1984; Rhoads & Klein 1993).

TAXONOMY

Chrysogonum L., Sp. Pl. 2:920. 1753. TYPE: *Chrysogonum virginianum* L.

Diotostephus Cass., Dict. Sci. Nat. 48:543. 1827. TYPE: *Diotostephus repens* Cass. (see comments below, under var. *brevistolon*).

Chrysogonum virginianum L., Sp. Pl. 2:920. 1753. TYPE: U.S.A. VIRGINIA: [No other data], J. Clayton 298 (LECTOTYPE, Stuessy 1977 [or ISOLECTOTYPE" fide Reveal 1989 by annotation]; BM, John Clayton Herbarium image!).

Plants herbaceous, perennial, arising from a fibrous-rooted rhizome up to 5 cm long, sometimes stoloniferous, sometimes producing basal offsets. *Stems* erect to erect-ascending (flowering), mostly 10–30 (rarely to 50) cm, or prostrate (non-flowering stolons), up to 50 cm, villous. *Leaves* opposite, basal and cauline, 3(–5)-nerved from the base, elliptic-ovate to deltate-ovate, 2.5–10 cm, petiolate, crenate-dentate to subentire, minutely strigose-hirsutulous to hirsute-villous, also minutely stipitate-glandular above and beneath with hairs ca. 0.1 mm long. *Capitula* axillary, 1–2 per node, solitary on naked peduncles 2–22 cm or appearing to arise from the basal rosette; involucre cupulate-hemispheric, 7–10 cm wide; phyllaries 10 in 2 series, outer oblong-ob lanceolate, distal half foliaceous and spreading, inner greenish, rigidly erect and somewhat scarious; receptacles flat to shallowly convex; paleae oblanceolate, ca. 4 mm long, scarious. *Ray florets* 5(–6), pistillate, fertile, corolla laminae yellow, broadly elliptic, 6–17 mm, apically 3-toothed; cypselae each basally adnate to a single inner phyllary, 3 paleae, and 3 sterile disc florets, this “cypselae-complex” deciduous as a unit. *Disc florets* ca. 25–50, functionally staminate, corollas yellow, 2.5–2.7 mm, tubes much shorter than the narrowly funnelform throats, lobes 5, deltate; ovaries sterile; anthers brown to black; styles filiform, the branches mostly undivided; ovaries filiform, epappose. *Cypselae* (ray) obovoid, strongly flattened radially, 3–4.5 mm × 2–2.5 mm, blackish-brown; pappus a low, irregular, ‘half-cup-shaped’ crown, incomplete on the adaxial face. Base chromosome number, $x = 16$.

An elaiosome is developed at the base of the cypselae-complex (formerly termed “achene-complex”). This is a fleshy, oil-bearing structure elaborated at the base of the phyllary and the two associated outer paleae (Fig. 2). All three taxa of *Chrysogonum* produce elaiosomes; variation in the degree of elaboration of the elaiosome tissue occurs but without apparent geographical pattern.

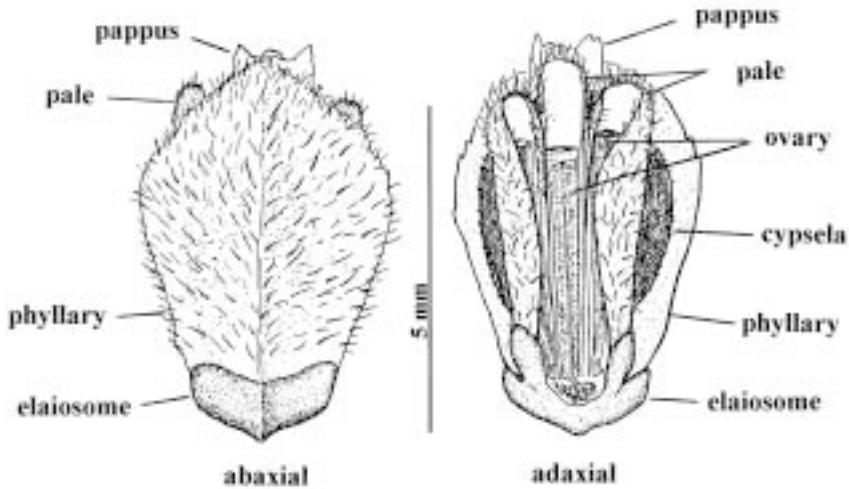


FIG. 2. Cypselo-complex and elaiosome morphology in *Chrysogonum virginianum*.

Native species of ants carry the cypselo-complexes into their nests, chew off the elaiosomes, and return the undamaged cypselae or the whole complexes to the surface (Nesom 1978).

The stolons of var. *brevistolon* and var. *australe* presumably are derived from erect leafy stems (as in var. *virginianum*) where developmental processes have re-oriented them into lateral, prostrate or decumbent branches. In var. *australe*, the stolons commonly produce leaves and rooting plantlets only at the apex; another pair of leaves less commonly is produced proximal to the stolon apex. In var. *brevistolon*, the stolons are shorter and produce leaves more frequently at rooting nodes along the length. The basal offsets that are uncommonly produced in var. *virginianum* apparently are essentially subterranean rhizomes produced from the caudex or main rhizome without the herbaceous nature that would indicate they are directly derived from erect branches.

In all three varieties of *Chrysogonum virginianum*, the first (earliest-flowering) capitula are borne on leafless, ebracteate scapes. These scapes apparently are homologous with the leafless and ebracteate peduncles of later capitula that are raised on leafy stems in var. *virginianum* and var. *brevistolon*. In this view, the permanently 'acaulescent' flowering stems of var. *australe* remain in an early development stage and can be interpreted as neotonous.

Chromosome numbers are invariantly $2n = 32$ for var. *virginianum* and var. *brevistolon*. A count has not been made for var. *australe* sensu stricto. Chromosome counts reported below as "Nesom unpublished" were made by the author in 1975 and 1976 from field-collected meiotic materials from North Caro-

lina localities. In all observations, meiosis and tetrad formation were regular; 16 bivalents were observed in populations from Lee, Montgomery, Moore, and Orange cos. (var. *virginianum*) and Wilkes Co. (var. *brevistolon*). Eight tetravalents were regularly produced in one population from Orange Co., N.C. (UNC campus); in one population from Wake Co., N.C. (Umstead State Park), four to eight tetravalents were commonly formed.

All three taxa of *Chrysogonum* are now used as garden plants and are sold in nurseries under various horticultural names.

KEY TO THE VARIETIES OF *CHRYSOGONUM VIRGINIANUM*

1. Plants occurring individually, without stolons; earliest flowering stems leafless, later ones leafy; leafy flowering stems mostly 15–35(–50) cm high _____ var. **virginianum**
1. Plants colonial, mat-forming by stolons; flowering stems leafless and/or leafy; leafy flowering stems (if present) mostly 15–25 cm high.
 2. Earliest flowering stems leafless, mostly 2–10 cm high, later ones leafy, 15–25 cm high; longest stolon internodes 2–6 cm _____ var. **brevistolon**
 2. All flowering stems leafless, 2–10 cm high; longest stolon internodes 12–60 cm _____ var. **australe**

1a. *Chrysogonum virginianum* L. var. **virginianum** (Fig. 1)

Chrysogonum virginianum L. var. *dentatum* A. Gray, Bot. Gaz. 7:31. 1882. TYPE: U.S.A. MARYLAND. MONTGOMERY CO.: High Island in the Potomac River, 6 Jun 1881, *J.D. Smith s.n.* (HOLOTYPE: GH!).

Plants without stolons, not colonial or mat-forming. Stems (flowering) 15–35(–50) cm tall, the earliest leafless, becoming leafy. Leaves: blades deltate-ovate, basally abruptly cuneate to truncate or subcordate, minutely strigose-hirsutulous with ascending-appressed hairs 0.1–0.3 mm long. Capitula: peduncles 2–22 cm long; outer phyllaries 6–11(–15) mm long, 3–7 mm wide. Chromosome number, $2n = 32$ (Montgomery Co., Md.–Kovanda 1978; Lee Co., Montgomery Co., Moore Co., Orange Co., and Wake Co., N.C.–Nesom unpublished).

Flowering spring–early summer or longer with moisture (late Mar–Jun, –Jul and later). Moist to dry woodlands and forests, usually in partially sunny sites, especially in clearings and along edges; D.C., Ky, Md., N.Y., N.C., Ohio, Pa., S.C., Va., W.Va. The report from New York (Mitchell & Tucker 1999) is noted as an escape from cultivation.

Plants of var. *virginianum* do not produce leafy stolons, but basal offsets sometimes increase the size of the plant. Elongation of basal offsets or the primary rhizome may produce the effect of separate but interconnected plants, but such offsets/rhizomes are not commonly produced, except (apparently) in Maryland, D.C., and adjacent regions of Virginia. Plants of var. *virginianum* occur as discrete individuals but they are usually clustered, probably as a result of the pattern of cypsela-complex dispersal by ants. The flowering stems are erect; the first are leafless; they are later leafy as the lower internodes elongate.

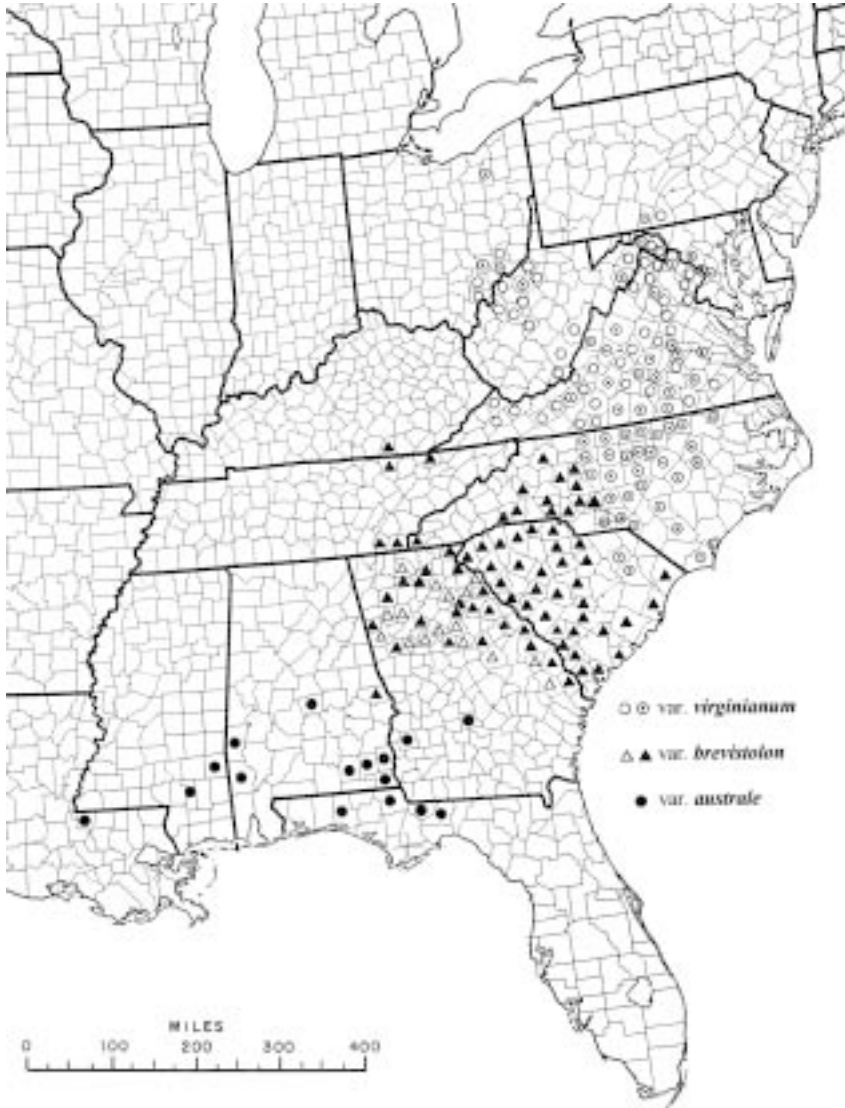


FIG. 3. Geographic distribution of the three varieties of *Chrysogonum virginianum*. Distribution points added from literature references (without vouchers seen by the author) are indicated as open (unfilled) symbols. A record for Greene County, Tenn., shown in Chester et al. (1997) is vouchered by a specimen collected from cultivation (B.E. Wofford pers. comm.) and is not included in the present account.

1b. *Chrysogonum virginianum* var. *brevistolon* Nesom, var. nov. (**Fig. 1**). TYPE: U.S.A. SOUTH CAROLINA. LEXINGTON CO.: Riverbanks Zoo Botanical Garden, old Saluda Mill site, shaded slope near ravine just S of tram line clearing, occasional herbs, somewhat trailing but with flowering stems generally erect, 7 May 1993, *J.B. Nelson 14,062* (HOLOTYPE: BRIT!; ISOTYPE: USCH!).

Differt a var. *virginiano* stolonibus et habitu coloniali; differt a var. *australi* stolonibus brevioribus foliaceis internodiis brevibus.

Diotostephus repens Cass., Dict. Sci. Nat. 48:544. 1827. *Chrysogonum diotostephus* DC., Prodr. 5:510. 1836 (nom. nov. illegit.). TYPE: "Nous avons fait cette description, générique et spécifique, sur un très petit échantillon sec, incomplet, en mauvais état, et dont nous ignorons l'origine" (HOLOTYPE: P?). As noted by Stuessy (1977), Cassini's description of this taxon is explicit enough that its identity as *C. virginianum* seems reasonable, and de Candolle, who saw the specimen, treated it within *Chrysogonum* (as *C. diotostephus*, see below). Its association here with var. *brevistolon* rather than var. *australe* is based on de Candolle's description of its habitat as "in siccis pinguibus Carolinae."

Plants stoloniferous, colonial and mat-forming; stolons (leafy above-ground runners) with longest internodes 2–6 cm, these often becoming lignescent, partially to fully buried and rhizome-like. Stems (flowering) mostly 2–25 cm tall, the earliest leafless, becoming leafy. Leaves: blades deltate-ovate, basally abruptly cuneate to truncate or subcordate, strigose-hirsutulous with hairs 0.5–0.3 mm long. Capitula: peduncles 2–22 cm long; outer phyllaries 6–10 mm long, 3–4 mm wide. Chromosome number, $2n = 32$ (Clarke Co., Ga.–Jones 1968; Lancaster Co., S.C.–Solbrig et al. 1972; Rutherford Co., N.C.–Morton 1981; Wilkes Co., N.C.–Nesom unpublished).

Flowering spring–early summer (Mar–May, –early Jun). Moist to dry woodlands, usually in partially sunny sites; Ala., Ga., Ky., N.C., S.C., Tenn.

Variety *brevistolon* differs from var. *virginianum* primarily by elongation and lateral re-orientation of the basally produced stems of the latter into stolons or stoloniform branches. Stolon production in var. *brevistolon* results in colonies of closely interconnected plants (often densely matted), in contrast to the individuals of var. *virginianum*. The distinction between var. *virginianum* and var. *brevistolon* usually can be determined from herbarium collections, but early-flowering plants commonly produce only a single head from a basal rosette of leaves and observation of later growth is necessary to observe stolon production. In a few instances, it is possible that intermediates and infra-population variation occur (e.g., in NCU and USCH collections from Darlington and Florence cos., S.C.), and lignescent stolons (becoming partially buried and rhizome-like) of var. *brevistolon* may be very similar to structures in var. *virginianum* that originate as basal offsets or rhizomes. Using the criteria discussed here for their distinction, however, var. *virginianum* and var. *brevistolon* have closely contiguous, non-overlapping geographic ranges.

Stolon length appears to vary in var. *brevistolon*, although the stolons are never like those of var. *australe* and intermediates between var. *brevistolon* and

var. *australe* have not been observed. In earlier phases of the present study, however, no distinction was made between var. *brevistolon* and var. *australe* (as recognized here), and all were annotated as var. *australe*, based on their production of distinct stolons (in contrast to var. *virginianum*).

The erect stems of var. *brevistolon* tend to be shorter than in var. *virginianum* but are of ten otherwise indistinguishable. In both taxa, the erect stems become leafy, with 2–3 internodes.

In var. *virginianum*, a flower bud is produced in each leaf axil, and two capitula on naked peduncles are produced at each node (from a pair of opposite leaves). On the prostrate to decumbent stoloniform branches of var. *brevistolon*, one of the axillary flower buds commonly is suppressed and a node produces only a single capitulum, which is held erect. This mechanism for bud suppression tends to be active even on the erect branches of var. *brevistolon*, and on a plant collected without complete lower parts, observation of a single axillary shoot per node on erect stems is a reliable indication of its identity. The converse is not true, because plants of var. *brevistolon* may also produce both axillary buds at a node.

1c. *Chrysogonum virginianum* var. *australe* (Alexander ex Small) Ahles, J. Elisha Mitchell Sci. Soc. 80:173. 1964. (**Fig. 1**). *Chrysogonum australe* Alexander ex Small, Man. Southeast. Fl., 1415, 1509. 1933. TYPE: U.S.A. FLORIDA. JACKSON CO.: dry woods, somewhat calcareous, about a mile E of Marianna, 16 Mar 1925, R.M. Harper s.n. (HOLOTYPE: NY; ISOTYPES: GH!, US!).

Plants stoloniferous, mat-forming; stolons (leafy above-ground runners) with longest internodes 12–60 cm, apparently remaining herbaceous. Stems (flowering) 2–10 cm tall, leafless. Leaves: blades elliptic-ovate, gradually tapered to the petiole, villous-hirsute with spreading hairs 1–3 mm long. Capitula: peduncles 2–10 cm long; outer phyllaries 7–10 mm long, 2.5–4 mm wide. Chromosome number unknown.

Flowering spring (mid Mar–Apr, –May). Pine-oak, longleaf pine, beech-oak-magnolia woods, ravine slopes, limestone outcrops, floodplains and terraces, sand or sandy loam; Ala., Fla., Ga., La., Miss.

Variety *australe*, as recognized here, corresponds in geographic range almost exactly to the “East Gulf Coastal Plain” phytogeographic pattern outlined by Sorrie and Weakley (2001). Plants of this taxon are recognized by their leafless flowering stems and whip-like stolons with long internodes. They are so strikingly different in appearance from those of var. *virginianum* that treatment of var. *australe* as a separate species might be justified. This is further emphasized by the apparent allopatry (and corresponding genetic isolation) of var. *australe*. The existence of a broad region of morphologically and geographically intermediate populations (var. *brevistolon*), however, makes it reasonable to view var. *australe* and var. *virginianum* as extremes of a three-segmented array of variation within a single species.

Besides the features of stolons and flowering stems, var. *australe* is distinguished from the other two varieties by a tendency for the leaf blades to be basally attenuate, a tendency for stems and petioles to be more villous (with longer trichomes), and a tendency for the phyllaries to be narrower. Variability in these features of var. *australe* overlaps with that in the other two varieties.

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