

TAXONOMY OF *TETRANEURIS* (ASTERACEAE: HELENIEAE: TETRANEURINAE)

Mark W. Bierner and B. L. Turner

Plant Resources Center, The University of Texas, Austin, Texas 78712

Abstract: *Tetraneuris* is recognized as a genus separate from *Hymenoxys* and a taxonomic treatment is presented for the 14 taxa recognized as constituting *Tetraneuris*: *T. acaulis* var. *acaulis*, *T. acaulis* var. *arizonica*, *T. acaulis* var. *caespitosa*, *T. acaulis* var. *epunctata*, *T. argentea*, *T. herbacea*, *T. ivesiana*, *T. linearifolia* var. *linearifolia*, *T. linearifolia* var. *arenicola*, *T. scaposa* var. *scaposa*, *T. scaposa* var. *argyrocaulon*, *T. torreyana*, *T. turneri*, and *T. verdiensis*. The revision includes synonymies, typifications, descriptions, discussions, and range maps for each of the accepted species.

Resumen: Se reconoce a *Tetraneuris* como un género distinto de *Hymenoxys*, y se presenta un tratamiento taxonómico para los 14 taxones reconocidos en *Tetraneuris*: *T. acaulis* var. *acaulis*, *T. acaulis* var. *arizonica*, *T. acaulis* var. *caespitosa*, *T. acaulis* var. *epunctata*, *T. argentea*, *T. herbacea*, *T. ivesiana*, *T. linearifolia* var. *linearifolia*, *T. linearifolia* var. *arenicola*, *T. scaposa* var. *scaposa*, *T. scaposa* var. *argyrocaulon*, *T. torreyana*, *T. turneri*, and *T. verdiensis*. La revisión incluye sinónimias, tipificaciones, descripciones, discusiones, y mapas de distribución para cada una de las especies aceptadas.

Keywords: Asteraceae, Helenieae, Tetraneurinae, *Hymenoxys*, *Tetraneuris*.

Tetraneuris Greene belongs to Helenieae, which is sometimes positioned in Heliantheae (Turner and Powell, 1977; Robinson, 1981). Karis and Ryding (1994), after presenting a history of the circumscription of Helenieae, recognized a paraphyletic Helenieae on what were said to be "practical" grounds, commenting that it "eventually will have to be split into smaller, monophyletic units." Most recently, Baldwin and Wessa (2000) recognized a much more tightly defined, apparently monophyletic Helenieae, along the lines of what we envision as a natural grouping that includes *Tetraneuris*.

Tetraneuris has been variously treated, either as an infrageneric grouping within *Hymenoxys* (sensu lato) or as a distinct genus. Many recent workers (e.g., Barkley, 1986; Cronquist, 1994; Karis and Ryding, 1994; Welsh, 1987) have accepted *Hymenoxys* in the broad sense. Karis and Ryding (1994), for example, included *Tetraneuris* within *Hymenoxys* and placed it in Gaillardiiinae, commenting, "Most of the generic segregates from *Hymenoxys*, namely, *Mac-*

dougalia [A. Heller], *Rydbergia* [Greene], and *Tetraneuris*, are not recognized as genera here, because it has not been shown that these taxa are more closely related to other parts of the Gaillardiiinae than to *Hymenoxys* sensu stricto." Robinson (1981) recognized both *Hymenoxys* and *Tetraneuris*, along with twelve other genera, these constituting his Gaillardiiinae, which was part of his expanded Heliantheae. Spring et al. (1994) recognized *Hymenoxys* and *Tetraneuris* as members of Gaillardiiinae within Heliantheae, and presented compelling evidence based mainly on sesquiterpene lactone and monoterpene glycoside chemistry for recognition of *Tetraneuris* as a genus separate from *Hymenoxys*. Bierner (1994), who also recognized *Hymenoxys* and *Tetraneuris* as members of Gaillardiiinae within Heliantheae, merged the long-recognized *Dugaldia* Cass. and *Plummera* A. Gray into an expanded *Hymenoxys* and recognized *Tetraneuris* at the generic level based on features that distinguish it from *Hymenoxys* (most notably subequal, free involucre bracts, ability to synthesize 6, 8-dimethoxy

flavone aglycones and monoterpene glycosides, and apparent inability to synthesize seco-pseudoguaianolides).

Turner (1972) was inclined to accept *Hymenoxys* in the broad sense, including the segregates mentioned by Karis and Ryding (1994) and also including *Plummera*, which was retained by Karis and Ryding. Turner took *Hymenoxys* to be a monophyletic assemblage of taxa with an ancestral base chromosome number of $x = 15$, largely confined to xeric regions of temperate North America, with a secondary diversification in temperate regions of South America. Turner viewed *Hymenoxys* as having two subgeneric groupings, *Hymenoxys* and *Tetraneuris*, the former comprising about 20 species, the latter about 8 or 9 species.

In spite of its widespread distribution and commonness, *Hymenoxys* (sensu lato) has never been comprehensively monographed. This is perhaps due in part to the procrastinational proclivities of the late Dr. Kittie Parker of the U.S. National Museum, who had most of the North American specimens of the genus "tied up" for nearly 30 years through loans to that institution. Parker was forever in the process of monographing *Hymenoxys*, at first in the broad sense including *Tetraneuris* (e.g., Parker, 1950, 1970), and later in the narrow sense excluding *Tetraneuris* (e.g., Parker, 1980). Unfortunately, she was never able to get her work in final form. To some considerable extent this must have reflected her inability to draw satisfactory lines among the groupings concerned; i.e., should *Tetraneuris* be recognized? should it not? what about *Plummera*?, etc. The junior author knew her personally, visiting with her many times over the years. She was a wonderfully informed worker on *Hymenoxys* and expounded well and often upon its morphological characters; nonetheless, one always left her presence with the feeling that she really was not sure about relationships in the group.

Bierner and Jansen (1998) took up the

hymenoxian generic gauntlet, using DNA restriction site data. Their results suggested strongly that *Tetraneuris* should be separated from *Hymenoxys* for phyletic reasons. Because of this, the junior author has given up his arguments for the recognition of *Hymenoxys* as including *Tetraneuris*.

Bierner and Jansen (1998) presented DNA data bearing upon the relationship of *Tetraneuris* to *Hymenoxys* and related genera; a modified version of their phylogenetic tree is presented in Figure 1. *Plummera*, *Dugaldia*, and *Macdougalia* are close to one another and to *Hymenoxys* (i.e., *Hymenoxys* subg. *Picradenia* represented by *H. brachyactis*, *H. cooperi*, *H. helenioides*, *H. jamesii*, *H. lemmonii*, *H. quinquesquamata*, *H. richardsonii*, *H. rusbyi*, and *H. subintegra*). There is some separation of *H. odorata* (of the subgenus *Phileozero*), and an even greater separation of the oddball dysploid, *H. texana* (cf. Strother and Brown, 1988). Unfortunately, Bierner and Jansen had no samples of the South American taxa (subg. *Hymenoxys*), or of *H. grandiflora*, *H. brandegeei*, or *H. insignis* (subg. *Rydbergia*). Figure 1 shows marked separation of *Tetraneuris* from all other hymenoxian genera (including *Plummera*, *Dugaldia*, and *Macdougalia*). The *Tetraneuris* taxa share 52 mutations that are not in *Hymenoxys*; the hymenoxian taxa share 33 mutations that do not occur in *Tetraneuris*. Indeed, the DNA restriction site data suggest that *Tetraneuris* is more closely related to the morphologically remote *Psilostrophe* DC. than to *Hymenoxys*.

Recognition of *Tetraneuris* as a genus separate from *Hymenoxys* was accepted by Baldwin and Wessa (2000) and supported by their work. Using analyses of nuclear 18S–26S rDNA sequences of the internal transcribed spacer region, they classified *Tetraneuris* (sensu Bierner, 1994) along with *Amblyolepis* DC., *Baileya* Harv. & A. Gray, *Hymenoxys*, and *Psilostrophe* in "Riddelliinae" (an illegitimate name for the subtribe correctly known as Tetraneurinae), reserving Gaillardinae for *Gaillardia* Foug., *He-*

TABLE 1. Chromosome numbers in *Tetraneuris*. All counts are given as haploid numbers regardless of whether they were reported as haploid or diploid. Only one collection or voucher is shown for each count. Vouchers examined as part of this study are cited in Representative Specimens.

Taxon	<i>n</i>	Collection or bibliographic reference
<i>T. acaulis</i> var. <i>acaulis</i>	14	Powell and Turner, 1963
	15, 30	Strother, 1966
	28	Johnston and Bonde, 1969 (as var. <i>arizonica</i>)
<i>T. acaulis</i> var. <i>arizonica</i>	14	Windham 97-207 (UT!)
	15, 30	Strother, 1966
	28	Windham 98-161 (UT!)
<i>T. acaulis</i> var. <i>caespitosa</i>	14	Johnston and Bonde, 1969
	15	Wiens 2866 (COLO!)
<i>T. acaulis</i> var. <i>epunctata</i>	14	Windham 93-143 (COLO!, UT!)
	15	Watson 889 (MONTU!)
	28	Windham 99-158 (UT!)
<i>T. argentea</i>	15, 30	Strother, 1966
<i>T. herbacea</i>	14	Cusick, 1991
<i>T. ivesiana</i>	14, 28	Johnston and Bonde, 1969
	15, 30	Strother, 1966
<i>T. linearifolia</i> var. <i>arenicola</i>	15	Bierner et al., 1992
<i>T. linearifolia</i> var. <i>linearifolia</i>	14	Strother, 1983
	15, 30	Zhao, 1996
<i>T. scaposa</i> var. <i>argyrocaulon</i>	15	Strother 555 (TEX!)
<i>T. scaposa</i> var. <i>scaposa</i>	15, 30	Strother, 1966
<i>T. torreyana</i>	14	Windham 96-140 (UT!)
<i>T. turneri</i>	45	Parker, 1970
<i>T. verdiensis</i>	Unknown	

dular or sparsely to densely dotted with sessile glands, adaxial faces glabrous, eglandular. DISC FLORETS 20–250+, bisexual, fertile; corollas yellow proximally, yellow to purple-red distally, throats cylindric to cylindric-campanulate, lobes 5. RECEPTACLES hemispheric to conic; paleae none. CYPSELAE obpyramidal to narrowly obpyramidal, sparsely to densely pubescent; pappi 4–8, usually aristate scales.

CHROMOSOME NUMBERS: $2n = 28, 30, 56, 60, 90$ (Table 1 and chromosome count vouchers included in Representative Specimens). *Hymenoxys* shows relatively little chromosomal variability with only two taxa exhibiting dysploidy, *H. odorata* (Sanderson and Strother, 1973) and *H. texana* (Strother and Brown, 1988), and none exhibiting polyploidy. *Tetraneuris* exhibits dysploidy and polyploidy at both the inter- and intra-

specific levels (Table 1). Given the commonness of $2n = 30$ in both *Tetraneuris* and *Hymenoxys* (for the latter, see Bierner, 2001), we believe $x = 15$ to be the ancestral base chromosome number for both genera.

DISTRIBUTION: *Tetraneuris* as herein recognized consists of 14 taxa, 13 distributed from southwestern Canada to northeastern Mexico, and 1 (*T. herbacea*) disjunct to central and northeastern Illinois (probably now extinct according to Cusick, 1991), northern Ohio, and Ontario, Canada.

KEY TO THE SPECIES OF *TETRANEURIS*

1. Annuals; caudices none 5. *T. linearifolia*
1. Perennials; caudices present.
2. Caudices not thickened distally; leaves all basal-

proximal, not tightly clustered, arising at various levels near bases of stems.

- 3. Stems erect; leaf blades sparsely to densely pubescent, not woolly; northeastern Mexico through south, central, west, and north Texas to New Mexico, western Oklahoma, eastern Colorado, western Kansas, and southwestern Nebraska 6. *T. scaposa*
- 3. Stems erect or \pm decumbent; leaf blades moderately to densely woolly; south Texas and northeastern Mexico (Coahuila) 8. *T. turneri*
- 2. Caudices thickened distally; leaves all basal or basal and cauline, basal leaves tightly clustered, appearing to arise from the same level at bases of stems.
- 4. Leaves basal and cauline.
 - 5. Leaf blades moderately to, usually, densely strigoso-canescens* . . . 2. *T. argentea*
 - 5. Leaf blades sparsely to moderately pubescent, not strigoso-canescens 4. *T. ivesiana*
- 4. Leaves all basal.
 - 6. Heads discoid; leaves densely pubescent, not strigoso-canescens; Yavapai County, Arizona 9. *T. verdiensis*
 - 6. Heads usually radiate, if discoid then leaf blades strigoso-canescens; widespread.
 - 7. Ray florets 14–27; pappus scales usually not aristate; Ontario, Illinois (?), Ohio 3. *T. herbacea*
 - 7. Ray florets 7–15(–21); pappus scales aristate; Texas to North Dakota and westward.
 - 8. Leaf blades usually with conspicuously distinct midribs, glabrous or, usually, sparsely to, sometimes, moderately or even densely pubescent, not strigoso-canescens or sericeous, densely glandular; outer phyllaries 4–8, margins usually conspicuously scarious 7. *T. torreyana*
 - 8. Leaf blades with distinct midribs, glabrous or sparsely to densely pubescent, often strigoso-canescens or sericeous, eglandular or sparsely to densely glandular; outer phyllaries 6–12, margins sometimes to

often inconspicuously scarious 1. *T. acaulis*

1. TETRANEURIS ACAULIS (Pursh) Greene, Pittonia 3: 265. 1898.

PERENNIALS. CAUDICES \pm branched, thickened distally. AERIAL STEMS 1–35(–60), erect, unbranched. LEAVES all basal, new leaves tightly clustered, appearing to arise from the same level at bases of stems, blades spatulate to oblanceolate to linear-oblanceolate, entire, glabrous or sparsely to densely pubescent, often strigoso-canescens, lanuginose, or sericeous, eglandular or sparsely to densely dotted with impressed glands, bases usually densely woolly or long-pubescent. HEADS 1–35(–60) per plant, usually radiate, borne singly. PEDUNCLES green throughout to purple-red-tinted throughout, 0.5–30 cm, sparsely to densely pubescent, often lanate below involucre, eglandular or sparsely to moderately dotted with sessile glands. INVOLUCRES 7–12 \times 8–16 mm. PHYLLARIES: outer phyllaries 6–12, often purple-red-tinted on apices and margins, sometimes purple-red-tinted throughout, obovate to ovate to lanceolate, 3.9–9(–11.5) \times 1–3.8 mm, margins sometimes to often slightly scarious, abaxial faces sparsely to densely pubescent, eglandular or sparsely to moderately dotted with sessile and/or impressed glands; mid phyllaries often purple-red-tinted on apices and margins, sometimes purple-red-tinted throughout, obovate to ovate to lanceolate, (3–)4–7.2(–8.5) \times 0.8–3 mm, margins often scarious, abaxial faces sparsely to densely pubescent, eglandular or sparsely dotted with sessile glands; inner phyllaries sometimes purple-red-tinted on apices, 3.5–6 \times 1–2.5 mm, abaxial faces sparsely to moderately pubescent, eglandular or sparsely dotted with sessile glands. RAY FLORETS 8–15(–21); corollas 9–19 \times 3–8 mm, abaxial faces glabrous or sparsely to moderately pubescent, eglandular or sparsely to moderately dotted with sessile glands. DISC FLORETS 25–200+; corollas yellow, 2.7–4.3 \times 0.7–1.3 mm, gla-

* The term strigoso-canescens is used to describe the tightly appressed, often silvery pubescence composed of relatively short hairs (ca 1.0–1.5 mm long) observed in *Tetranneuris argentea* and *T. acaulis* var. *acaulis*. This is in contrast to spreading, lanuginose, or sericeous pubescence composed of longer hairs (ca 1.5–3 mm long) in various taxa including *T. ivesiana* and the other three varieties of *T. acaulis*.

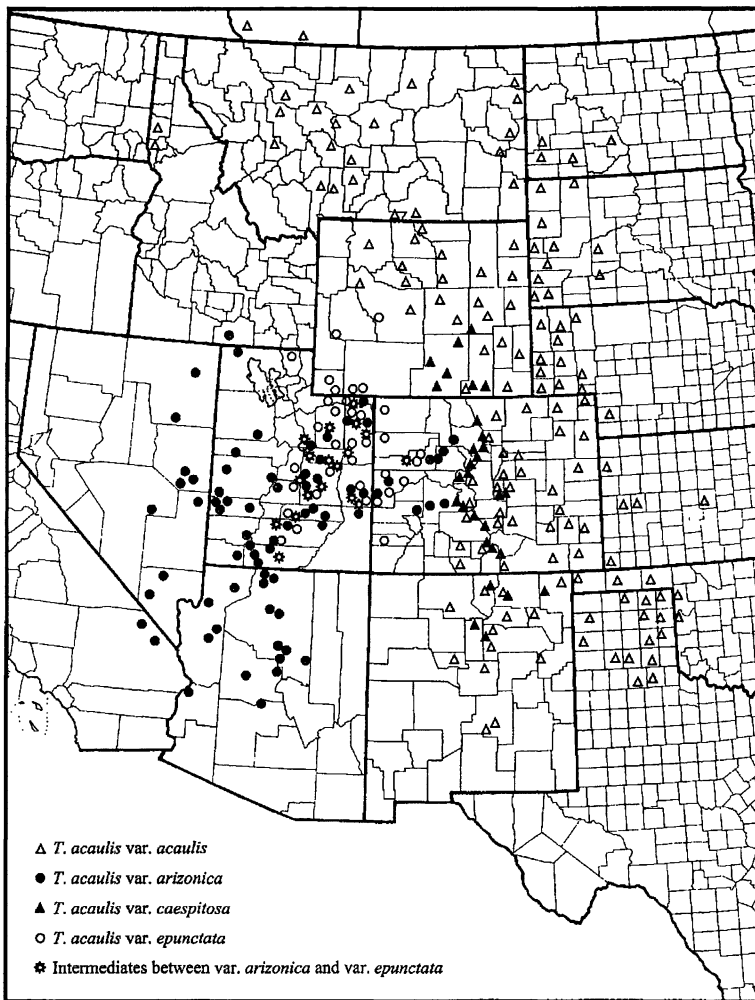


FIG. 2. Distribution of *Tetraneuris acaulis* var. *acaulis*, *T. acaulis* var. *arizonica*, *T. acaulis* var. *caespitosa*, and *T. acaulis* var. *epunctata*. Also shown are intermediates between *T. acaulis* var. *arizonica* and *T. acaulis* var. *epunctata*.

brous or sparsely pubescent, eglandular or sparsely dotted with sessile glands. CYPSE-LAE 2–4 × 0.8–1.2 mm, surfaces white, moderately to densely pubescent, eglandular or sparsely dotted with sessile glands; pappi 5–8, obovate- to oblanceolate-aristate scales, 2.2–3.7 × 0.5–1.2 mm.

Tetraneuris acaulis is very widespread and variable, and some 14 original names have been applied to what in our opinion constitute four recognizable infraspecific taxa (Fig. 2). Varieties of *T. acaulis* overlap

with one another and with other taxa with which they appear to hybridize.

Tetraneuris acaulis var. *acaulis* ranges from central New Mexico and the panhandle of Texas through parts of Oklahoma, Colorado, Kansas, Nebraska, South Dakota, North Dakota, Wyoming, and Montana into southern Alberta and Saskatchewan (Fig. 2). Throughout its range, which is east of the continental divide except for two Idaho collections (the type of *T. septentrionalis* and a collection at LL; see representative specimens), it is usually easily identified by

dense strigoso-canescens leaf pubescence and paucity of impressed leaf glands. In various parts of Colorado and southeastern Wyoming, the leaves may be rather sparsely pubescent and/or densely glandular, and it is not unusual to find specimens from those areas identified as *T. acaulis* var. *arizonica*, *T. scaposa*, or *T. simplex*, the last applied to such plants from southeastern Wyoming and northern Colorado.

We have observed plants that appear to be hybrids between *Tetraneuris acaulis* var. *acaulis* and *T. scaposa* var. *scaposa*, and it is possible that the Colorado and Wyoming populations with sparsely pubescent and/or densely glandular leaves are the result of long-time and widespread hybridization between these two taxa. We have included such morphologic variants under *T. acaulis* var. *acaulis* because they have caudices that are thickened distally and leaves that are tightly clustered; *T. scaposa* var. *scaposa* has caudices that are not thickened distally and leaves that are basal-proximal rather than tightly clustered. We are confident that these plants are not referable to *T. acaulis* var. *arizonica*. The pubescence, while sparse in many cases, is composed of closely appressed hairs ca 1–1.5 mm long, identical to those found in typical densely strigoso-canescens plants. The leaf pubescence of *T. acaulis* var. *arizonica* is composed of spreading rather than closely appressed hairs ca 1.5–3 mm long.

Taxonomic problems in *Tetraneuris acaulis* along and east of the continental divide are further complicated by the existence of a high-elevation taxon, *T. acaulis* var. *caespitosa*, which ranges from northern New Mexico to southcentral Wyoming (Fig. 2). We were inclined to include those plants within *T. acaulis* var. *acaulis* as high-elevation variants; however, the more we examined them the clearer it became that they are morphologically distinct and occupy a well defined geographic range. Compared to *T. acaulis* var. *acaulis*, such plants typically have shorter peduncles that are lanate below the involucre, lanuginose or seri-

ceous leaf pubescence, and longer outer phyllaries. They generally grow at considerably higher elevations and are most commonly found along the Sangre de Cristo range from northern New Mexico into southern Colorado and north from there along the continental divide into northern Colorado and parts of southern Wyoming. They are also found in adjacent areas east of the continental divide including the Pike's Peak vicinity in Teller County, Colorado, where such plants were described as *T. brevifolia*.

On the west side of the continental divide, *Tetraneuris acaulis* var. *arizonica* ranges from northern Arizona and southeastern California into eastern Nevada, Utah, southern Idaho, and western Colorado (Fig. 2). It overlaps in distribution with *T. acaulis* var. *epunctata* in eastern Utah and western Colorado (Fig. 2), and with *T. ivesiana* in northern Arizona, southern Utah, and western Colorado (Fig. 2 and 3). While it is generally not too difficult to separate *T. acaulis* var. *arizonica* from *T. acaulis* var. *epunctata* by its densely glandular leaves, and from *T. ivesiana* by its generally broader basal leaves and lack of cauline leaves, it is not uncommon to find plants that have all basal, moderately glandular, oblanceolate leaves (intermediates, perhaps hybrids, between *T. acaulis* var. *arizonica* and *T. acaulis* var. *epunctata*) or all basal, densely glandular, linear-oblanceolate leaves (perhaps hybrids between *T. acaulis* var. *arizonica* and *T. ivesiana*). For the most part, we have included only plants with densely glandular leaves and no cauline leaves in *T. acaulis* var. *arizonica*; it seems quite likely that some of these are *T. ivesiana* plants that simply lack cauline leaves or are hybrids or hybrid derivatives between the two taxa. Dwarf-form/pincushion plants in Emery County, Utah, along the San Rafael Swell (e.g., Anderson 87-39, UTC) have been described as *Hymenoxys acaulis* var. *nana*; we have included them in synonymy under *T. acaulis* var. *arizonica*. They are quite distinctive, but similar dwarf-form/pincushion plants occur in

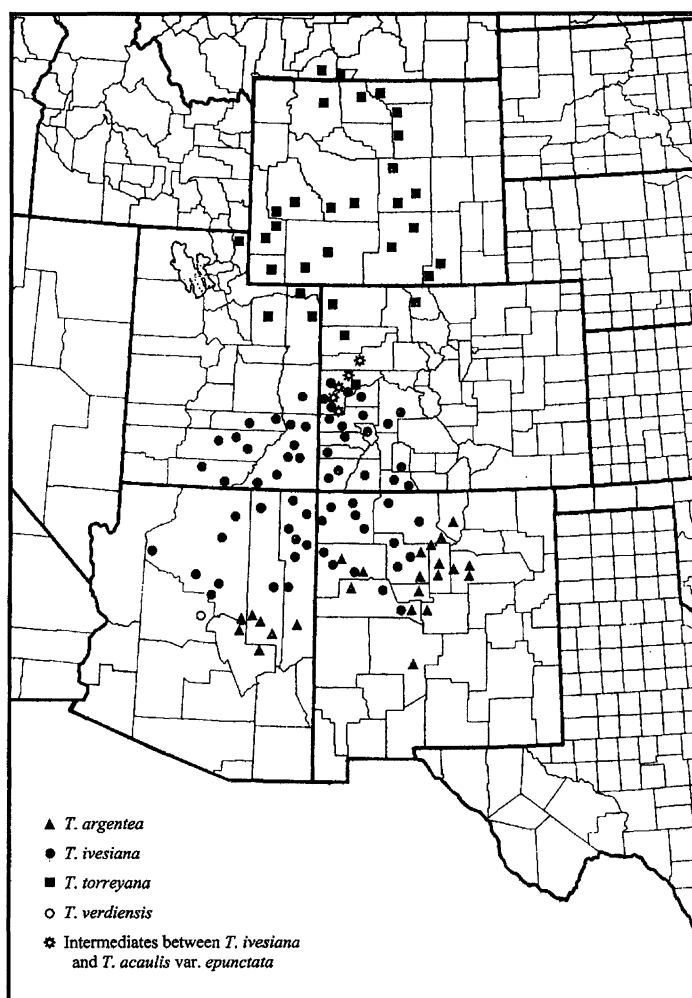


FIG. 3. Distribution of *Tetraneuris argentea*, *T. ivesiana*, *T. torreyana*, and *T. verdiensis*. Also shown are intermediates between *T. ivesiana* and *T. acaulis* var. *epunctata*.

several other *Tetraneuris* species and we do not believe that they warrant formal taxonomic recognition. This situation is discussed further under *T. torreyana*.

Tetraneuris acaulis var. *epunctata* ranges from southcentral Utah to northeastern Utah, western Colorado, and southwestern Wyoming (Fig. 2). Most of the plants have distinctly eglandular or very sparsely glandular leaves, but it is not unusual to find intermediate plants that have moderately glandular leaves (Fig. 2). In westcentral Colorado, where the ranges of *T. acaulis* var. *epunctata* and *T. ivesiana* overlap most sig-

nificantly (there is also some minor overlap in southern Utah), one finds intermediate plants (Fig. 3) that have eglandular or sparsely glandular basal and cauline leaves (typically, *T. ivesiana* has densely glandular leaves).

REPRESENTATIVE SPECIMENS INTERMEDIATE BETWEEN *TETRANEURIS ACAULIS* VAR. *EPUNCTATA* AND *T. ACAULIS* VAR. *ARIZONICA*: **UNITED STATES. Colorado.** Garfield Co.: 5 mi N of Rifle on Government Creek, 1770 m, 17 May 1947, Weber 3315 (COLO, CS, RM, UTC). **Utah.** Carbon Co.:

Price, Apr 1930, *Flowers s.n.* (UT); Near Emery County line, Hwy 124, 9 mi S of Dragerton (East Carbon City), 1770 m, 30 May 1992, *Holmgren & Holmgren 11662* (MONTU). Daggett Co.: 3 mi S of Manila, 1935 m, $2n = 60$, 29 Jun 1947, *Parker & McClintock 6985* (TEX). Duchesne Co.: S of Starvation Reservoir along Hwy 40, ca 3.3 mi W of the Strawberry River bridge at the W edge of Duchesne, 1770 m, $n = 28$, 19 May 1995, *Windham 95-65* (COLO, UT). Emery Co.: W Tavaputs Plateau above Book Cliffs, SE of E Carbon City, near Turtle Canyon, 1750 m, 12 May 1978, *Albee 3945* (UT); San Rafael Swell, 1525 m, 15 May 1931, *Cottam 5594* (UT); Nelson Mt top, ca 6 mi SW of Ferron, 2802 m, 20 Jul 1983, *Tuhy 931* (UTC); First turnoff E of Castle Valley Ridge, Woodward Canyon Trail S along ridge, 20 Jul 1973, *Woodruff 619* (UT). Garfield Co.: Table Cliff Plateau, 1 mi E of Pine Lake, 2745 m, 26 Jun 1940, *Maguire 19116* (UTC). Grand Co.: NE of Moab, Porcupine Rim, 1830 m, 10 May 1986, *Chandler et al. 2884* (RM); NE slope of LaSal Mts, above Beaver Creek, 2500 m, 10 Jun 1986, *Franklin 3575* (RM). Kane Co.: W of Skutumpah Ranch, Skutumpah Terrace, ca 1830 m, 4 Jun 1981, *Grimes 2040* (UTC). Sevier Co.: 20 mi E of Salina, 2360 m, 19 Jun 1947, *Parker & McClintock 6910* (TEX). Uintah Co.: 16.3 mi N of jct of Hwys 40 and 44 (jct in Vernal), 15 Jun 1971, *Bierner 323* (TEX); 5 mi S of Bonanza, 1630 m, 19 Jun 1975, *Howard s.n.* (UTC); Flat Rock Spring area, ca 48 mi SW of Ouray, 2195 m, 30 Jun 1980, *Mutz 80-102* (UT). Utah Co.: 8 mi E of Soldier Summit, 5 Jun 1940, *Maguire 18403* (UTC). Wasatch Co.: 6 mi E of Soldier Summit on Hwy 50, 2165 m, 6 Aug 1965, *Hatch 84* (UTC). Wayne Co.: Slopes above Grover, 13 Jun 1953, *Holmgren & Tillett 9435* (UTC).

REPRESENTATIVE SPECIMENS INTERMEDIATE BETWEEN *TETRANEURIS ACAULIS* VAR. *EPUNCTATA* AND *T. IVESIANA*: **UNITED STATES. Colorado.** Garfield Co.: Flat

Tops/White River Plateau, Grand Hogback, ca 3 air mi N of Rifle, 1740 m, 24 May 1991, *Vanderhorst 2140* (COLO, RM). Mesa Co.: 22 mi NE of Gateway, N side of West Creek, 2135 m, 18 Jun 1983, *Neese 13685* (CS); Hills below Mount Low, NE of De Beque, 1565 m, 23 May 1986, *O'Kane 2377* (RM); Uncompahgre Nat'l Forest, along Hwy 408 between Uncompahgre Butte and Monument Hill, 2745 m, 4 Sep 1981, *Siplivinsky 2330* (COLO, MONTU); Colorado Nat'l Monument, 1530 m, 21 May 1948, *Weber 3752* (COLO, CS, MONTU, RM, TEX, UTC).

KEY TO THE VARIETIES

1. Leaf blades sparsely to densely pubescent, often lanuginose, sometimes sericeous, not strigoso-canescens; peduncles 0.5–8(–12) cm; outer phyllaries 6.8–9(–11.5) mm; growing at (2100–)3000–3850 m 1c. *T. acaulis* var. *caespitosa*
1. Leaf blades sparsely to densely pubescent, often strigoso-canescens; peduncles (1–)5–20(–30) cm; outer phyllaries 4–7.5 mm; growing at 700–2930(–3475) m.
 2. Leaf blades sparsely to densely pubescent, usually densely strigoso-canescens; east of the continental divide 1a. *T. acaulis* var. *acaulis*
 2. Leaf blades glabrous or sparsely to moderately to, sometimes, densely pubescent, not strigoso-canescens; west of the continental divide.
 3. Leaf blades glabrous or, usually, sparsely to moderately or, sometimes, densely pubescent, densely glandular; northern Arizona to southeastern California, eastern Nevada, Utah, western Colorado, and southern Idaho 1b. *T. acaulis* var. *arizonica*
 3. Leaf blades glabrous or sparsely to moderately pubescent, at least some (usually most or all) eglandular or sparsely glandular; southcentral to northeastern Utah, western Colorado and southwestern Wyoming 1d. *T. acaulis* var. *epunctata*

1a. *TETRANEURIS ACAULIS* (Pursh) Greene var. *ACAULIS*.

Gaillardia acaulis Pursh, Fl. Amer. Sept. 2: 743. 1814, as *Galardia*. TYPE: UNITED STATES. North Dakota? "In Upper Louisiana" (protologue), "Louisiana" (ho-

- lotype label), 1810–1811, *J. Bradbury* (HOLOTYPE: PH!).
- Actinella acaulis* (Pursh) Nutt., Gen. N. Amer. Pl. 2: 173. 1818.
- Actinea acaulis* (Pursh) Spreng., Syst. 3: 574. 1826.
- Cephalophora acaulis* (Pursh) DC., Prodr. 5: 663. 1836.
- Actinea acaulis* (Pursh) Kuntze, Revis. Gen. Pl. 1: 303. 1891, nom. superfl.
- Ptilepida acaulis* (Nutt.) [sic] Britton, Mem. Torrey Bot. Club 5: 339. 1894.
- Tetraneuris acaulis* (Pursh) Greene, Pittonia 3: 265. 1898.
- Picradenia acaulis* (Nutt.) [sic] Britton in N. L. Britton and A. Brown, Ill. Fl. N. U.S. 3: 449. 1898.
- Hymenoxys acaulis* (Pursh) K. L. Parker, Madroño 10: 159. 1950.
- Actinella depressa* Torr. & A. Gray. var. *pygmaea* A. Gray, Mem. Amer. Acad. Arts (Series 2) 4: 100. 1849. TYPE: UNITED STATES. New Mexico. Colfax Co.: "Raton Mountains" (protologue), "In the Cañon of the Colorado, Raton Mountains" (MO isotype label), Apr 1848, A. Gordon s.n. (HOLOTYPE: GH!; ISOTYPES: GH!, MO-208206!).
- Tetraneuris pygmaea* (A. Gray) Wooton & Standl., Contr. U.S. Natl. Herb. 16: 193. 1913.
- Actinea depressa* (Torr. & A. Gray) Kuntze var. *pygmaea* (A. Gray) J. F. Macbride, Contr. Gray Herb. 56: 42. 1918.
- Tetraneuris simplex* A. Nelson, Bot. Gaz. 28: 127. 1899. TYPE: UNITED STATES. Wyoming. Albany Co.: "Laramie Hills" (lectotype label), 16 Jun 1897, A. Nelson 3177 (LECTOTYPE here designated: RM-15210!; ISOLECTOTYPE: MO-208304!).
- Actinella simplex* (A. Nelson) A. Nelson, New Man. Centr. Rocky Mts. 558. 1909.
- Actinea acaulis* (Pursh) Spreng. var. *simplex* (A. Nelson) J. F. Macbride, Contr. Gray Herb. 56: 43. 1918.
- Actinea simplex* (A. Nelson) A. Nelson, Univ. Wyoming Publ. Sci., Bot. 1: 60. 1924.
- Tetraneuris incana* A. Nelson, Bot. Gaz. 28: 128. 1899. TYPE: UNITED STATES. Wyoming. Natrona Co.: "Wallace Creek" (protologue and holotype label), 30 Jul 1898, A. Nelson 5006 (HOLOTYPE: RM-15392!; ISOTYPE: NY!).
- Actinella incana* (A. Nelson) A. Nelson, New Man. Centr. Rocky Mts. 559. 1909.
- Actinea incana* (A. Nelson) A. Nelson, Univ. Wyoming Publ. Sci., Bot. 1: 62. 1924.
- Tetraneuris eradiata* A. Nelson, Bot. Gaz. 37: 275. 1904. TYPE: UNITED STATES. Wyoming. Washakie Co.: "Steep slopes. Head of Middle Fork of Powder River, Big Horn Co., Wyo." (holotype label), 18 Jul 1901, L. N. Goodding 276 (HOLOTYPE: RM-42587!; ISOTYPES: F-215537!, GH!, MO-208049!, NY!, UC-51039!, US-485147!). The type specimen labels give the locality as being in Big Horn County, which was correct in 1901. The creation of Washakie County in 1911 out of the southern portion of Big Horn County included this locality (Ron Hartman, University of Wyoming, personal communication).
- Actinella eradiata* (A. Nelson) A. Nelson, New Man. Centr. Rocky Mts. 559. 1909.
- Actinea eradiata* (A. Nelson) A. Nelson, Univ. Wyoming Publ. Sci., Bot. 1: 62. 1924.
- Tetraneuris septentrionalis* Rydb., Bull. Torrey Bot. Club 37: 447. 1910. TYPE: UNITED STATES. Idaho. "Palouse Country, Idaho" (holotype label), Jun-Jul 1892, G. B. Aiton s.n. (HOLOTYPE: NY!; ISOTYPE: NY!). Palouse Country would encompass areas around Moscow Idaho and adjacent Washington and include Latah County and Nez Perce County, Idaho (Anita F. Cholewa, J. F. Bell Museum of Natural History, University of Minnesota, personal communication).

Actinea acaulis (Pursh) Spreng. var. *septentrionalis* (Rydb.) A. Nelson, Univ. Wyoming Publ. Sci., Bot. 1: 62. 1924.

Actinea osterhoutii A. Nelson, Univ. Wyoming Publ. Sci., Bot. 1: 62. 1924. TYPE: UNITED STATES. Colorado. Otero Co.: "Rocky Ford, Otero Co. Colo." (holotype label), 8 Jun 1900, G. E. Osterhout 2035 (HOLOTYPE: RM-23590!; ISOTYPE: NY!).

AERIAL STEMS 1–10(–15). LEAVES: blades spatulate to oblanceolate to linear-oblanceolate, sparsely to densely pubescent, usually densely strigoso-canescens, sparsely to, sometimes, moderately or densely dotted with impressed glands. HEADS 1–10(–15) per plant, usually radiate. PEDUNCLES green throughout to purple-red-tinted throughout, (2–)8–20(–30) cm, sparsely to densely pubescent, not lanate below involucre, eglandular or sparsely dotted with sessile glands. INVOLUCRES 7–10 × 8–14 mm. PHYLLARIES: outer phyllaries 6–10, 4–7 × 1.1–2.5 mm, margins sometimes slightly scarious, abaxial faces usually densely pubescent, eglandular or sparsely dotted with sessile and/or impressed glands; mid phyllaries often purple-red-tinted on apices and margins, obovate to ovate, 4.2–7 × 1.3–2.5 mm, margins often scarious, abaxial faces moderately to densely pubescent, eglandular or sparsely dotted with sessile glands; inner phyllaries 3.5–5.5 × 1–2.5 mm, abaxial faces sparsely to moderately pubescent, eglandular or sparsely dotted with sessile glands. RAY FLORETS 8–14; corollas 9–15 × 3–7 mm, abaxial faces glabrous or sparsely to moderately pubescent, sparsely to moderately dotted with sessile glands. DISC FLORETS 25–150+; corollas 3–3.5 × 0.7–1 mm, eglandular or sparsely dotted with sessile glands. CYPSELAE 2.5–3 × 0.8–1 mm, eglandular or sparsely dotted with sessile glands; pappi 5–8, obovate to oblanceolate-aristate scales, 2.2–2.9 × 0.8–1 mm.

CHROMOSOME NUMBERS: $2n = 28, 30, 56, 60$.

DISTRIBUTION (Fig. 2) AND HABITAT: Central New Mexico and the panhandle of Texas through parts of Oklahoma, Colorado, Kansas, Nebraska, South Dakota, North Dakota, Wyoming, Idaho, and Montana into southern Alberta and Saskatchewan (the latter according to Cronquist, 1994). Growing at roadsides, on hillsides, in grasslands, and at edges of woods, 700–2000(–3000) m.

FLOWERING AND FRUITING: April through October, mainly May through July.

REPRESENTATIVE SPECIMENS: CANADA. **Alberta.** Oldman River Valley, N of Pincher, 21 Jun 1940, Moss 847 (RM); Coulee Verdigris entre Milk River et Allerton, 26 Jun 1958, Boivin & Perron 12237 (RM). UNITED STATES. **Colorado.** Alamosa Co.: Sangre de Cristo Range, vicinity of Zapata Falls, 3000 m, 30 Jun 1998, Hogan 3351 (COLO). Arapahoe Co.: Bombing range, 17 Jun 1960, Brunquist B-11 (CS). Baca Co.: Springfield, 13 Jun 1948, Taylor 67 (TEX). Bent Co.: Arkansas River near Hasty, 3 May 1947, Porter 4112 (TEX). Boulder Co.: Near Boulder, Dry Mesa, 28 May 1901, Ramaley 688 (COLO). Chaffee Co.: Salida, 2440 m, 27 Jul 1917, Johnston 239 (RM). Conejos Co.: Basalt ridge above La Jara Creek E of González-Martínez ranches, 2444 m, 10 Jul 1984, Bye & Linares 12910 (COLO). Custer Co.: 5 mi E of Wetmore, 1710 m, 28 May 1954, Harrington 7335 (CS). Denver Co.: Denver, Valverde Hills, Jun 1886, Eastwood s.n. (COLO). Douglas Co.: Palmer Lake, 20 May 1925, Nelson 10518 (MONTU, RM). El Paso Co.: Garden of the Gods E of Manitou Springs, 1890 m, $2n = 60$, 1 Jul 1947, Parker & McClintock 6994 (COLO, RM, TEX, UTC). Elbert Co.: 5 mi SW of Elbert, 16 Jun 1937, Ownbey 1269 (COLO, MONTU, RM, UTC). Fremont Co.: Hwy 120, 3.1 mi W of Hwy 50, 15 Jun 1975, Bierner 51298 (TEX). Kiowa Co.: Hwy 96, S of Haswell, 1320 m, 29 Jun 2000, Clark & Crawford 1192 (COLO). Kit Carson Co.: 12 mi N of Stratton, 1270 m, 19 May 2000, Clark & Crawford 897 (COLO). Larimer Co.:

Hwy 287, 2.3 mi N of Hwy 14, 13 Jun 1975, *Bierner 51295* (TEX). Las Animas Co.: Hwy 111, ca 4 mi S of Stonewall, 2620 m, 15 Jun 1941, *Robbins 536* (TEX); 4 mi N of Andrix at jct of Hwys 48 & 215, 1610 m, 31 May 1991, *Wittmann & Weber 18159* (COLO). Lincoln Co.: Just W of Little Horse Creek, 1615 m, 22 May 2000, *Clark & Crawford 976* (COLO). Logan Co.: Flattop Butte, ca 20 mi NNW of Sterling, 1295 m, 31 May 1997, *Lederer 97-32* (COLO). Otero Co.: Hwy 50, 15.8 mi W of Hwy 101 (5.8 mi W of the Otero-Bent county line), 16 Jun 1975, *Bierner 51300* (TEX). Park Co.: Hwy 120, 2 mi N of the jct to Sunlight Basin, 1710 m, 16 Jun 1989, *Shaw 4589* (UTC). Prowers Co.: Hwy 287, 14 mi S of Lamar, 4 May 1949, *Weber 4547* (COLO). Pueblo Co.: E side of I-25, ca 10 mi S of Pueblo at the Burnt Mill Rd exit, 15 Jun 1975, *Bierner 51299* (TEX). Rio Grande Co.: Del Norte, 1 Jul 1921, *Bethel et al. 4377* (RM). Saguache Co.: Sage plains 6 mi S of summit of Poncha Pass, 2530 m, 14 Jun 1951, *Weber & Livingston 6156* (COLO). Sedgwick Co.: Julesburg, 11 Jun 1913, *Osterhout 4914* (COLO, RM). Teller Co.: 2 mi S of Florissant at Petrified Forest, 2850 m, 16 Aug 1961, *Iltis & Iltis 18794* (COLO). Washington Co.: Hwy 34, ca 17.3 mi E of Brush, 8 May 1966, *Johnston 1002* (COLO). Weld Co.: 6.5 mi E of Grover, 1650 m, 16 Apr 1954, *Douglass 549* (COLO). Yuma Co.: Wray, 15 Jul 1909, *Osterhout 4010* (RM).

Idaho. Latah Co.: Palouse Country, Jun-Jul 1892, *Aiton s.n.* (NY). Nez Perce Co.: Lewistown, Jun 1930, *Curtis s.n.* (LL). **Kansas.** Sherman Co.: 7 mi S, 2 mi W, 3 mi S of Goodland, 25 May 1971, *McGregor 23725* (OKL). Barton Co.: Great Bend, Aug 1886, *Smyth 3970* (KSC). Morton Co.: 8 mi N of Elkhart, 16 Jun 1972, *Hulbert 4495* (KSC). Scott Co.: 7 mi W of Scott City, 19 Jun 1957, *Hulbert 2919* (KSC, OKLA). Wichita Co.: 1 Aug 1895, *Hitchcock 289* (KSC, RM).

Montana. Big Horn Co.: 14 mi W of Wyola, 14 Jun 1976, *Turner & Plettman, s.n.* (TEX). Carbon Co.: Ca 18 mi N of Lovell, 2045 m, 16 Jun 1990, *Evert 18986* (RM).

Carter Co.: Medicine Rocks State Park, 11 mi N of Ekalaka, 1040 m, 19 May 1986, *Shelly 1047* (MONTU). Cascade Co.: Black Eagle Dam, 1175 m, 16 Jun 1934, *Marsh 745* (MONTU). Chouteau Co.: Little Sandy Creek Missouri River access site, 5 May 1981, *Beyer 24* (MONTU). Custer Co.: Ismay, 1220 m, 17 Jun 1936, *Nerenz 244* (MONTU). Dawson Co.: Hodges, 24 May 1936, *Stentz & Clary s.n.* (MONTU). Fergus Co.: Heath, 8 Aug 1971, *Olmstead & Wendt G-32* (TEX). Gallatin Co.: Bozeman, Horse Shoe Hills, 27 Jun 1937, *Cotner s.n.* (MONTU). Judith Basin Co.: 8 mi S of Raynesford, 8 Aug 1971, *Olmstead & Wendt G-43* (TEX). Lewis & Clark Co.: W of Great Falls on Hwy 200, 5 mi W of Hwy 287, 5 Jun 1979, *Ramsden & Lackschewitz 463* (MONTU). Meagher Co.: Jefferson Nat'l Forest, 1740 m, 28 Jun 1931, *Flint 25-31* (MONTU). Park Co.: Livingston, 8 Jun 1906, *Blankinship 725* (NEB). Phillips Co.: E side of the Coburn Ditch valley 1 mi N of the Matador Ranch headquarters, 915 m, 18 May 2000, *Lesica 8058* (MONTU). Powell Co.: 25 mi E of Drummond, 8 Jun 1938, *Barkley & Jenen 2490* (MONTU, UTC). Richland Co.: Fairview, 5 Jun 1937, *Hanson s.n.* (MONTU). Roosevelt Co.: 4 km N of Culbertson, 700 m, 30 May 1986, *Mooers & Mooers 1108* (MONTU). Stillwater Co.: I-90 rest area ca 9 mi E of Columbus, 1100 m, 2 Jun 1993, *Evert 24615* (RM). Sweet Grass Co.: Big Coulee Creek, 15 Jun 1902, *Blankinship s.n.* (UTC). Teton Co.: 15 mi W of Choteau, 1220 m, 28 Jun 1981, *Shaw 3465* (MONTU). Wheatland Co.: 15 mi SW of Harlowton, 26 Jun 1934, *Hitchcock 2409* (MONTU).

Nebraska. Banner Co.: S bluffs of Rocky Hollow (12 mi S of jct to Harrisburg on Hwy 71), 5 Jul 1974, *Churchill 3793* (NEB). Box Butte Co.: 15 mi N of Hemingford on Hwy 2, 10 Jun 1973, *Churchill 1039* (NEB). Chase Co.: SE of Enders, 8 Aug 1941, *Tolstead 411587* (NEB). Cheyenne Co.: 3 mi E of Potter on Hwy 30, 5 Jul 1974, *Churchill 3772* (NEB). Dawes Co.: Hwy 385 S of Chadron, 15 mi from jct with Hwy 87, 13 Aug 1983, *Keil et al. 17722*

(TEX). Deuel Co.: 5 mi N, 3.5 mi W of Chappell, 3 Jun 1992, *Rolfsmeier* 10127 (NEB). Garden Co.: Near S end of McCuligan Canyon, 3.5 mi S, 2 mi SW of Oshkosh, 14 Jun 1992, *Rolfsmeier* 10349 (NEB). Kimball Co.: 1 mi W of Kimball on Hwy 30, 6 Jul 1974, *Churchill* 3810 (NEB). Morrill Co.: 0.5 mi S of Angora on Hwy 385, 1 Jun 1973, *Churchill* 864 (NEB). Scotts Bluff Co.: S of Minatare, 1265 m, 29 Jul 1951, *Kiener* 47417 (NEB). Sheridan Co.: Near Hay Springs, 1000 m, 6–7 Jun 1901, *MacDougal* 53 (MONTU). Sioux Co.: 1 mi W of entrance of Soldier Creek Management Unit Nebraska Nat'l Forest, W of Fort Robinson State Park, 17 Jun 1991, *Rolfsmeier* 8950 (NEB). **New Mexico.** Bernalillo Co.: Sandia Mt, 19 Aug 1926, *Arsene & Benedict* 16567 (LL). Colfax Co.: 2 mi NE of Cimarron on Hwy 64, ca 2010 m, 26 Jun 1965, *Strother* 418 (TEX). Harding Co.: Ca 10 mi NNW of Mills, ca 1830 m, $n = 15$, 2 Jul 1981, *Spellenberg et al.* 6038 (TEX). Lincoln Co.: Capitan Mts, Johnnie Canyon, 9 Aug 1977, *Fletcher* 2500 (UNM); N edge of Ruidoso, $2n = 15\text{II}$, 10 Jun 1965, *Strother* 321 (TEX). Mora Co.: 4.5 mi E of Golondrinas, 9 Jun 1961, *Potter* 408 (UNM). Quay Co.: 5 mi E of Montoya, 1340 m, 4 Jun 1955, *Parker & Parker* 8319 (TEX). Rio Arriba Co.: Gypsum hills N of Coyote, 25 May 1982, *Fletcher* 6045 (UNM). San Miguel Co.: 18 mi SW of Las Vegas on Hwy 85/85, 1980 m, $2n = 30\text{II}$, 26 Jun 1965, *Strother* 416 (TEX); 2 mi N of Sapello, 2165 m, $2n = 30\text{II}$, 26 Jun 1965, *Strother* 417 (TEX); 20 mi S of Las Vegas, 1950 m, $2n = 60$, 29 Aug 1946, *Parker & McClintock* 6476 (RM). Taos Co.: Between Questa and Taos, 30 Jul 1932, *Nelson & Nelson* 157 (RM). Torrance Co.: Hwy 285, ca 20 mi N of Hwy 60 (jct just W of Encino), 23 May 1989, *Bierner* 89-29 (TEX). Union Co.: 4 mi S of Moses on Hwy 18, 27 Jun 1965, *Strother* 422 (TEX). **North Dakota.** Billings Co.: Little Missouri Nat'l Grasslands, SW corner of Kinley, 855 m, 22 Jun 1992, *DiGiacomo* 1 (UTC). Hettinger Co.: W of Mott, 24 Jun 1942, *Hotchkiss s.n.* (RM). Morton Co.:

Sentinel Butte, 23 Jun 1916, *Tidestrom s.n.* (LL). Slope Co.: 15 May 1962, *Mueller* 287 (OKLA). **Oklahoma.** Beaver Co.: 7 mi E of Elmwood, 29 Apr 1974, *Stephens* 74795 (OKL). Cimarron Co.: Ca 0.5 mi E and 4 mi N of Kenton, 30 Apr 1992, *McPherson* 634 (OKLA). Ellis Co.: 9 mi W and 3.5 mi S of Arnett, 23 May 1970, *Nighswonger & Carey* 656 (KSC, OKL). Roger Mills Co.: 4 mi NE of Durham, 21 May 1965, *Taylor & Baalman* 2630 (OKL). Texas Co.: 26 mi W of Optima, 22 Jun 1941, *Rigney* 119 (OKLA). **South Dakota.** Butte Co.: Redwater Ridge, 11 Jul 1975, *Sisk s.n.* (SDU). Custer Co.: Pringle, 15 Jun 1914, *Over* 1687 (SDU). Fall River Co.: Hot Springs, 6 Jun 1997, *Holland* 9001 (KSC); 2 mi S of Edgemont, 6 Jul 1927, *Shantz* 280 (LL). Haakon Co.: Grindstone Buttes, 10 mi N and 6 mi W of Philip, North Butte, 26 Jun 1982, *Ode* 82-39 (SDU). Harding Co.: Tableland, Cave Hills, 15 Jul 1920, *Over & Solem* 10723 (SDU). Jackson Co.: Badlands Nat'l Monument, 24 May 1967, *Stockert* 57-67 (SDU). Lawrence Co.: Deadwood, 9 Jul 1913, *Rydberg* 37 (SDU). Meade Co.: E of Tilford, 1020 m, 25 May 1938, *Benson* 618 (NEB). Pennington Co.: Rapid City, 22 May 1924, *Lee B-345* (SDU). Perkins Co.: Near Lemon, 11 Jun 1966, *Lindstrom* 1708 (KSC). **Texas.** Armstrong Co.: Ca 15 mi S of Claude, 10 Oct 1964, *Correll* 30380 (LL). Briscoe Co.: 4 mi W of Quitaque, 29 Jun 1961, *Johnston* 6576a (LL). Donley Co.: 7 mi NW of Memphis, 10 Jun 1941, *Rose-Innes & Moon* 1011 (TEX). Gray Co.: 8.7 mi W of McLean, 28 May 1964, *Rowell* 10141 (OKLA). Hall Co.: Dry rocky limestone hills, 7 Aug 1940, *Smith* 304 (OKL). Hansford Co.: 16 mi NW of Gruver, 9 Oct 1965, *Rowell* 10978 (OKLA). Hartley Co.: N side of Rita Blanca Lake, 100–500 ft NW of boat ramp rd leading S from Hwy 281 ca 0.6 mi SE of Lake Drive, S side of Dalhart, ca 1195 m, 3 Jun 1991, *Carr & Diamond* 11188 (TEX). Hemphill Co.: Cliff on breaks of the Canadian River just S of Canadian, 25 Jun 1957, *Correll & Johnston* 17064 (LL). Lipscomb Co.: Ca 2 mi W of Darrouzett, 24

May 1961, *Correll 24047* (LL). Ochiltree Co.: 8.7 mi SE of Perryton on Hwy 83, 6 Jun 1958, *Wallis 7200* (OKLA, TEX). Oldham Co.: 8 mi W of Adrian, Aug 1949, *York & Rogers 393* (TEX). Randall Co.: Rim of Palo Duro Canyon, 1 May 1942, *Lundell & Lundell 11419* (LL). Roberts Co.: N side of Canadian River, 27 mi S of Perryton on Hwy 70, 15 Jul 1957, *Wallis 4977* (OKLA, TEX). Wheeler Co.: Mobeetie, 22 Sep 1926, *Tharp 4570* (TEX). **Wyoming.** Albany Co.: W foothills Laramie Range, ca 6.5 air mi SE of Laramie, 2370 m, 18 Jul 1995, *Fertig 16003* (RM); Ca 25 mi SW of Wheatland, 1875 m, 11 Jun 1985, *O'Brian 1342* (RM). Big Horn Co.: Big Horn Mts, John Blue Canyon Rd, ca 5.9 mi NNE of Hwy 14A, 1830 m, 28 May 1980, *Dueholm & Hartman 9664* (TEX). Campbell Co.: Ca 6.25 mi S of Reno Junction, 1495 m, 11 Jun 1978, *Dueholm & Hartman 2185* (RM). Converse Co.: 8 mi N of Douglas on Hwy 87, 1495 m, 12 Jun 1946, *Porter 3851* (TEX); Ca 40 air mi NW of Douglas, 1540 m, 14 Jun 1978, *Skelton s.n.* (RM). Crook Co.: Ca 9 air mi ESE of Sundance, 1585 m, 11 Jul 1984, *Marriott 7929* (TEX). Fremont Co.: Ca 18 air mi S of Moneta, 1800 m, 28 May 1985, *Hartman & Haines 19856* (RM); Wind River Basin, ca 1.6 air mi NE of Dubois, 2195 m, 26 Jun 1984, *Nelson 10786* (RM). Goshen Co.: Ca 6.5 air mi SSE of Lingle, 1370 m, 16 Jun 1994, *Nelson 31639* (RM). Hot Springs Co.: Ca 5 mi S of Thermopolis, 22 Jun 1961, *Fisser 524* (RM). Johnson Co.: Ca 7 air mi S of Buffalo, 1585 m, 4 Jun 1979, *Dueholm 6431* (RM); Ca 17.5 air mi WSW of Kaycee, 1950 m, 4 Jul 1979, *Nelson 3057* (RM). Laramie Co.: I-80, just W of Cheyenne, 13 Jun 1975, *Biernier 51294* (TEX). Natrona Co.: Ca 20 air mi N of Natrona, 1650 m, 3 Jul 1979, *Dueholm 7694* (RM); Casper Mt area, vicinity of Garden Creek Falls, 1950 m, 1 Jun 1962, *Jozwik 84* (RM). Niobrara Co.: S of Boner House, 35 mi NW of Lusk, 27 May 1940, *Gilbert s.n.* (RM). Park Co.: Along S side of Buffalo Bill Reservoir ca 10 mi SW of Cody, 9 Jun 1989, *Evert 16562* (RM). Platte Co.: Ca 15 air mi N of Wheatland,

1410 m, 29 Jun 1994, *Nelson 32344* (RM). Sheridan Co.: E slope Bighorn Mts, ca 7.3 air mi WNW of Dayton, 3 Jun 1994, *Fertig & Britt 14775* (RM). Washakie Co.: Hwy 431 at Hot Springs County line, 1555 m, 7 Jun 1995, *Dorn 5936* (RM). Weston Co.: Ca 16 air mi SSE of Newcastle, 16 May 1984, *Marriott 6181* (RM).

1b. *TETRANEURIS ACAULIS* (Pursh) Greene var. *ARIZONICA* (Greene) K. L. Parker.

Tetranneuris arizonica Greene, *Pittonia* 3: 266. 1898. TYPE: UNITED STATES. Arizona. Mohave Co.: "Treadwell, Arizona" (protologue), "Trumbull, Arizona" (lectotype label), 1877, *E. Palmer 259* (LECTOTYPE here designated: NY!; ISOLECTOTYPES: GH!, MO-208039!, MO-208040!, US-63695!). The name "Treadwell," which is given by Greene (1898) as the locality for the *Palmer 259* collection in the original description, does not appear on any of the type material labels that we have examined. The labels on the lectotype (NY) and the GH isoelectotype say "Trumbull, Arizona", the label on the US isoelectotype says "Northern Arizona", and the labels on the MO isoelectotypes have no locality information at all. The U.S. Department of the Interior National Atlas of the United States (web site at <http://nationalatlas.gov>) lists only Mount Trumbull in Mohave County as a site with that name in Arizona. The atlas does not list Treadwell. Type material was not located at NDG, hence the selection of a NY specimen, also referred to by Cronquist (1994).

Actinea acaulis (Pursh) Spreng. var. *lanata* (Nutt.) J. F. Macbride forma *arizonica* (Greene) J. F. Macbride, *Contr. Gray Herb.* 56: 42. 1918.

Actinea arizonica (Greene) A. Nelson, *Univ. Wyoming Publ. Sci., Bot.* 1: 60. 1924.

Actinea acaulis (Pursh) Spreng. [subsp.] *arizonica* (Greene) S. F. Blake, *Contr. U.S. Natl. Herb.* 25: 596. 1925.

Actinea acaulis (Pursh) Spreng. var. *arizo-*

- nica* (Greene) S. F. Blake ex Munz, Man. S. Calif. 570, 601. 1935, nom. superfl.
- Hymenoxys acaulis* (Pursh) K. L. Parker var. *arizonica* (Greene) K. L. Parker, Madroño 10: 159. 1950.
- Tetrandeum acaulis* (Pursh) Greene var. *arizonica* (Greene) K. L. Parker, Phytologia 45: 467. 1980.
- Hymenoxys acaulis* (Pursh) K. L. Parker var. *nana* S. L. Welsh, Rhodora 95: 398. 1993. TYPE: UNITED STATES. Utah. Emory Co.: "ca. 3 mi. E of the Muddy River, San Rafael Reef" (protologue), 6 May 1982, *Atwood & Goodrich* 8652 (HOLOTYPE: BRY, illustrated in Rhodora 95: 394!; ISOTYPE: NY—as database image!).
- Tetrandeum acaulis* (Pursh) Greene var. *nana* (S. L. Welsh) Kartesz & Gandhi, Phytologia 78: 2. 1995.

AERIAL STEMS 1–20(–35). LEAVES: blades spatulate to oblanceolate to linear-oblanceolate, sparsely to, usually, moderately or, sometimes, densely pubescent, not strigoso-canescens or sericeous, densely dotted with impressed glands. HEADS 1–20(–35) per plant, radiate. PEDUNCLES green throughout to, usually, purple-red-tinted throughout, (1–)5–15(–30) cm, sparsely to densely pubescent, sometimes lanate below involucre, eglandular or sparsely to moderately dotted with sessile glands. INVOLUCRES 7–12 × 12–16 mm. PHYLLARIES: outer phyllaries 7–10, 3.9–6.5 × 1.3–3.8 mm, margins often slightly scarious, abaxial faces sparsely to, usually, moderately to, sometimes, densely pubescent, sparsely to moderately dotted with sessile and/or impressed glands; mid phyllaries often purple-red-tinted on apices and margins, sometimes purple-red-tinted throughout, obovate to ovate to lanceolate, 4–6.2 × 1.4–3 mm, margins usually scarious, abaxial faces sparsely to moderately pubescent, sparsely dotted with sessile glands; inner phyllaries 3.7–5.8 × 1.1–1.6 mm, abaxial faces sparsely to moderately pubescent, eglandular or sparsely dotted with sessile

glands. RAY FLORETS 9–15; corollas 11–17 × 3.8–7.4 mm, abaxial faces glabrous or sparsely to moderately pubescent, sparsely to moderately dotted with sessile glands. DISC FLORETS 50–150+; corollas 2.7–4.3 × 1–1.3 mm, eglandular or sparsely dotted with sessile glands. CYPSELAE 3–3.7 × 1–1.2 mm, eglandular or sparsely dotted with sessile glands; pappi 5–7, oblanceolate-aristate scales, 2–3.5 × 0.8–1.2 mm.

CHROMOSOME NUMBERS: $2n = 28, 30, 56, 60$.

DISTRIBUTION (Fig. 2) AND HABITAT: Northern Arizona and southeastern California into eastern Nevada, Utah, southern Idaho, and western Colorado. Growing at roadsides and in grasslands, pine forests, and aspen meadows, 1280–2930 m.

FLOWERING AND FRUITING: April through September, mainly May through July.

REPRESENTATIVE SPECIMENS: UNITED STATES. Arizona. Coconino Co.: S rim Grand Canyon ca 2 mi W of town, 15 May 1963, *Barr* 63-193 (ARIZ, UT); Hwy 64, 24.6 mi W of Hwy 89, in Kaibab Nat'l Forest, 29 May 1975, *Bierner* 51263 (TEX); Hwy alt 89, 6.7 mi S of Hwy 67 (jct in Jacob Lake), 22 Jun 1992, *Bierner* 92-35 (TEX); Open area in pine woods S of Walnut Canyon Nat'l Monument, 2165 m, 25 May 1961, *Demaree* 44274 (ARIZ, ASU); Vicinity of Flagstaff, 2135 m, 2 Jun 1898, *MacDougal* 26 (ARIZ, RM); 12 mi N of Sedona, 1525 m, 6 May 1961, *Nickerson & Edwards* s.n. (ARIZ); 9 mi E of Jacob Lake, 2075 m, $2n = 60$, 15 Aug 1946, *Parker et al.* 6195 (COLO, RM); 20 mi SE of Fredonia on alt 89, 1910 m, $n = 30 \pm$, 17 Jun 1965, *Strother* 370 (TEX-2); SW of Winslow along Jacks Canyon below Chavez Draw ca 3.25 km NNE of the summit of Quayle Hill, 1880 m, $n = 14$, 11 Aug 1997, *Windham et al.* 97-207 (UT); N slope of the Kaibab Plateau on rim of Le Fevre Canyon along Hwy 89A ca 2.8 mi S of Le Fevre Overlook, 2245 m, $n = 14$, 5 May 2000, *Windham* 2030 (UT). La Paz Co.: Parker, 2165 m, *McCleary* s.n.

(ASU). Maricopa Co.: Ca 42 mi NNE of Mesa, 23 Apr 1960, *Crosswhite* 759 (ASU). Mohave Co.: Peach Springs, 1465 m, 20 Sep 1935, *Kearney & Peebles* 12752 (ARIZ); S end of Twin Point near Grand Canyon rim, Shivwits Plateau, 1830 m, 24 May 1981, *Phillips et al.* 80-94 (ARIZ); Tuweep Valley, along rd 42 mi S of Hwy 389 turnoff, 51 airline mi SW of Kanab, UT, 1650 m, 27 May 1969, *Holmgren* 3379 (COLO, UTC); Hackberry, 26 May 1884, *Jones s.n.* (UTC). Yavapai Co.: 5 mi S of Prescott, 1615 m, 7 Jun 1945, *Bostick* 23 (ARIZ, TEX); At Red Rock below Sedona, on border between Yavapai and Coconino Co, 1280 m, 20 May 1965, *Coffee* 28 (UNM). **California.** San Bernardino Co.: Mojave Desert, New York Mts, mouth of Keystone Canyon, 1525 m, 10 May 1974, *Tilforth* 44457 (RM); Near summit of Clark Mt, 2075 m, 4 Jun 1949, *Weatherby* 603 (UT). **Colorado.** Eagle Co.: Park Range, vicinity of McCoy, 2165 m, 13 Jun 1989, *Kastning & Culp* 1637 (RM); Flat Tops/White River Plateau: ridge between E and W forks of Sheep Creek, ca 17 air mi NW of Eagle, 2440–2680 m, 4 Jun 1990, *Vanderhorst* 154 (RM). Garfield Co.: Flat Tops/White River Plateau, Heart Lake Rd, ca 15 air mi W of Eagle, 2380–2410 m, 27 May 1990, *Hartman* 24881 (COLO, RM). Grand Co.: Kremmling, 23 Jun 1907, *Osterhout* 3496 (RM). Gunnison Co.: 6 mi E of Gunnison, 2590 m, 22 May 1938, *Rollins* 2100 (UTC); Sagebrush knoll above Soap Creek, 4 mi N of Sapinero, 2290 m, 29 May 1952, *Weber* 7449 (COLO). Mesa Co.: Grand Junction, 31 May 1921, *Osterhout* 6117 (RM); Due W of Gateway, Gateway Canyon, 2 Jun 1986, *Franklin* 3354 (RM). Montrose Co.: Cimarron, 2135 m, 18 May 1898, *Crandall* 3253 (RM). **Idaho.** Cassia Co.: Mt. Harrison, 14 Jul 1941, *Davis* 1337 (LL). **Nevada.** Clark Co.: S of Deer Creek, Charleston (Spring) Mts, 2670 m, 18 Jun 1937, *Clokey* 7754 (COLO, MONTU, NEB, OKLA, RM, TEX, UT, UTC); N of Las Vegas near Mormon Pass in the Sheep Range ca 3.94 km SW of Wamp Spring, 2045 m, 28 May 1998, *Windham* 98-245 (UT). Elko

Co.: Pequop Mts, ca 2 air mi due S of Pequop Summit, near relay tower, 2440 m, 10 Jun 1985, *Tiehm & Williams* 9612 (UTC); Cherry Creek Mts, High Peak, 10 airline mi WSW of Currie, 2930 m, 15 Jun 1979, *Holmgren & Holmgren* 9301 (RM). Lincoln Co.: ESE of Atlanta on knoll near base of Limestone Hills ca 4.15 km ENE of Bradshaw Spring, 2075 m, $n = 14$, 29 May 1998, *Windham* 98-267 (UT). Nye Co.: Ridge N of Cherry Creek Pass, Quinn Canyon Range, 20 Jun 1945, *Maguire & Holmgren* 25536 (COLO, UT, UTC). White Pine Co.: Mt. Wheeler, 2745 m, 20 Jun 1928, *Cottam* 3315 (UT); Connor's Pass, 5 mi NW of Connor's Station, 2135 m, 21 Jun 1946, *McMillan et al.* 98940 (UT); Egan Range, 0.5 mi W of Hwy 50 on rd to Ruth, 2060 m, 10 Jul 1982, *Tiehm & Tucker* 7337 (UT). **Utah.** Beaver Co.: N of Hwy 21 in the Wah Wah Mts ca 4.86 km ENE of the summit of Lime Point, 1990 m, $n = 14$, 4 May 1992, *Windham & Windham* 92-55 (UT); W side of The Needles near McCune Pass ca 2.49 km ESE of Cottonwood Spring, 2050 m, $n = 14$, 6 May 1966, *Windham* 96-077 (UT); Needle Range, 1 mi NW of Forked Spring, 2470 m, 1 Jun 1964, *Holmgren* 316 (KSC, RM); 7 mi W of Beaver, E slope of Mineral Mts, 1720 m, 23 May 1987, *Franklin* 4782 (MONTU). Box Elder Co.: Raft River Mts, N slope of George Creek Canyon, 5.5 air mi SE of Yost, 2740 m, 15 Jul 1984, *Holmgren & Holmgren* 10640 (COLO, UTC). Carbon Co.: Hwy 53 NE of Wellington ca 3.13 km ESE of the confluence of Coal Creek and Alkali Creek, 1860 m, $n = 14$, 21 May 1993, *Windham* 93-78 (COLO, UT). Daggett Co.: N slope of Uinta Mts, Jul 1959, *Richens* 40 (UTC). Duchesne Co.: Hwy 40, 2 mi W of Duchesne, 19 Jul 1938, *Garrett* 7805 (UT). Emery Co.: Oil Well Flat N of I-70 in the San Rafael Swell ca 3.73 km SE of Mexican Seep, 1830 m, $n = 14$, 15 May 1998, *Windham* 98-198 (UT); Isolated hill NW of Rattlesnake Bench in the San Rafael Swell ca 1.99 km E of The Sinkhole, 1990 m, $n = 14$, 15 May 1998, *Windham* 98-196 (UT); Along N rim of Cat Canyon in the San Ra-

fael Swell ca 6.7 km WNW of Sulphur Spring, 2030 m, $n = 14$, 15 May 1998, *Windham* 98-192 (UT); Near Lone Tree Crossing rd in the San Rafael Swell ca 2.73 km NNW of the summit of Deadman Peak, 1700 m, $n = 28$, 15 May 1998, *Windham* 98-190 (UT); NW rim of Segers Hole in the San Rafael Swell ca 6.6 km SE of East Cedar Mountain Spring, 2075 m, $n = 28$, 15 May 1998, *Windham* 98-184 (UT); On hill E of Cedar Mt in the San Rafael Swell ca 4.56 km SSE of the summit of Pissant Knoll, 1860 m, $n = 14$, 14 May 1998, *Windham* 98-178 (UT); Along small tributary of Road Draw at SE base of Calf Mesa ca 4.15 km WSW of the summit of Window Blind Peak, 1660 m, $n = 14$, 17 Apr 1992, *Windham & Ungerman* 92-8 (COLO, UT); 5.4 mi NW of I-70 on dirt rd to Moore, $2n = 15$ II, 21 May 1988, *Bierner* 88-59 (TEX); Buzzard Bench, SW of Castle Dale, 5 Jun 1975, *Allen* 585 (UT). Garfield Co.: N of Kodachrome Basin along small tributary of Henrieville Creek ca 1.5 km SW of its confluence with Little Creek, 1875 m, $n = 28$, 3 May 1992, *Windham & Windham* 92-35 (UT); SSE of Cannonville on ridge overlooking the Paria River ca 0.92 km NW of its confluence with Wildcat Wash, 1815 m, $n = 28$, 13 May 1998, *Windham & O'Kane* 98-161 (UT); Along Bull Creek, a little SW of Bull Mt; Henry Mts, 20 mi S of Hanksville, 2440 m, 17 Jun 1961, *Cronquist & Holmgren* 9298 (TEX, UTC); Dixie Nat'l Forest, Escalante Mts, along FS rd 132 ca 1.3 km E of Pine Lake, 2560 m, 7 Jul 1988, *Bayer et al.* UT-815 (RM). Grand Co.: 20 mi up the river from Moab, 30 Apr 1940, *Meek* M-10 (UTC); SSE of Crescent Junction near base of ridge NE of Hwy 191 ca 8.24 km NNW of Burrow Seep, 1455 m, $n = 14$, 10 May 1997, *Windham et al.* 97-085 (UT). Iron Co.: Rd between Panguitch Lake and Duck Creek, 9 Jul 1941, *Plummer* 138a (UT). Juab Co.: Drum Mts, ca 2 mi SW of Schoenburger Spring, 1760 m, 4 Jun 1997, *Shultz & Aitken* 17247 (UTC). Kane Co.: 8 mi N of Mt. Carmel Jct on Hwy 89, ca 1770 m, $2n = 30$ II, 18 Jun 1965, *Strother* 372 (TEX); N

side of Hwy 14 near edge of Harris Flat on the Markagunt Plateau ca 3.78 km NE of Harris Spring, 2365 m, $n = 28$, 4 Jun 1996, *Windham* 96-168 (UT); 15 mi S of Orderville, Hwy 89, 18 Jun 1951, *Preece & Turner* 2489 (COLO); 4 mi S of Cannonville, 1555 m, 28 May 1965, *Cronquist* 10216 (UTC). Millard Co.: E side of Warm Cove Ridge at W edge of Pine Valley ca 3.55 km ENE of the highest point in the Halfway Hills, 1700 m, $n = 14$, 7 May 1996, *Windham* 96-081 (UT); Crest of Confusion Range near Hwy 6/50 ca 5.98 km SSE of Conger Reservoir, 1950 m, $n = 14$, 7 May 1996, *Windham* 96-091 (UT); Desert Range Experiment Station, on rd through Halfway Hills, 1905 m, 23 Jun 1963, *Holmgren* 257 (KSC, RM); Along state route at mile post 40 between Scipio and Salina, 27 Jun 1985, *Nelson & Nelson* 7894 (RM). San Juan Co.: 12 mi SE of Moab, 1710 m, 23 Apr 1986, *Franklin* 2803 (RM). Sevier Co.: SE slope of the Valley Mts ca 3.59 km NW of the jct of Hwys 63 and 256, 1740 m, $n = 28$, 2 May 1992, *Windham & Windham* 92-10 (UT); Ridge S of I-70 in Gooseberry Valley ca 4.52 km SW of the confluence of Salina Creek and Cottonwood Creek, 1930 m, $n = 28$, 2 May 1996, *Windham* 96-026 (UT). Tooele Co.: Sheeprock Mts, on S side of Red Pine Mt, 14 Jun 1995, *Bates* 362 (UT, UTC). Uintah Co.: 5 mi N of Whiterocks, 1980 m, Summer 1943, *Murphey* 13 (UTC); Dinosaur Nat'l Monument, above Morris Ranch, W of Hog Canyon on S side of Split Mt, 1725 m, 29 Jun 1989, *Naumann* 353 (COLO). Utah Co.: Colton, 19 Aug 1929, *collector ? s.n.* (UT). Washington Co.: Near Zion Nat'l Park tunnel, 1525 m, 3 Jun 1930, *Cottam s.n.* (UT). Wayne Co.: S of Hwy 24 on ridge above Fremont River near rd to Notom ca 7.53 km NW of the summit of Golden Throne, 1590 m, $n = 28$, 8 May 1997, *Windham et al.* 97-063 (UT); N slope of Henry Mts along rd to Lonesome Beaver Campground ca 3.04 km NNW of the summit of Bull Mt, 1905 m, $n = 14$, $2n = 28$, 22 May 2001, *Windham et al.* 2424 (UT); Hwy 24, 40.4 mi W of Hwy 95, in Capitol

Reef Nat'l Monument, 9 Jun 1975, *Bierner* 51274 (TEX).

1c. *TETRANEURIS* ACAULIS (Pursh) Greene var. *CAESPITOSA* A. Nelson.

Tetraneuris acaulis (Pursh) Greene var. *caespitosa* A. Nelson, Bot. Gaz. 28: 127. 1899. TYPE: UNITED STATES. Wyoming. Albany Co.: "Laramie Hills" (protologue and lectotype label), 30 May 1898, A. Nelson 4314 (LECTOTYPE here designated: RM-15391!; ISOLECTOTYPES: BM!, GH!, MO-208030!).

Actinella acaulis (Pursh) Nutt. var. *caespitosa* (A. Nelson) A. Nelson, New Man. Centr. Rocky Mts. 558. 1909.

Actinea acaulis (Pursh) Spreng. var. *lanata* (Nutt.) J. F. Macbride forma *caespitosa* (A. Nelson) J. F. Macbride, Contr. Gray Herb. 56: 42. 1918.

Hymenoxys acaulis var. *caespitosa* (A. Nelson) K. L. Parker, Madroño 10: 159. 1950.

Actinella lanata Nutt., Trans. Amer. Philos. Soc. 7: 379. 1841. (Not *Actinella lanata* Pursh, Fl. Amer. Sept. 2: 560. 1814 = *Eriophyllum lanatum* [Pursh] J. Forbes). TYPE: UNITED STATES. Wyoming. Natrona Co.: "On the lofty hills or mountains, called the 'Three Butes [sic]' of the upper Platte" (by implication from the protologue, which says, "Hab. With the above," in reference to that given for *Actinella torreyana*), "Platte" (holotype label), "Red Butes" with the "Red" struck through and a "3" written above (BM possible isotype label), T. Nuttall s.n. (HOLOTYPE: PH!; possible ISOTYPES: BM!, NY!). The type locality of this taxon is believed to be Red Buttes, ca 2 mi S of the Oregon Trail SW of Casper, Wyoming. This locality is discussed more completely under *Tetraneuris torreyana*.

Tetraneuris lanata (Nutt.) Greene, Pittonia 3: 265. 1898.

Tetraneuris lanigera Daniels, Univ. Missouri

Stud., Sci. Ser. 2(2): 245. 1911. Nom. nov. based on *Actinella lanata* Nutt.

Actinea acaulis (Pursh) Spreng. var. *lanata* (Nutt.) J. F. Macbride, Contr. Gray Herb. 56: 42. 1918.

Actinea acaulis (Pursh) Spreng. [subsp.] *lanigera* (Daniels) S. F. Blake, Contr. U.S. Natl. Herb. 25: 596. 1925.

Tetraneuris brevifolia Greene, Pittonia 3: 266. 1898. TYPE: UNITED STATES. Colorado. El Paso Co.: "Summit of a bleak ridge above timber line, on Pike's Peak; collected only by Mr. Canby" (protologue), "Alpine ridges, Pike's Peak" (lectotype label), Aug 1871, Canby s.n. (LECTOTYPE here designated: NY-00622293, plant at bottom left of the sheet—as database image!). Original material was not located at NDG.

AERIAL STEMS 1–35(–60). LEAVES: blades spatulate to oblanceolate to linear-oblanceolate, sparsely to densely pubescent, often lanuginose, sometimes sericeous, sparsely to, sometimes, moderately or densely dotted with impressed glands. HEADS 1–35(–60) per plant, radiate. PEDUNCLES green throughout to purple-red-tinted throughout, 0.5–8(–12) cm, sparsely to, usually, densely pubescent, usually lanate below involucre, eglandular or sparsely dotted with sessile glands. INVOLUCRES 7–11 × 8–15 mm. PHYLLARIES: outer phyllaries 6–12, 6.8–9(–11.5) × 1–2(–2.5) mm, margins sometimes slightly scarious, abaxial faces moderately to, usually, densely pubescent, eglandular or, sometimes, sparsely dotted with sessile and/or impressed glands; mid phyllaries often purple-red-tinted on apices and margins, rarely purple-red-tinted throughout, obovate to ovate to lanceolate, 5.7–7.2(–8.5) × 0.8–1.8 mm, margins often scarious, abaxial faces moderately to, usually, densely pubescent, eglandular or sparsely dotted with sessile glands; inner phyllaries 4–6(–7) × 1–2.1 mm, abaxial faces moderately to densely pubescent, eglandular. RAY FLORETS 9–15(–21); corol-

las 9–13 × 3–7 mm, abaxial faces glabrous or sparsely to moderately pubescent, eglandular or sparsely to moderately dotted with sessile glands. DISC FLORETS 25–200+; corollas 3–4 × 0.8–1 mm, eglandular. CYPSSELAE 2–3(–4) × 0.8–1 mm, eglandular; pappi 5–8, obovate- to oblanceolate-aristate scales, 2.5–3.5 × 0.5–1.2 mm.

CHROMOSOME NUMBERS: $2n = 28, 30$.

DISTRIBUTION (Fig. 2) AND HABITAT: Northwestern New Mexico, central Colorado, and southcentral Wyoming. Edges of montane forests, alpine meadows above timberline, and open savannas. (2100–) 3000–3850 m.

FLOWERING AND FRUITING: May through September, mainly June through August.

REPRESENTATIVE SPECIMENS: **UNITED STATES.** **Colorado.** Alamosa Co.: Sangre de Cristo Range, N ridge of California Peak, 3660 m, 20 August 1998, *Hogan 3530* (COLO). Boulder Co.: Ca 8 mi N of Nederland, 3660 m, $n = 15$, 16 Jun 1961, *Wiens 2866* (COLO); On Rollins Pass, 0.3 mi N of Needle Eye Tunnel, 3475 m, $2n = 28$, 3 Aug 1965, *Johnson 902* (COLO); Niwot Ridge, 15 mi W of Boulder, 3460 m, $2n = 28$, 28 Jul 1965, *Johnson 802* (COLO). Chaffee Co.: Monarch Pass, Observatory Hill at microwave tower, ca 3570 m, 24 Jun 1962, *Gillett & Taylor 11468* (COLO). Clear Creek Co.: Ridge W of Berthoud Pass, 3660–3810 m, 17 Jul 1957, *Beaman & Erbach 1359* (COLO). Costilla Co.: SW end of Lost Lake, 6 mi ENE of Stonewall Gap, 3565 m, 5 Aug 1986, *Neely 3763* (CS). Custer Co.: Sangre de Cristo Range, North Colony Lakes basin, ca 3505 m, 30 Jul 1995, *Hogan 2789* (COLO, UNM). El Paso Co.: Above timberline, Pike's Peak, 3660 m, 11 Aug 1935, *Ownbey 937* (RM). Gilpin Co.: Rollins Pass area ca 15 mi SW of Rollinsville, 3660 m, 2 Sep 1967, *Taylor & Taylor 4728* (OKL). Grand Co.: Berthoud Pass, 3355–3660 m, Jul 1903, *Tweedy 5849* (RM). Gunnison Co.: Monarch Pass, 3470 m, 27 Aug 1935, *Maguire et al. 12718* (UTC). Huerfa-

no Co.: Cuchara Pass, 3050 m, 13 Jun 1934, *Stigall s.n.* (COLO). Lake Co.: Vic. Weston Pass, 3690 m, 1 Jul 1964, *Gierisch 2955* (COLO, CS, RM). Larimer Co.: Knoll above Iceberg Lake, Rocky Mts Nat'l Park, 3535 m, 26 Jun 1960, *Welsh & Charette 1346b* (COLO). Park Co.: Tundra ridge just W of Hoosier Pass toward North Star Mt, 3810 m, 7 Jul 1951, *Weber et al. 6505* (COLO). Saguache Co.: Sangre de Cristo Range, N Fork of Crestone Creek, ca 3660 m, 13 Jul 1991, *Hogan 1318* (COLO, UNM). Summit Co.: W side of Hoosier Pass, 3600 m, 17 Aug 1995, *Redner s.n.* (COLO). Teller Co.: Cripple Creek, 3350 m, 3 Jul 1920, *Clokey 3953* (RM). **New Mexico.** Colfax Co.: Philmont Scout Ranch, near Cimarron, trail 1 mi NE of Comanche Peak, 3290 m, 27 Jul 1968, *Hartman 2160* (RM). San Miguel Co.: Santa Fe Nat'l Forest, Elk Mt, near summit, ca 14 mi NNE of Pecos, 3535 m, 19 Aug 1991, *Dunmire 1183* (UNM). Santa Fe Co.: SW flank of Lake Peak, 3780 m, 13 Jul 1964, *Martin & Smith 287* (UNM). Taos Co.: Wheeler Peak, 3855 m, 15 Jun 1967, *Mackay 4T-55* (UNM). Union Co.: Sierra Grande, 2590 m, 2 Jul 1976, *Hubbard s.n.* (UNM). **Wyoming.** Albany Co.: Medicine Bow Nat'l Forest, 2515 m, 1 Jun 1972, *Asplund 72-1* (RM); 5.6 mi SW of Centennial on top of Centennial Ridge, 2960 m, 12 Jun 1973, *Nelson 480* (RM). Carbon Co.: Sierra Madre, ca 14 air mi NNW of Bridger Peak, 2410 m, 14 Jun 1988, *Hartman & Kastning 23644* (RM); NW exposure of Elk Mt, 2305 m, 1 Jul 1965, *Gartner 41* (RM); Rawlins Uplift, W hillside above BLM District Office, just N of Rawlins, 2135 m, 2 Jun 1983, *Warren 582* (RM); Shirley Basin, NE rim of Chalk Mt ca 3.5 mi W of Hwy 77 and 1.25 mi SE of Horse Peak, 2290 m, 30 May 1999, *Fertig & Welp 18639* (RM). Converse Co.: T27N R72W Sec 19 NE1/4, 2195 m, 24 May 1986, *Dorn 4332* (RM).

1d. TETRANEURIS ACAULIS (Pursh) Greene var. EPUNCTATA (A. Nelson) Kartesz & Gandhi.

Tetraneuris epunctata A. Nelson, Bot. Gaz. 37: 275. 1904. TYPE: UNITED STATES. Utah. Uintah Co.: "Stony subalpine slopes. Dyer Mine, Uintah Mts." (holotype label), 3 Jul 1902, *L. N. Goodding* 1236 (HOLOTYPE: RM-42063!; ISOTYPES: BRY-192692!, COLO!, GH!, MO-208048!, NY!, UC-51306!, US-485655!).

Actinella epunctata (A. Nelson) A. Nelson, New Man. Centr. Rocky Mts. 560. 1909.

Actinea epunctata (A. Nelson) A. Nelson, Univ. Wyoming Publ. Sci., Bot. 1: 60. 1924.

Hymenoxys acaulis (Pursh) K. L. Parker var. *epunctata* (A. Nelson) Cronquist in A. Cronquist et al., Intermount. Fl. 5: 79. 1994.

Tetraneuris acaulis (Pursh) Greene var. *epunctata* (A. Nelson) Kartesz & Gandhi, Phytologia 78: 2. 1995.

Tetraneuris crandallii Rydb., Bull. Torrey Bot. Club 32: 127. 1905. TYPE: UNITED STATES. Colorado. Mesa Co.: "Grand Junction" (protologue and holotype label), 28 May 1894, *C. S. Crandall s.n.* (HOLOTYPE: NY!).

AERIAL STEMS 1–10(–15). LEAVES: blades oblanceolate to linear-oblanceolate, glabrous or sparsely to moderately pubescent, not strigoso-canescens or sericeous, eglandular or sparsely dotted with impressed glands. HEADS 1–10(–15) per plant, radiate. PEDUNCLES green throughout to, usually, purple-red-tinted throughout, (1–) 5–15(–25) cm, sparsely to densely pubescent, often lanate below involucre, eglandular or sparsely to moderately dotted with sessile glands. INVOLUCRES 8–12 × 10–15 mm. PHYLLARIES: outer phyllaries 6–12, 5–7.5 × 1–2.2 mm, margins sometimes slightly scarious, abaxial faces sparsely to densely pubescent, usually eglandular, sometimes sparsely dotted with sessile and/or impressed glands; mid phyllaries often purple-red-tinted on apices and margins, obovate to ovate to lanceolate, 5.5–6.7 × 1.2–2.5 mm, margins often scarious, abaxial faces

sparsely to moderately pubescent, usually eglandular, sometimes sparsely dotted with sessile glands; inner phyllaries 4.8–6 × 1–2.5 mm, abaxial faces sparsely to moderately pubescent, usually eglandular, sometimes sparsely dotted with sessile glands. RAY FLORETS 10–14; corollas 11–19 × 5–8 mm, abaxial faces glabrous or sparsely pubescent, eglandular or sparsely dotted with sessile glands. DISC FLORETS 50–150+; corollas 3.5–4 × 1–1.3 mm, eglandular or sparsely dotted with sessile glands. CYPSELAE 3–4 × 0.9–1 mm, eglandular; pappi 5–6, obovate to oblanceolate-aristate scales, 2.8–3.7 × 0.7–1.2 mm.

CHROMOSOME NUMBERS: $2n = 28, 30, 56$.

DISTRIBUTION (Fig. 2) AND HABITAT: Southcentral Utah to northeastern Utah, western Colorado, and southwestern Wyoming. Growing at roadsides, on hillsides, and at edges of woods, 1600–2700(–3475) m.

FLOWERING AND FRUITING: May through September, mainly May through July.

REPRESENTATIVE SPECIMENS: UNITED STATES. Colorado. Dolores Co.: Plateau Creek 7 mi N of its confluence with McPhee Reservoir, 2470 m, 9 Jun 1993, *Komarek* 154 (COLO). Garfield Co.: 2 mi N of Rifle, 10 May 1941, *Porter* 2832 (RM, UTC); Flat Tops/White River Plateau, Main Elk Creek, ca 4 air mi NW of New Castle, 23 May 1990, *Hartman & Vanderhorst* 24496 (RM). Mesa Co.: On top of Grand Mesa, 30 mi E of Grand Junction, 3200 m, 25 Aug 1946, *Parker et al.* 6378 (TEX); 2.2 mi S, 17.2 mi W of DeBeque, 2100 m, 1 Jun 1999, *Morse* 3414 (COLO); 10 mi SW of Gateway, 2290 m, 10 Jun 1949, *Harrington* 4328 (UTC); Ca 25 mi SW of White-water, 2135 m, 25 May 1947, *Harrington* 2794 (CS). Moffat Co.: Near Irish Canyon Rd W of Vermillion Creek ca 1.84 km N of the summit of Blue Hill, 2075 m, $n = 28$, 12 Jun 1993, *Windham & Windham* 93-96 (COLO, UT). Rio Blanco Co.: Drill Hole in upper Taylor Draw, 4 mi E of Rangely, 1814

m, 13 Jun 1979, *Bartman & Erickson* 552 (CS). **Utah.** Cache Co.: Sink basins between Mt. Magog and Mt. Naomi, 2685 m, 19 Jul 1936, *Maguire et al.* 14113 (UTC). Daggett Co.: NE slope of the Uinta Mts at base of Windy Ridge ca 3.32 km NW of Dowd Spring, 2390 m, $n = 28$, 6 Jun 1999, *Windham* 99-158 (UT). Duchesne Co.: Hwy 40, 23.7 mi W of Duchesne, 11 Jun 1967, *Mears* 2055 (TEX); 27 mi S of Myton, on rd to Wellington, 10 Jun 1961, *Cronquist & Holmgren* 9237 (TEX); E flank of Mt Emmons, 3475 m, 7 Aug 1968, *West* 1018 (UTC). Emery Co.: SE of Price along Hwy 6 on pediment of Book Cliffs ca 3.13 km NNE of Coon Spring, 1625 m, 11 May 1997, *Windham et al.* 97-091 (UT); Calf Canyon, San Rafael Swell, 2.2 mi N of bridge over San Rafael River, 1–2 mi into rt fork of canyon, 28 May 1978, *Shultz & Shultz* 2488 (UTC). Garfield Co.: 10 mi N of Escalante, 2110 m, 4 Jun 1972, *Arnow* 3339 (UT); Bryce Canyon Nat'l Park, 0.25 mi NW of Museum, on hill below Inn, 2425 m, 19 Jul 1957, *Buchanan* 209 (UT). Grand Co.: La Sal Mts, W ridge of Gold Mt, 2775 m, 12 Jul 1933, *Maguire et al.* 5640 (UTC); Ca 25 mi due NE of Moab, Sevenmile Mesa, 1650 m, 17 May 1986, *Franklin* 3069 (RM). Sanpete Co.: S rim of Block Mt on the Wasatch Plateau ca 5.81 km SW of the summit of Heliotrope Mt, 3280 m, $n = 28$, 9 Jul 2000, *Windham* 2223 (UT). Sevier Co.: White Mt, Southern Wasatch Range, ca 14 mi NW of Emery, 3424 m, 6 Aug 1983, *Tuhy* 1033 (UTC). Summit Co.: Uinta Mts, 9 mi SE of Lonetree [WY], N of Hale, near Rock Ranger Station, 2440 m, 28 Jun 1947, *Parker & McClintock* 6980 (TEX). Uintah Co.: 2.9 mi SW of Santio Crossing at Willow Creek, on rd to Little Pack Mt, ca 25 air mi S of Ouray, 1815 m, 28 May 1979, *Shultz* 3274 (UTC); Ca 3 km E of Evacuation Creek and 2 km N of Park Canyon, ca 20 km airline SE of Bonanza, 1800 m, 27 May 1976, *Cronquist* 11459 (UTC); Diamond Mt Plateau, 7.2 mi E of Hwy 44, the jct of which is 23.8 mi N of Vernal, 2440 m, 8 Jun 1971, *Holmgren & Holmgren* 5088

(UTC); Hwy 191, 6.2 mi S of the Uintah-Daggett county line, 23 Jun 1992, *Bierner* 92-41 (TEX); East Tavaputs Plateau, rd to Hill Creek Ranger Station, 13–15 Jul 1956, *Vickery & Wiens* 1611 (UT); Utah Co.: Colton, 18 mi NW of Helper, 1780 m, 23 Aug 1946, *Parker et al.* 6358 (TEX). Wayne Co.: WSW of Teasdale near the base of Boulder Mt ca 1.01 km ESE of the highest point of Black Ridge, 2235 m, $n = 14$, 21 Jul 1993, *Windham* 93-143 (COLO, UT). **Wyoming.** Fremont Co.: Wind River Range, Brown Canyon area, ca 10 mi S of Lander, on N slopes, 24 Jul 1961, *Fisser* 631 (RM). Sweetwater Co.: NE end of Little Mt, ca 33.5 air mi S of Rock Springs, 2710 m, 21 Jul 1079, *Aldrich* 561 (RM); Cedar Mt, ca 5 air mi NW of McKinnon, 2510–2590 m, 22 Jun 1994, *Rafsdal* 976 (RM). Sublette Co.: Upper Green River Basin, Cretaceous Mt/Hogsback Ridge area, Big Mesa, S end, ca 7 air mi NW of La Barge, 2440 m, 26 May 1993, *Hartman* 38005 (RM). Uinta Co.: Ca 7.5 mi W of Hwy 414 on Hwy 291, ca 6 air mi SW of Lonetree, 2580–2610 m, 3 Jul 1994, *Rafsdal* 1412 (RM); Ft. Bridger, 9 Jun 1898, *Nelson* 4607 (RM). Ca 5 mi E of Lonetree, $n = 15$, 16 May 1973, *Watson* 889 (MONTU).

2. TETRANEURIS ARGENTEA (A. Gray) Greene.

- Actinella argentea* A. Gray, Mem. Amer. Acad. Arts (Series 2) 4: 100. 1849. TYPE: UNITED STATES. New Mexico. Santa Fe Co.: "Gravelly and stony hills, around Santa Fé; April to June" (protologue), 1847, *A. Fendler* 457 (HOLOTYPE: GH!; ISOTYPES: BM!, GH-two sheets!, K!, MO-208033!, NY!, PH-two sheets!, UC-711297!, US-637111!, US-1084850!, photographs of three additional sheets at K!).
Actinea argentea (A. Gray) Kuntze, Revis. Gen. Pl. 1: 303. 1891.
Ptilepida argentea (A. Gray) A. Heller, Plant World 1: 22. 1897.
Tetraneuris argentea (A. Gray) Greene, Pittonia 3: 269. 1898.

Hymenoxys argentea (A. Gray) K. L. Parker, Madroño 10: 159. 1950.

Actinella leptoclada A. Gray in War Department [U.S.], Pacif. Railr. Rep. 4(5): 107. 1857. TYPE: UNITED STATES. New Mexico. Bernalillo Co.: "In mountains and rocky places near Santa Antonita [San Antonito], New Mexico" (protologue), "Camp B. San Antonita . . . mountains & rocky places" (NY isotype labels), "Santa Antonita N. Mexico" (US isotype label), 9 Oct 1853, J. M. Bigelow 968 (HOLOTYPE: GH!; ISOTYPES: NY-two sheets!, US-47376!).

Actinea leptoclada (A. Gray) Kuntze, Revis. Gen. Pl. 1: 303. 1891.

Tetraneuris leptoclada (A. Gray) Greene, Pittonia 3: 269. 1898.

Tetraneuris trinervata Greene, Pittonia 3: 267. 1898. TYPE: UNITED STATES. New Mexico. Bernalillo Co.: "Sandia Mountains, New Mexico" (protologue), "Camp B Douglass . . . Crest of Sandia Mts" (holotype label), 10 Oct 1853, J. M. Bigelow 996 (HOLOTYPE: NY!; probable ISOTYPES: GH!, US-47637!).

Actinea scaposa (DC.) Kuntze [var.] *trinervata* (Greene) Kittell, Fl. Ariz. New Mex. 470. 1941.

Tetraneuris formosa Greene ex Wooton & Standl., Contr. U.S. Natl. Herb. 16: 192. 1913. TYPE: UNITED STATES. New Mexico. Sierra Co.: "Kingston, Dry hills" (holotype label), 22 Aug 1904, O. B. Metcalfe 1235 (HOLOTYPE: US-498042!; ISOTYPES: BM!, CAS-10417!, F-187579!, GH!, MO-208051!, NMC-50366!, NY!, RM-90034!, UC-891086!, US-890368!).

Actinea formosa (Greene ex Wooton & Standl.) A. Nelson, Univ. Wyoming Publ. Sci., Bot. 1: 61. 1924.

PERENNIALS. CAUDICES \pm branched, thickened distally. AERIAL STEMS 1–8(–12), erect, leafy, unbranched or sparingly branched distally, green throughout to, oc-

asionally, purple-red-tinted throughout, 5–25(–42) cm, moderately to, usually, densely pubescent, eglandular or sparsely to moderately dotted with sessile glands. LEAVES basal and cauline, entire, moderately to, usually, densely strigoso-canescens, moderately to, sometimes, densely dotted with impressed glands; basal leaves tightly clustered, appearing to arise from the same level at bases of stems, blades spatulate to oblanceolate, bases usually densely woolly or long-pubescent; proximal cauline blades oblanceolate; mid blades oblanceolate to linear-oblanceolate, 2.5–5 mm wide; distal blades linear-lanceolate to linear. HEADS 1–10(–30) per plant, 1–3(–7) per stem, radiate, borne singly or in paniculiform to corymbiform arrays. PEDUNCLES 2–13.5 cm, moderately to, usually, densely pubescent, sparsely to moderately dotted with sessile glands. INVOLUCRES (5–)7–10 \times 8–15 mm. PHYLLARIES: outer phyllaries 8–11, often purple-red-tinted on apices, obovate to ovate to lanceolate, 4–6.5 \times 1.5–3 mm, margins usually scarious, abaxial faces densely pubescent, moderately dotted with sessile and/or impressed glands; mid phyllaries often purple-red-tinted on apices, obovate to oblanceolate, 4.5–6.5 \times 2–2.8 mm, margins scarious, abaxial faces moderately to, usually, densely pubescent, sparsely to moderately dotted with sessile glands; inner phyllaries 4.5–6 \times 1.2–1.8(–2.3) mm, abaxial faces moderately to densely pubescent, sparsely to moderately dotted with sessile glands. RAY FLORETS 8–14; corollas 11.8–17 \times 5–7 mm, abaxial faces glabrous or sparsely to moderately pubescent, sparsely to moderately dotted with sessile glands. DISC FLORETS 25–75(–100+); corollas yellow proximally, yellow to rarely purple-red-tinted distally, 2.8–3.8 \times 0.8–1.4 mm, glabrous or sparsely pubescent, eglandular or sparsely dotted with sessile glands. CYPSELAE 2.4–3.1 \times 1–1.3 mm, surfaces white, moderately to densely pubescent, eglandular or sparsely dotted with sessile glands; pappi 5–6, obovate-aristate scales, 2.1–3.5 \times 1–1.5 mm.

CHROMOSOME NUMBERS: $2n = 30, 60$.

DISTRIBUTION (Fig. 3) AND HABITAT: Northern New Mexico and eastern Arizona. Growing at roadsides, on hillsides, in open treeless areas, and at edges of juniper woodlands and pine forests, (1555–)1950–2365(–2590) m.

FLOWERING AND FRUITING: April through September, mainly May through August.

REPRESENTATIVE SPECIMENS: **UNITED STATES. Arizona.** Apache Co.: 1 mi E of St. Johns on Hwy 666 then 1 mi E to East Side Cemetery then 1 mi ENE to edge of wash then 1 mi N past fence line, top of mesa in sandy soil, 1785 m, 2 Sep 1984, *Mohlenbrock 2431* (ASU). Coconino Co.: Woods Canyon Lake area, 2290–2410 m, 19 May 1963, *Schmidt 65* (ARIZ). Gila Co.: 1 mi S of White River Junction along Hwy 60–70, 1555 m, 23 Apr 1962, *Gardner 145* (ASU); 18 mi SW of Heber near Mogollon Rim rd, 1950 m, 14 June 1947, *Parker & McClintock 6802* (RM). Navajo Co.: Just outside of Heber on the NW side, 1980 m, 18 May 1980, *Fischer & Yatskiyevych 6773* (ARIZ); ridge above Aripine, 12 mi NW of Pinedale, 1920 m, 15 Jun 1947, *Parker & McClintock 6830* (ARIZ, COLO, LL, RM, UT); rim rd 7 mi E of Show Low, 1950 m, 28 Jun 1965, *Sutherland s.n.* (ASU). **New Mexico.** Bernalillo Co.: Sandia Crest rd (Hwy 536), 1 mi W of Hwy 14 (jct in San Antonito), 25 Jun 1992, *Bierner 92-44* (TEX); Ca 3 mi S of San Antonito, 2010 m, $n = 15$, 19 May 1956, *Jackson 2038* (UNM). Catron Co.: Datil Mts, ca 2590 m, 13 Jun 1976, *Fletcher 384* (UNM). Cibola Co.: Zuni Mts, vicinity of Bluewater Creek, 2330 m, 16 Jun 1982, *Fletcher 6174* (UNM). Los Alamos Co.: E of Los Alamos, 2.4 mi W of Hwy 30 on Hwy 502, 23 May 1988, *Bierner 88-62* (TEX). McKinley Co.: 23 mi E of Gallup on Hwy 66, 2135 m, 20 Jun 1965, *Strother 390* (TEX); Ca 5 mi NE of Thoreau, 2225 m, 24 May 1994, *Sivinski & Lightfoot 2691* (UNM). Rio Arriba Co.: 2 mi S of Truchas Village, 1980 m, 28 Aug 1946,

Parker & McClintock 6448 (ARIZ, COLO, LL, OKLA, RM, UT, UTC). San Miguel Co.: Las Vegas, 7 Jul 1927, *Arsene 18658* (LL); 20 mi S of Las Vegas, 29 Aug 1946, *Parker & McClintock 6475* (ARIZ); 5 mi N of Pecos on Hwy 63, 2225 m, $2n = 15II$, 26 Jun 1965, *Strother 415* (TEX). Sandoval Co.: Bandelier Nat'l Monument, 1980 m, 12 May 1939, *Sholly 46* (ARIZ); 15 mi E of Bernalillo on Hwy 44, 1890 m, 22 Jun 1965, *Strother 392* (TEX). Santa Fe Co.: Hwy 41, 9.2 mi S of Hwy 285, 20 May 1972, *Bierner 374* (TEX); hills N of Santa Fe on rd to Hyde Park, 2135 m, $2n = 30$, 29 Aug 1946, *Parker & McClintock 6464* (ARIZ, COLO, LL, OKLA, RM, TEX, UT, UTC). Socorro Co.: 31,000 ft from crater fence NW-facing alluvial slope, atomic bomb test site, 31 Aug 1965, *Hess et al. 581* (RM). Taos Co.: 1 mi up Rio Chiquito Creek on rd 437, Carson Nat'l Forest, 2365 m, 2 Aug 1996, *Atwood 21182* (UNM). Torrance Co.: East View school house, 16 mi NW of Mountainair, 1995 m, 31 Aug 1946, *Parker & McClintock 6521* (ARIZ, COLO, LL, OKLA, RM, UT, UTC). Valencia Co.: Zuni Mts, FS rd 349 near La Jara Spring, 2330 m, 14 Jun 1969, *Riffle 1126* (UNM).

Tetraneuris argentea is similar to *T. ivesiana* in that both have one or more well-defined stem leaves. The former is readily distinguished by its closely appressed silvery vestiture that mostly or nearly obscures the glandular punctations on the leaf surfaces. This is aptly discussed by Cronquist (1994), who opted to treat *T. ivesiana* as a variety of *T. argentea*, noting that in New Mexico the former "largely gives way to var. *argentea*."

Our examination of a wide suite of specimens, including independent fieldwork by both of us, suggests that two species can be easily recognized. In fact, *Tetraneuris argentea* is essentially allopatric with *T. ivesiana*, their distributions overlapping only slightly in northwestern New Mexico (Fig. 3). We have not encountered the two taxa growing together, and we have not seen any

specimens that suggest hybridization between the two.

The ranges of *Tetraneris argentea* and *T. acaulis* var. *acaulis* overlap in northcentral New Mexico (Fig. 2 and 3). Their proximity and the rather striking similarity of their strigoso-canescens leaf pubescence lead us to speculate that they may be sister taxa. This contention appears to be supported by the work of Bierner and Jansen (1998); their phylogenetic tree based on restriction site DNA data places *T. argentea* and *T. acaulis* var. *acaulis* as sister species.

3. TETRANEURIS HERBACEA Greene.

Tetraneris herbacea Greene, Pittonia 3: 268. 1898. TYPE: UNITED STATES. "Central Illinois and Ohio" (protologue), (HOLOTYPE: NDG? not located). Greene cited no specimens of this taxon in his protologue; he noted the taxon occurs in "Central Illinois and Ohio." Perhaps he saw material at US or elsewhere. NEOTYPE here designated: UNITED STATES. Illinois. Will Co.: Near Rockdale, "original prairie, stony soil," 23 May 1951, *Virginius H. Chase 11908* (TEX!; ISONEOTYPE: OKL!).

Actinea herbacea (Greene) B. L. Rob., Rhodora 10: 68. 1908.

Hymenoxys herbacea (Greene) Cusick, Rhodora 93: 238. 1991.

Actinella scaposa (DC.) Nutt. var. *glabra* A. Gray, Man. Bot. N. U. S., ed. 5, 263. 1867. TYPE: UNITED STATES. Illinois. Will Co.: "Joliet, Illinois, on an Indian mound" (protologue), S. W. Boott s.n. (LECTOTYPE [per K. L. Parker annotation] selected here: GH!). Not *Actinella glabra* Nutt. (= *Tetraneris scaposa* var. *scaposa*).

Actinea acaulis (Pursh) Spreng. var. *glabra* (A. Gray) Cronquist, Rhodora 47: 403. 1945.

Hymenoxys acaulis (Pursh) K. L. Parker var. *glabra* (A. Gray) K. L. Parker, Madroño 10: 159. 1950.

PERENNIALS. CAUDICES \pm branched, thickened distally. AERIAL STEMS 1–10, erect, unbranched. LEAVES all basal or, occasionally, 1 leaf located 1–2 cm below the head, new leaves very tightly clustered, appearing to arise from the same level at bases of stems, blades spatulate to oblanceolate to linear-oblanceolate, entire, glabrous or sparsely to, rarely, moderately pubescent, moderately to densely dotted with impressed glands, often with 2 distinct lateral veins in addition to the midrib, bases usually densely woolly or long-pubescent. HEADS 1–10 per plant, radiate, borne singly. PEDUNCLES green throughout to purple-red-tinted throughout, 5–35 cm, sparsely to moderately pubescent proximally, very densely pubescent distally, eglandular or very sparsely dotted with sessile glands. INVOLUCRES 10–15 \times 12–20 mm. PHYLLARIES: outer phyllaries 8–12, often purple-red-tinted on apices and margins, lanceolate to linear-lanceolate, 5–7.5 \times 1.5–2.5 mm, margins sometimes slightly scarious, abaxial faces sparsely to densely pubescent, sparsely to moderately dotted with sessile and/or impressed glands; mid phyllaries often purple-red-tinted on apices and margins, obovate to oblanceolate, 5.5–6.5 \times 1.8–2 mm, margins scarious, abaxial faces sparsely to densely pubescent, sparsely to moderately dotted with sessile glands; inner phyllaries sometimes purple-red-tinted on apices, 4.2–6 \times 1–2.3 mm, abaxial faces sparsely to moderately pubescent, eglandular or sparsely dotted with sessile glands. RAY FLORETS 14–27; corollas 11.8–20 \times 3.8–10.2 mm, abaxial faces glabrous or sparsely to moderately pubescent, sparsely to moderately dotted with sessile glands. DISC FLORETS 50–100+; corollas yellow, 3.4–4 \times 1.1–1.3 mm, glabrous or sparsely to moderately pubescent, eglandular or sparsely dotted with sessile glands. CYPSELAE 2.4–3.4 \times 1–1.2 mm, surfaces white, moderately to densely pubescent, eglandular or sparsely dotted with sessile glands; pappi 4–7, ovate to, rarely, obovate-aristate scales, 1.9–2.2 \times 0.8–1.1 mm.

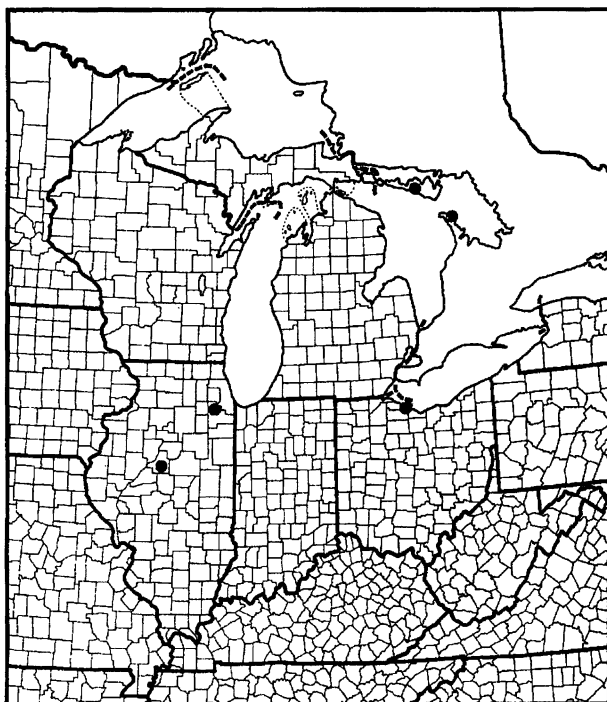


FIG. 4. Distribution of *Tetraneuris herbacea* (Illinois populations now believed extinct; the Tazwell County locality is from Cusick, 1991).

CHROMOSOME NUMBER: $2n = 28$.

DISTRIBUTION (Fig. 4) AND HABITAT: Central and northeastern Illinois (extinct according to Cusick, 1991), northern Ohio, and Canada in Ontario. Growing on limestone flats and in openings in woods, ca 180 m.

FLOWERING AND FRUITING: April through October, mainly May and June.

REPRESENTATIVE SPECIMENS: **CANADA.** **Ontario.** Bruce Co.: Lindsay Township, Cabot Head, Bruce Peninsula, 20 Jun 1994, *Oldham et al.* 16259 (MICH). Manitoulin Co.: Manitoulin Island, near Hensley Bay (W of Misery Pt), ca 9 mi SE of Silver Water, 22 May 1997, *Voss* 16570 (MICH). **UNITED STATES.** **Ohio.** Ottawa Co.: Marblehead Quarry, 0.5–0.8 mi NE of jct of Hartshorn & Quarry Rds, Danbury Twp, 22 May 1980, *Cusick & Brandenburg* 20008 (OS). **Illinois.** Will Co.: Along Hwy 6 near

Rockdale (4 mi S of Joliet), 14 May 1939, *Wadmond* 15539 (MICH).

This rare and threatened or endangered species is discussed in detail by Cusick (1991) and by Moran-Palma and Snow (1997). Its distally thickened caudices and tightly clustered leaves suggest that it is a dysploid derivative ($2n = 28$) that has evolved out of the *Tetraneuris acaulis* complex. Cusick (1991) suggested that the ancestors of *T. herbacea* “probably migrated from the western cordillera into the Great Lakes region during the Xerothermic interval about 8000 years B.P. This period marked the eastward expansion of many drought-tolerant western taxa, a phenomenon known as the prairie peninsula.” The junior author suggests that *T. herbacea* may have arisen from divergent populations of *T. scaposa* var. *scaposa* along the receding glacial front during the last glaciation, now largely

restricted to localized peripheral habitats of lakes Erie and Michigan.

4. *TETRANEURIS IVESIANA* Greene.

Tetranneuris ivesiana Greene, Pittonia 3: 269.

1898. TYPE: UNITED STATES. Arizona. Apache Co.: "Rio Zuñi" (protologue and lectotype label), 26 Sep 1851, Woodhouse s.n. (LECTOTYPE here designated: NY!).

Actinea leptoclada (A. Gray) Kuntze var. *ivesiana* (Greene) J. F. Macbride, Contr. Gray Herb. 56: 44. 1918.

Hymenoxys acaulis (Pursh) K. L. Parker var. *ivesiana* (Greene) K. L. Parker, Madroño 10: 159. 1950.

Hymenoxys ivesiana (Greene) K. L. Parker, Leaflet. W. Bot. 9: 92. 1960.

Hymenoxys argentea (A. Gray) K. L. Parker var. *ivesiana* (Greene) Cronquist in A. Cronquist et al., Intermount. Fl. 5: 79. 1994.

Tetranneuris mancosensis A. Nelson, Bot. Gaz. 28: 129. 1899. TYPE: UNITED STATES. Colorado. Montezuma Co.: "Mancos" (protologue and holotype label), 29 Jun 1898, C. S. Crandall s.n. (HOLOTYPE: RM-13212!).

Tetranneuris intermedia Greene, Pl. Baker. 3: 29. 1901. TYPE: UNITED STATES. Colorado. Montrose Co.: "Dry hills at Cimarron, southern Colorado" (protologue), "Cimarron . . . Common in mats on stony hillsides" (holotype label), 6 Jun 1901, C. F. Baker 34 (HOLOTYPE: NDG-061662!; ISOTYPES: GH!, KI!, MO-208090!, NY!, RM-157791!, US-411735!).

Tetranneuris pilosa Greene in P. A. Rydberg, Fl. Colorado 379. 1906. TYPE: UNITED STATES. Colorado. La Plata Co.: "Los Pinos (Bayfield)" (protologue and lectotype label), 17 May 1899, C. F. Baker 726 (LECTOTYPE here designated: NDG-061657!; ISOLECTOTYPES: BM!, GH!, KI!, MO-208152!, NY!, US-369980!). The collection number "726" does not ap-

pear on the lectotype; it does appear on all of the isolectotypes. The date "17 May" appears on the lectotype; only "May" appears on the isolectotypes. The notation "*Tetranneuris pilosa* Greene n. sp." appears on all. This name has caused a bit of confusion, because some of the plants from the original collection do not have cauline leaves. Cauline leaves are clearly visible on a number of plants including the lower one on the lectotype sheet and various others on the isolectotype sheets at BM, K, MO, and NY.

PERENNIALS. CAUDICES \pm branched, thickened distally. AERIAL STEMS (1–)5–20(–30), erect, leafy, unbranched or sparingly branched distally, green throughout to purple-red-tinted throughout, 9–26 cm, sparsely to moderately pubescent, sparsely to moderately dotted with sessile glands. LEAVES basal and cauline, entire, glabrous or sparsely to moderately pubescent, usually very strongly dotted with impressed glands; basal leaves tightly clustered and appearing to arise from the same level at bases of stems, blades linear-oblongate, bases usually densely woolly or long-pubescent; proximal cauline blades linear-oblongate; mid blades linear-oblongate to linear, 1.7–2 mm wide; distal blades linear-oblongate to linear. HEADS (1–)5–30(–40) per plant, 1–2(–5) per stem, radiate, borne singly or in paniculiform to corymbiform arrays. PEDUNCLES 5–18.5 cm, sparsely to moderately pubescent, usually densely pubescent distally, sparsely to moderately dotted with sessile glands. INVOLUCRES 8–12 \times 13–17 mm. PHYLLARIES: outer phyllaries 7–12, often purple-red-tinted on apices and margins, obovate to ovate to lanceolate, 5–6.4 \times 1.5–2.7 mm, margins usually scarious, abaxial faces sparsely to, usually, moderately to, sometimes, densely pubescent, sparsely to moderately dotted with sessile and/or impressed glands; mid phyllaries often purple-red-tinted on apices and margins, obovate to oblongate, 4.3–6.5 \times

1.8–2.8 mm, margins scarious, abaxial faces sparsely to moderately pubescent, sparsely to moderately dotted with sessile glands; inner phyllaries 4.3–6 × 1.2–2 mm, abaxial faces sparsely to moderately pubescent, sparsely dotted with sessile glands. RAY FLORETS 7–10; corollas 10–20 × 3.8–8.5 mm, abaxial faces glabrous or sparsely to moderately pubescent, sparsely to moderately dotted with sessile glands. DISC FLORETS (40–)80–150+; corollas yellow, 3.3–4.5 × 1–1.4 mm, glabrous, eglandular or sparsely dotted with sessile glands. CYPSELAE 3–4.1 × 1–1.3 mm, surfaces white, moderately to densely pubescent, sparsely to moderately dotted with sessile glands; pappi 5–7, obovate- to oblanceolate- to lanceolate-aristate scales, 2.7–4.5 × 0.7–1.5 mm.

CHROMOSOME NUMBERS: $2n = 28, 30, 56, 60$.

DISTRIBUTION (Fig. 3) AND HABITAT: Southeastern Utah, southwestern Colorado, northwestern New Mexico, and northeastern Arizona. Growing at roadsides, on hill-sides, in open treeless areas, and at edges of juniper woodlands and pine forests, 1265–2830 m.

FLOWERING AND FRUITING: April through August.

REPRESENTATIVE SPECIMENS: **UNITED STATES.** **Arizona.** Apache Co.: Winter Canyon 1 mi from Ganado, 1950 m, 8 Jun 1968, *Anderson & Young 15* (ARIZ); Crossing of Chinle Creek between Dinnehotso and Mexican Water, 1495 m, 17 Jul 1948, *Gould & Phillips 4789* (ARIZ); 1 mi W of Sawmill, 2255 m, 11 Jul 1961, *Harrington 9554* (CS); Natural Bridge, Petrified Forest, 15 Jun 1928, *Harrison 5534* (ARIZ); Navajo Reservation, Chuska Mts, Lukachukai Mts, Hwy 13 ca 3.3 mi NE of Lukachukai, 1.4 mi SW of Wagon Wheel picnic area, 2140 m, 2 Jun 1986, *Reeves 8369* (ASU); Just E of Rough Rock, 1890 m, $n = 30$, 24 Jun 1965, *Strother 397* (TEX); 14 mi S of Chinle, 1830 m, $n = 15$, 24 Jun 1965, *Strother 400* (TEX). Coconino Co.: 20 mi NE of Tuba

City, 26 Jun 1967, *Cazier 71* (ASU); 50 mi S of Grand Canyon S rim, 26 Jun 1940, *Maguire 12219* (UTC); Flagstaff, Jun 1891, *McDougal s.n.* (RM); Just E of Sedona, S end of Oak Creek, 1740 m, $n = 30 \pm$, 14 Jun 1965, *Strother 337* (TEX); 3 mi W of Little Colorado River Gorge, ca 18 mi W of Cameron, 1830 m, $n = 15$, 15 Jun 1965, *Strother 341* (TEX). Navajo Co.: Ca 1 mi E of Marsh Pass (a few mi W of Kayenta), 19 May 1966, *Alston 6* (TEX); Hwy 180, 3.0 mi E of Hwy 77 (jct in Holbrook), 28 May 1975, *Bierner 51259* (ARIZ, TEX). **Colorado.** Archuleta Co.: 2 mi E of Pagosa Springs, $2n = 30$, 27 Aug 1946, *Parker & McClintock 6429* (COLO, LL, OKLA, RM, TEX, UT, UTC). Delta Co.: Near Austin, Jun 1920, *Burritt 79* (COLO). Dolores Co.: Ca 4 air mi NE of Dove Creek . . . along the Dolores River, 1830–1860 m, 22 Jun 1995, *Moore 5958* (CS). Gunnison Co.: Gunnison Basin, 4 mi N of Gunnison, just E of Cranor Hills Ski Area, 9 Jul 1999, *Orthner 871* (COLO); 3.8 mi W of Sapinero Bridge on S-facing rocky slope above Curicanti Reservoir just W of Dry Gulch and W of Lake City turnoff, 2250 m, 28 May 1982, *Weber et al. 16017* (COLO, RM, UT, UTC); N side of Blue Mesa Reservoir near mouth of Dry Gulch ca 3.93 km SE of the summit of Tenderfoot Hill, 2315 m, $n = 14$, 18 May 2000, *Windham 2105* (UT). La Plata Co.: 9 mi S of Ignacio; 0.7 mi SE of La Boca, 2828 m, 30 Apr 1985, *O'Kane 85-28* (COLO, CS); 4 mi S of Durango, 1980 m, $2n = 15II + 1$ or 2 fragments, 20 Jun 1965, *Strother 387* (TEX). Mesa Co.: Grand Mesa, 1980 m, 13 May 1963, *Frary 630* (CS); 20 air mi SE of Grand Junction, 1980 m, 15 Jun 1983, *Neese & Abbott 13573* (UTC); Uncompahgre Plateau, 2745 m, 24 Jun 1946, *Simonds AS1* (CS); Colorado Nat'l Monument, 10 May 1982, *Siplivinsky 3163* (COLO). Mineral Co.: Open slope, Wolf Creek Camp Ground, 2440 m, 2 Jul 1948, *Harrington 4126* (CS). Montezuma Co.: McElmo Canyon, SW of Cortez, 1 Jun 1965, *Davis 307* (CS); Park Point, Mesa Verde Nat'l Park, 2590 m, 6 Aug 1965, Sa-

lamun & *Erdman* 2194 (COLO). Montrose Co.: Hwy 141, 19.0 mi N of Hwy 90, 11 Jun 1975, *Bierner* 51286 (TEX); Near Montrose, 17 Jun 1928, *Osterhout* 6926 (RM); Naturita, 1650 m, 30 Apr 1914, *Payson* 266 (COLO, RM). Ouray Co.: Ridgeway, 18 Jun 1924, *Payson* & *Payson* 3849 (RM, TEX). San Miguel Co.: Uncompahgre Nat'l Forest S of Norwood, 2380 m, 4 Jun 1982, *Sipl* & *Beck* 3586 (COLO, UT, UTC). **New Mexico.** Cibola Co.: 0.5 mi N of Mesita Pueblo, 1 mi N of I-40, 21 May 1991, *Lowrey* 1341 (UNM). McKinley Co.: Mexican Springs, 1980 m, 1934, *Klinger* 137 (UNM); 18 mi E of Gallop, 2135 m, 5 Jul 1947, *Parker* & *McClintock* 7011 (COLO, LL, OKLA, RM, UT, UTC); Haystack Mt, ca 5 mi W of Pre-witt, 19 May 1995, *Sivinski* 3002 (UNM). Rio Arriba Co.: Hwy 84, 1.4 mi NW of Abiquiu, 23 May 1988, *Bierner* 88-61 (TEX); Carson Nat'l Forest, Canyon Bancos ca 14 air mi W of Dulce, 2105-2180 m, 28 May 1987, *Hartman et al.* 22481 (COLO, RM). San Juan Co.: Breaks of Animas River, E of Aztec, 1 Jun 1952, *Clark* 16268 (UNM); 1.5 mi E of Arizona border; up Sanostee Wash to about 13 mi W of Sanostee, 1950 m, 8 Jun 1995, *Holmes* 363 (COLO); 28 mi W of Farmington, 1770 m, $n = \text{ca } 15$, 20 Jun 1965, *Strother* 386 (TEX); 5 mi S of Bloomfield, 1585 m, $2n = 15\text{II}$, 25 Jun 1965, *Strother* 406 (TEX); 3 mi S of Nageezi, ca 2195 m, $2n = 15\text{II}$, 25 Jun 1965, *Strother* 407 (TEX). Sandoval Co.: Ca 6 mi SSW of San Ysidro, 1830 m, 6 Jun 1994, *Heil* 8438 (UNM); 10 mi NW of Cuba, 2290 m, $n = 15$, 25 Jun 1965, *Strother* 409 (TEX); Ca 2 mi N of Jemez Springs on Hwy 4, ca 2075 m, $n = 15$, 25 Jun 1965, *Strother* 411 (TEX). Valencia Co.: Zuni Mts, SE slope of Mt Sedgwick, 2745 m, 17 Aug 1968, *Riffle* 814a (UNM). **Utah.** Emery Co.: Ca 27 mi W of Green River, along rd to Castle Dale, 25 May 1961, *Cronquist* 9105 (UTC). Garfield Co.: SW of the Henry Mts along Bullfrog-Capitol Reef rd, ca 4.3 km NNW of Brush Corral Reservoir, 1600 m, $n = 14$, 9 May 1997, *Windham* 97-068 (UT); W of Henry Mts along Burr Canyon in Capitol Reef, ca

3.54 km SE of Double Arch, 1540 m, $n = 14$, 9 May 1997, *Windham* 97-065 (UT); N of Escalante along Posey Lake rd near Pine Creek ca 4.66 km SE of Skull Spring, 1890 m, $n = 14$, 24 May 2001, *Windham* 2433 (UT). Grand Co.: Arches Nat'l Park, 5.8 mi N of Balanced Rock, 10 Jun 1975, *Bierner* 51281 (RM, TEX). Kane Co.: 2 mi W of Glen Canyon City and ca 56 mi E of Kanab, 1340 m, 23 May 1965, *Cronquist* 10168 (RM, TEX, UTC); SE of Kodachrome Basin State Park along rd to Grosvenor Arch ca 2.64 km SSE of the confluence of Dry Valley Creek and Wiggler Wash, 1825 m, $n = 14$, 9 Jun 1999, *Windham* 99-186 (UT). San Juan Co.: Monument Valley, 5 mi N of Goulding Trading Post, 19 May 1966, *Alston* 13 (TEX); Hwy 46, 0.7 mi E of Hwy 191 (La Sal Junction), 22 May 1988, *Bierner* 88-60 (TEX); 60 mi N of Mexican Hat via Hwys 95 and 261, 1675 m, $2n = 30\text{II}$, 19 Jun 1965, *Strother* 382 (TEX); 8 mi N of Mexican Hat, Valley of Gods on Hwy 261, $2n = 15\text{II}$, 19 Jun 1965, *Strother* 385 (TEX); Bridger Jack Mesa, ca 15 mi WNW of Monticello, 1950 m, 30 Jun 1984, *Tuhy* 1564 (RM); SW of Moab in Kane Springs Canyon ca 0.83 km SSE of the crest of Hurrah Pass, 1390 m, $n = 14$, $2n = 28$, 20 May 1994, *Windham* 94-52 (UT, UTC); SE of Hite Crossing bridge along Hwy 95 at turn-off to marina ca 3.57 km NW of the summit of Brown's Rim, 1265 m, $n = 14$, $2n = 28$, 9 May 1997, *Windham et al.* 97-077 (UT). Wayne Co.: W side of Colorado River in Canyonlands Nat'l Park, 10 May 1968, *botany majors s.n.* (UT); 10.2 mi E of Hwy 160 on Hwy 46, 7 Jun 1968, *Mears & Mears* 2814 (TEX).

The distribution of *Tetranneuris ivesiana* overlaps that of *T. acaulis* var. *arizonica* in northern Arizona, southern Utah, and western Colorado, and that of *T. acaulis* var. *epunctata* in southern Utah and westcentral Colorado (Fig. 2 and 3). Where the taxa come into contact, one finds plants that may represent hybrids. The hybrids might account for Welsh's (1983) acceptance of

Parker's (1950) treatment of *T. ivesiana* as a varietal element of her broad concept of *Hymenoxys acaulis*.

Although one might hypothesize a sister species relationship between *Tetranneuris ivesiana* and *T. argentea* (because they both possess cauline leaves), it seems far more likely that *T. ivesiana* is most closely related to *T. acaulis* var. *arizonica*. It is not infrequent that plants of *T. ivesiana* lack cauline leaves, not only in areas of overlap with *T. acaulis* var. *arizonica* but also in various parts of southwestern Colorado, most notably in La Plata and Archuleta counties. Populations in these areas have plants with and without cauline leaves that are otherwise indistinguishable. Furthermore, leaf width can be quite variable, and one is hard pressed to tell a *T. ivesiana* plant with densely glandular (typical) oblanceolate (broader than typical) basal leaves and no cauline leaves (atypical) from a plant of *T. acaulis* var. *arizonica*.

5. *TETRANEURIS LINEARIFOLIA* (Hook.) Greene, Pittonia 3: 269. 1898.

ANNUALS. CAUDICES none. STEMS 1–10, erect or \pm decumbent, leafy, unbranched or branched distally, green throughout to purple-red-tinted throughout, 15–50 cm, sparsely to densely pubescent, eglandular or sparsely dotted with sessile glands. LEAVES basal and cauline, sparsely to densely pubescent, sparsely to densely dotted with impressed glands, sessile glands sometimes present; basal blades spatulate to oblanceolate, entire or with 2–6 lateral teeth or lobes, bases often densely woolly or long-pubescent; proximal cauline blades narrowly spatulate to oblanceolate to linear-oblanceolate, entire or with 2–6 lateral teeth or lobes; mid blades oblanceolate to linear-oblanceolate to linear, 0.9–9.5(–16) mm wide, entire or with 1–2 lateral teeth or lobes; distal blades narrowly oblanceolate to linear-oblanceolate to linear, entire or, sometimes, with 1–2 lateral teeth or lobes. HEADS 8–50(–80) per plant, radiate,

borne singly or in corymbiform arrays. PEDUNCLES 8–29 cm, sparsely to densely pubescent, eglandular or sparsely dotted with sessile glands. INVOLUCRES 5–10 \times 7–15 mm. PHYLLARIES: outer phyllaries 8–21, sometimes purple-red-tinted on apices and margins, obovate to oblanceolate to lanceolate, 2.4–5.5 \times 0.5–1.4 mm, margins scarious or not scarious, abaxial faces moderately to densely pubescent, eglandular or sparsely to moderately dotted with sessile glands; mid phyllaries sometimes purple-red-tinted on apices, obovate to oblanceolate, 2.3–5 \times 0.8–1.5 mm, margins often scarious, abaxial faces sparsely to densely pubescent, eglandular or sparsely to moderately dotted with sessile glands; inner phyllaries 2.6–4 \times 0.7–1.4 mm, abaxial faces sparsely to densely pubescent, eglandular or sparsely dotted with sessile glands. RAY FLORETS 9–25; corollas 8.2–16.8 \times 2.8–7.1 mm, abaxial faces sparsely to moderately pubescent, sparsely to moderately dotted with sessile glands. DISC FLORETS 50–200+; corollas yellow, 1.6–3 \times 0.5–1 mm, glabrous or sparsely to moderately pubescent, eglandular or sparsely dotted with sessile glands. CYPSELAE 1.5–2.6 \times 0.5–0.9 mm, surfaces white or brown, moderately to densely pubescent, eglandular or sparsely to moderately dotted with sessile and/or impressed glands; pappi 4–8, obovate or obovate-aristate scales, 1–2.5 \times 0.5–1 mm.

REPRESENTATIVE INTERMEDIATE SPECIMENS: UNITED STATES. Texas. Bee Co.: 1 mi S of Normanna, along Medio Creek, 28 Mar 1948, *Cory 54100* (LL). Duval Co.: Hwy 1329, 8.3 mi S of Hwy 359 (jct in San Diego), $n = 15?$, multivalents and lagging chromosomes noted, 20 Mar 1991, *Bierner 91-10* (SWT, TEX); Hwy 1329, 11.4 mi S of Hwy 359 (jct in San Diego), $2n = 15II$, lagging chromosome noted in one anaphase I cell, 20 Mar 1991, *Bierner 91-11* (SWT, TEX); Hwy 16, 5.1 mi N of Hwy 44 (jct in Freer), 21 Mar 1991, *Bierner 91-16* (SWT, TEX). Live Oak Co.: Hwy 281, 2.8 mi S of Hwy 59 (jct in George West),

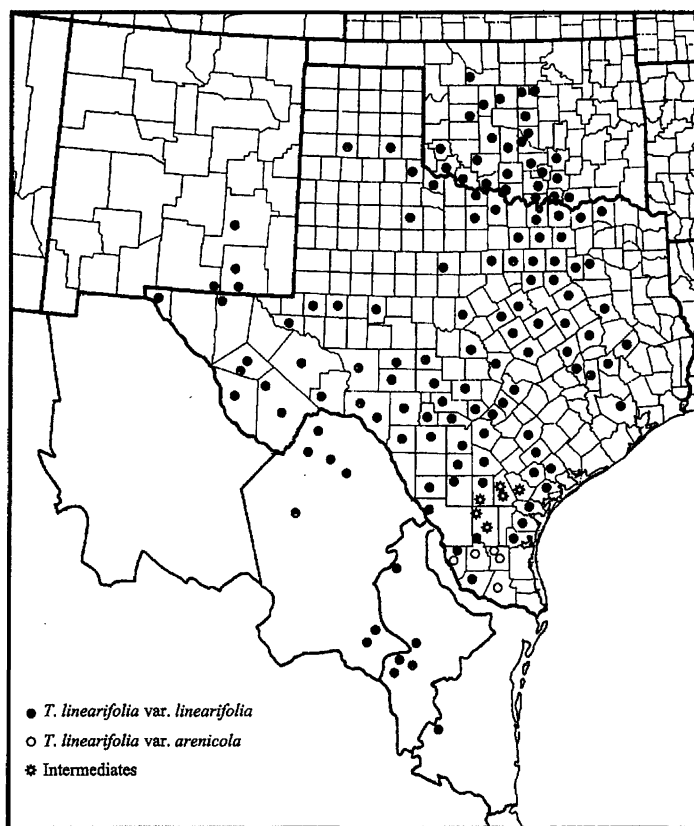


FIG. 5. Distribution of *Tetraneuris linearifolia* var. *linearifolia* and *T. linearifolia* var. *arenicola*. Also shown are intermediates between the two varieties.

$2n = 15II$, 19 Mar 1991, *Bierner 91-4* (SWT, TEX); Hwy 3162, 10.1 mi E of Hwy 281, $2n = 15II$, 19 Mar 1991, *Bierner 91-8* (SWT, TEX). McMullen Co.: Hwy 16, 3.6 mi N of Hwy 624 (jct in south-central part of county), 21 Mar 1991, *Bierner 91-17* (SWT, TEX).

The relationship of *Tetraneuris linearifolia* var. *linearifolia* and *T. linearifolia* var. *arenicola* to one another is discussed in detail in Bierner et al. (1992). The former is a morphologically variable, widespread taxon; the latter is much less morphologically variable and is known only from south Texas (Fig. 5). *Tetraneuris linearifolia* var. *arenicola* is distinguished from the typical variety by a syndrome of characteristics: basally branching habit, larger leaves, those at

the base usually markedly lobed, and long-pilose vestiture. Nevertheless, as can be seen from the specimens cited above, plants with intermediate morphology are fairly common in areas of distributional contact (Fig. 5), and those plants sometimes exhibit meiotic irregularities (e.g., *Bierner 91-10* and *91-11*, SWT, TEX). As might be expected, the populations of these two taxa (four of each) were very closely associated in the DNA phylogenetic tree presented by Bierner and Jansen (1998).

In addition to the morphological variability in *Tetraneuris linearifolia* var. *linearifolia*, some DNA restriction site variation was observed among populations examined by Bierner and Jansen (1998), and it is possible that additional morphogeographic infraspecific taxa might be culled from within

this complex. For example, in northcentral Mexico (Serranías del Burro, Coahuila) remarkably robust, broad-leaved, highly tomentose, large-headed plants, strikingly different from most other collections, occur in relatively mesic pine-oak woodlands (*Riskind 2336a* and *2381*, TEX). In the same area in seemingly more xeric sites, typical elements of the taxon occur (*Ruiz 81*, TEX; *Riskind 2094*, TEX). Also, robust, very tomentose plants occasionally occur elsewhere in its range. Therefore, we view such sporadic variation as unworthy of formal taxonomic recognition.

KEY TO THE VARIETIES

1. Stems erect, branched distally; leaves \pm pubescent, basal blades entire or, sometimes, with 2(–6) lateral teeth or lobes, proximal cauline blades entire or, rarely, with 1–2 lateral teeth or lobes, mid blades (0.9–)1.4–3(–4.8) mm wide; involucre (7–) 8–11(–12) mm in diameter; pappus scales obovate-aristate; Oklahoma and Texas to southeastern New Mexico and northeastern Mexico, growing in limestone-derived soils 5a. *T. linearifolia* var. *linearifolia*
 1. Stems erect or \pm decumbent, \pm branched distally; leaves usually densely pubescent, basal blades with 2–6 lateral teeth or lobes, proximal cauline blades with 2(–6) lateral teeth or lobes, mid blades (2.5–) 3.9–9.5(–16) mm wide; involucre 12–15 mm in diameter; pappus scales obovate, not aristate; south Texas, growing in sand 5b. *T. linearifolia* var. *arenicola*
- 5a. **TETRANEURIS LINEARIFOLIA** (Hook.) Greene var. **LINEARIFOLIA**.
- Hymenoxys linearifolia* Hook., Ic. Pl. 2: t. 146. 1837. TYPE: UNITED STATES. Texas. Austin Co.: “San Felipe, Texas” (protologue and holotype label), 1835, *T. Drummond 224* (HOLOTYPE: K! specimen to the left; ISOTYPES: BM!, GH!, PH-004025!, NY!, photograph of second plant at K!).
- Actinella linearifolia* (Hook.) Torr. & A. Gray, Fl. N. Amer. 2: 383. 1842.
- Actinea linearifolia* (Hook.) Kuntze, Revis. Gen. Pl. 1: 303. 1891.
- Ptilepida linearifolia* (Hook.) Britton, Mem. Torrey Bot. Club 5: 340. 1894.
- Tetraneuris linearifolia* (Hook.) Greene, Pittonia 3: 269. 1898.
- Picradenia linearifolia* (Hook.) Britton in N. L. Britton and A. Brown, Ill. Fl. N. U.S. 3: 448. 1898.
- Tetraneuris oblongifolia* Greene, Pittonia 3: 269. 1898. TYPE: MEXICO. Nuevo León. “Guajuco, State of Nuevo León, Mexico, 27 miles southeast of Monterey [sic]; a mountainous section” (PH and US-1415876 isotype labels), 1–8 Mar 1880, *E. Palmer 677* (LECTOTYPE here designated: US-27470!; ISOLECTOTYPES: GH!, K!, PH!, US-1415876!). Original material was not located at NDG.
- Tetraneuris linearifolia* (Hook.) Greene [var.] *oblongifolia* (Greene) Cockerell, Proc. Biol. Soc. Wash. 17: 112. 1904.
- Actinea linearifolia* (Hook.) Kuntze [var.] *oblongifolia* (Greene) Kittell, Fl. Ariz. New Mex. 470. 1941.
- Tetraneuris linearifolia* (Hook.) Greene var. *latior* Cockerell, Proc. Biol. Soc. Wash. 17: 112. 1904. TYPE: UNITED STATES. Texas. Kerr Co.: “Kerrville” (protologue and holotype label), 19–25 Apr 1894, *A. A. Heller 1619* (HOLOTYPE: MO-208112!; ISOTYPES: BM!, GH!, K!, MO-2486978!, NDG-061603!, NY!, PH-two sheets!, RM-3447!, UC-89945!, US-213516!, photograph of second plant at K!).
- Tetraneuris latior* (Cockerell) Rydb. in N. L. Britton et al., eds., N. Amer. Fl. 34: 108. 1915.
- Tetraneuris linearifolia* (Hook.) Greene subsp. *dodgei* Cockerell, Proc. Biol. Soc. Wash. 17: 112. 1904. TYPE: MEXICO. Nuevo León. “In fields: very common . . . Monterey [sic], Mexico” (holotype label), May 1891, *C. K. Dodge 109* (HOLOTYPE: US-27471!; probable ISOTYPE: MICH!).
- Tetraneuris dodgei* (Cockerell) Rydb. in N.

L. Britton et al., eds., N. Amer. Fl. 34: 108. 1915.

Actinea linearifolia (Hook.) Kuntze [var.] *dodgei* (Cockerell) A. Nelson, Univ. Wyoming Publ. Sci., Bot. 1: 62. 1924.

Actinea ursina Standl., Field Mus. Nat. Hist., Bot. Ser. 22: 126. 1940. TYPE: MEXICO. Nuevo León. "Scattered on drier, more open slopes. Las Canoas on Cerro Potosí, Municipio de Galeana" (protologue and holotype label), 17 Jul 1935, C. H. Mueller 2189 (HOLOTYPE: F, photograph at F!; ISOTYPES: GH!, MICH!, MO-1280217!).

STEMS 1(–6), erect, branched distally, 15–40 cm, sparsely to densely pubescent. LEAVES sparsely to moderately to, sometimes, densely pubescent, sparsely to densely dotted with impressed glands; basal blades spatulate to narrowly spatulate to oblanceolate, entire or, sometimes, with 2(–6) lateral teeth or lobes, bases often densely woolly or long-pubescent; proximal cauline blades narrowly spatulate to linear-oblan-ceolate, entire or, rarely, with 1–2 lateral teeth or lobes; mid blades linear-oblan-ceolate to linear, (0.9–)1.4–3(–4.8) mm wide, entire or, very rarely, with 1–2 lateral teeth or lobes; distal blades linear-oblan-ceolate to linear, entire. HEADS 10–50(–80) per plant, in corymbiform arrays. PEDUNCLES (8–)9.2–14.4(–19.5) cm, sparsely to moderately pubescent proximally, moderately to densely pubescent distally. INVOLUCRES (5–)6–7.8(–9) \times (7–)8–11(–12) mm. PHYLLARIES: outer phyllaries 8–16, sometimes purple-red-tinted on apices and margins, obovate to oblanceolate, (2.4–)3.4–4(–4.5) \times 0.7–1.3 mm, margins often scarious, abaxial faces moderately to densely pubescent, sparsely to moderately dotted with sessile glands; mid phyllaries sometimes purple-red-tinted on apices, (2.3–)3–4(–4.5) \times 0.8–1.5 mm, margins scarious, abaxial faces sparsely to moderately pubescent, eglandular or sparsely to moderately dotted with sessile glands; inner phyllaries 2.6–3.5(–4) \times 0.7–1.4 mm,

abaxial faces sparsely to moderately pubescent. RAY FLORETS 9–20; corollas (8.2–)9.1–12.1(–13.7) \times (3.3–)4.1–4.9(–5.8) mm. DISC FLORETS 50–200+; corollas 1.6–2.7 \times 0.5–0.8 mm, glabrous or sparsely pubescent proximally, sparsely to moderately pubescent distally. CYPSELAE 1.5–2.1(–2.5) \times 0.5–0.9 mm, surfaces white or brown, eglandular or moderately dotted with sessile and/or impressed glands; pappi 4–7, obovate-aristate scales, 1.2–1.9(–2.5) \times 0.5–1 mm.

CHROMOSOME NUMBERS: $2n = 28, 30$.

DISTRIBUTION (Fig. 5) AND HABITAT: Central Oklahoma, most of Texas, south-eastern New Mexico, and northeastern Mexico (Coahuila, Nuevo León, and Tamaulipas). Growing in limestone-derived soils at roadsides, on hillsides, in pastures and other open areas, and at edges of woods, 30–2700 m.

FLOWERING AND FRUITING: Throughout the year, mainly April through July.

REPRESENTATIVE SPECIMENS: **MEXICO. Coahuila.** Múzquiz, 1935, *Marsh 189* (TEX); Rancho Los Angeles, 54 km S of Saltillo, 28 Jul 1982, *Villaseñor et al. 1619* (TEX); Western side of Potrero de la Mula, about 20 km NW of Ocampo, on escarpment near mines, 18 Sep 1941, *Johnston 9229* (LL); Los Lirios to La Jacinta, Arteaga, 2390 m, 15 Sep 1995, *Hinton 25544* (TEX); Serranías del Burro, Rancho El Bonito, Mpio. de Villa Acuña, Canyon El Bonito, 4 May 1981, *Riskind 2336a* (TEX); Serranías del Burro, Rancho El Bonito, Mpio. de Villa Acuña, Canyon El Toro, 5 May 1981, *Riskind 2381* (TEX); Sierra La Encantada, cuesta Malena ca 170 km al NW de Múzquiz, brecha Boquillas del Carmen, 1600 m, 29 Mar 1992, *Carranza et al. 1510* (TEX); Rancho Florida, ca 100 km al NW de Múzquiz rumbo a Boquillas del Carmen, Hwy 53, 700 m, 29 May 1992, *Carranza et al. 1532* (TEX). **Nuevo León.** Hwy 85, S of Monterrey, 23.2 mi NW of Montemorelos, 20 May 1975, *Bierner 51208* (TEX); 30 mi S of Saltillo on Hwy 57, 24 Aug 1960, *Ellison 54*

(TEX); 1.5 mi N of Pablillo on Hwy 57, 28 Aug 1982, *Gieschen s.n.* (TEX); Sierra Madre Oriental: San Francisco Canyon, about 15 mi SW of Pueblo Galeana, 14 May 1934, *Mueller & Mueller* 337 (TEX); Municipio Bustamante, Sierra Gomas, Bustamante Canyon, 1100–1400 m, 13 Aug 1988, *Patterson* 6617 (TEX); Hwy 60 at village of Iturbide, 2n = 14II (possibly 13II + ring of 4), 8 Sep 1962, *Turner & Powell* 1066 (TEX). **Tamaulipas.** At Marcela, 21 Jul 1949, *Stanford et al.* 2622 (TEX). **UNITED STATES. New Mexico.** Chaves Co.: 3 mi S of the Pecos River, NE of Roswell, 16 Apr 1949, *Glassman* 2285 (OKL). Eddy Co.: Near Hwy 137, 5 mi W of Hwy 285 (10 mi NW and 5 mi W of Carlsbad), 26 Mar 1959, *Martin* 3008 (UNM); 6.2 mi SW of Whites City on Hwy 180, 0.25 mi E of Hwy, 27 Mar 1997, *Sivinski* 3540 (UNM). Otero Co.: N McKittrick Canyon near first crossing of Texas-New Mexico boundary on the NM side, 19 Oct 1973, *Patterson* 561 (LL). **Oklahoma.** Blaine Co.: Gypsum hills SE of Watonga, 13 Apr 1937, *Engelman* 1448 (OKL). Bryan Co.: 2 mi E, 1.25 mi S of Hwy 70 bridge across Lake Texoma, 8 May 1963, *Taylor & Taylor* 1579 (OKL). Caddo Co.: 5 mi E of Anadarko, 17 Apr 1937, *Kenworthy* 46 (TEX). Carter Co.: Ardmore Mts, 25 May 1966, *Wilson* 10695 (TEX). Cleveland Co.: 3 mi S and 2 mi E of Norman, 11 May 1944, *Hopkins et al.* 99 (LL, RM). Comanche Co.: Wichita Mt Wildlife Refuge, 29 Apr 1944, *Hopkins et al.* 197 (RM, TEX). Cotton Co.: 0.3 mi E of Red River Bridge on Hwy 281, 21 May 1970, *Ray et al.* 1064 (OKL). Custer Co.: 1 mi W and 0.5 mi S of Weatherford, 11 May 1952, *Waterfall* 10718 (TEX). Garvin Co.: Along Hwy 7, 5.1 mi E of Hennepin, ca 1.5 mi SW of site of old Fort Arbuckle, 25 Mar 1972, *Williams* 546 (OKL). Grady Co.: Hwy 9, 8 mi E of Chiskasha, 12 Apr 1968, *Massey & Brunken* 1933 (OKL, TEX). Greer Co.: 8 mi W of Granite, 2 May 1966, *Koch* 1049 (TEX). Jackson Co.: 2.5 mi W of Red River, 1 mi S of Hwy 5, 22 Apr 1970, *Black JB-110* (OKL). Jefferson Co.: Just N of Red

River bridge, W of Waurika on Hwy 79, 22 Apr 1957, *Rohrbaugh* 495 (OKL). Johnston Co.: 6 mi N of Millcreek, 14 Apr 1945, *Hopkins et al.* 996 (RM, TEX). Kingfisher Co.: Ca 2 mi W of Loyal, 13 May 1990, *Folley* 334 (OKL). Logan Co.: 12 mi W of Mulhall, 16 Apr 1937, *Engleman* 145 (OKL). Love Co.: Goodland limestone bluff, 8 mi W of Marietta, 26 Mar 1967, *Taylor & Taylor* 3599 (OKL). Major Co.: Slopes of gypsum hills 15 mi W of Fairview, 1 Jun 1955, *Engleman* 978 (OKL). Marshall Co.: Hwy 70 across from Lake Texoma Lodge, 23 Apr 1963, *Taylor & Taylor* 1450 (OKL). McClain Co.: Hwy 76, 10 mi N of Blanchard, 16 Jul 1980, *Huft* 1524 (OKL). Murray Co.: Turner Falls, 24 Apr 1936, *Demaree* 12278 (LL, TEX). Oklahoma Co.: 50th and Lincoln Blvd, Oklahoma City, 21 Apr 1973, *Sellers* 80 (OKL). Payne Co.: 9 mi S of Stillwater, 22 Apr 1938, *McLean* 139 (TEX). Pontotoc Co.: Pontotoc Ridge Preserve, 30 Apr 1997, *Benesh et al.* PON0078 (OKL). Stephen Co.: Waurika Wildlife Management Area, 10 May 1997, *Hoagland* 0282-97 (OKL). Tillman Co.: Davidson; 7 mi E of Hwy 70 from intersection with 183, 1.5 mi S on section line rd, 12 Apr 2000, *Hoagland & McCarty* BLM058 (OKL). **Texas.** Anderson Co.: Ca 350 m S of jct of Hwy 425 and 2201, 2 Jun 1999, *Holmes* 10137 (TEX). Archer Co.: Near N tip of main antenna array, ca 3.7 air mi E of jct Hwy 210 and 422 SW of Archer City, 335 m, 1 May 1996, *Carr* 15246 (TEX). Atascosa Co.: Hwy 791, 6.7 mi SW of Hwy alt 281 (jct in SE part of county), 21 Mar 1991, *Biernner* 91-18 (TEX). Bandera Co.: Hwy 173, 4.5 mi N of the Bandera-Medina county line, 18 May 1975, *Biernner* 51196 (TEX). Bell Co.: Morgan Point, Dam Rd, 8.6 mi N of Belton, 19 Mar 1966, *Cope* 10 (LL). Bexar Co.: Near Fredericksburg Rd, 7 mi NW of San Antonio, 6 May 1942, *Metz* 3263 (TEX). Bosque Co.: Morgan, 7 Jul 1927, *Tharp* 7308 (LL). Brazos Co.: College Station, 10 Apr 1927, *Cory s.n.* (LL). Brewster Co.: 7 mi SE of Alpine, 3 Apr 1929, *Clawson s.n.* (LL); Between Marathon and Persimmon Gap, 6

Apr 1937, *Warnock T108* (TEX). Brown Co.: 1.5 mi N of Owens, 24 May 1968, *Stanford 2311* (OKLA). Burnet Co.: Hwy 281, 12.3 mi S of Lampasas, 15 Apr 1957, *Chambers 1126* (LL). Childress Co.: 11 mi N of Childress, 1 mi N of Ted River Bridge, 9 Jun 1941, *Rose-Innes & Moon 1009* (TEX). Clay Co.: Just E of Wichita River on edge of Byers, 27 Apr 1964, *Correll & Correll 29444* (LL). Collin Co.: Field on W side of Preston Rd, opposite intersection of rd to Renner, 28 Jun 1964, *Correll & Correll 29907* (LL). Comal Co.: Comanche Spring, New Braunfels, etc, Jun 1849, *Lindheimer 853* (TEX). Cooke Co.: Tyler's Bluff, 11 May 1957, *Correll 16282* (LL). Coryell Co.: Hwy 36, ca 4 mi SE of Jonesboro, 30 Apr 1963, *Henderson 63-638* (TEX). Crockett Co.: Hwy 290, ca 23 mi W of Ozona, $2n = 14II$, 25 Apr 1979, *Strother 1299* (TEX); Hwy 290, ca 23 mi W of Ozona, $2n = 15II$, 25 Apr 1979, *Strother 1302* (TEX). Culbertson Co.: N fork of McKittrick Canyon, Guadalupe Mts, 25 Jul 1957, *Correll & Johnston 18476* (LL). Dallas Co.: E of Dallas, 22 Apr 1942, *Lundell 11317* (KSC, LL, MONTU, OKL, OKLA, RM). De Witt Co.: Western De Witt County, 21 Mar 1942, *Riedel s.n.* (TEX). Dimmit Co.: 9 mi W of Carrizo Springs, $2n = 15 II$ and $30II$ from same flower, 11 Mar 1994, *Turner 94-9* (TEX). Denton Co.: Roanoke, 6 Apr 1945, *Shinners 7079* (LL, OKLA). Donley Co.: 1 mi N of Ted River Bridge, 11 mi N of Childress, 9 Jun 1941, *Rose-Innes & Moon 1009* (TEX). Duval Co.: Mobil site, SW corner near entrance at Hwy 359 between Bruni and Hebronville, 6 May 1985, *Cowan 5269* (TEX). Ector Co.: N and NE of Notrees, 22 Apr 1966, *Collins 1209* (OKLA). Edwards Co.: 2 mi NW of Rocksprings, 16 May 1965, *Strother 309* (TEX). El Paso Co.: Frijoles to El Paso, 26 May 1931, *Nelson 11774* (RM). Ellis Co.: Along White Rock Creek, 11 mi S of Italy, 4 Jul 1957, *Correll & Johnston 17372* (LL). Fannin Co.: Ca 4 mi S of Honey Grove, Hwy 3225, 14 May 1999, *Holmes & Singhurst 10103* (TEX). Frio Co.: Near Pearsall, 11 Apr 1936, *Penzound 1-47* (TEX). Gi-

lespie Co.: Hwy 1, 5.1 mi E of its western jct with Hwy 290, 17 May 1975, *Bierner 51182* (TEX). Goliad Co.: Mar 1927, *Williams 8* (TEX). Gonzales Co.: 1 May 1935, *Le Sueur s.n.* (TEX). Grayson Co.: 5 mi ESE of Sherman, 0.5 mi S of Hwy 82, 8 May 1983, *Nee & Diggs 27191* (TEX). Grimes Co.: 2 mi SW of Anderson, $2n = 15II$, 9 May 1965, *Strother 224* (TEX). Hamilton Co.: 1.5 mi N of Fairy, 4 May 1970, *Stanford 3657* (OKLA). Hardeman Co.: Copper Breaks State Park, along equestrian trail, ca 300–500 ft W of parking area, 435 m, 26 Apr 1995, *Carr 14530* (TEX). Harris Co.: Huffman Rd, Houston NE 20 mi, 6 Mar 1943, *Boon 96* (TEX). Hays Co.: 5 mi S of Wimberly on Hwy 12, $2n = 15II$, 16 Aug 1965, *Strother 489* (TEX). Jeff Davis Co.: Upper slopes of Mt. Locke of Davis Mts., just below McDonald Observatory, 25 Jul 1969, *Marcks & Marcks 1322* (LL); 5 mi SE of Valentine, $n = 15$, 18 Apr 1962, *Turner 4737* (TEX). Johnson Co.: Hwy 67, S outskirts of Alvarado, 14 Apr 1957, *Chambers 1114* (LL). Kaufman Co.: Terrell, 8 May 1953, *Reed 1445* (LL). Kendall Co.: Hwy 473, 3.4 mi E of Hwy 1376, 24 May 1965, *Flyr 497* (NEB). Kerr Co.: Hwy 41, 1.4 mi NE of Hwy 83 (jct in Garven), 16 Apr 1988, *Bierner 88-51* (TEX). Kimble Co.: 21 mi SE of Junction, 13 May 1947, *McVaugh 8300* (OKLA, TEX). King Co.: 0.5 mi E of Guthrie, 6 May 1965, *Tully 13* (OKL). Kinney Co.: Ca 4 mi NE of Brackettville, $2n = 15II$, 15 May 1965, *Strother 270* (TEX). Kleberg Co.: Kingsville, Spring 1940, *Sinclair s.n.* (TEX). Lamar Co.: Hwy 2122, ca 3 mi from jct Hwy 1506 and ca 2 mi from jct Hwy 137, on W side of valley of Maxwell Creek, 24 Mar 1987, *Orzell & Bridges 4888* (TEX). LaSalle Co.: 3 mi S of Dilley, 26 Feb 1944, *Painter & Barkley 14313* (KSC, TEX UTC). Leon Co.: Top of the Marquez salt dome, 2 Jun 1954, *Tharp et al. 54983* (OKLA, TEX). Limestone Co.: Massey Farms, 6.25 mi SW of Ben Hur, 22 Apr 1967, *Massey 1552* (OKL). McLennan Co.: 2 mi W of Eddy, 8 May 1948, *Smith 1157* (TEX). McMullen Co.: 2 km al S del Rio Frio, 8

Apr 1989, *Hernandez 2327* (TEX). Medina Co.: Hwy 81, 1 mi S of Devine, 17 Mar 1963, *Sanchez 67* (TEX). Menard Co.: Menard, 28 Apr 1933, *Mahony s.n.* (TEX). Midland Co.: S of Midland on Hwy 349, 6–12 mi S of jct with I-20, 4 May 1992, *Nesom 7327* (TEX). Navarro Co.: Frost, May 1933, *Mitcham 35* (TEX). Nueces Co.: Mar 1923, *Stiles s.n.* (TEX). Palo Pinto Co.: Hwy 180, 1.5 mi E of the E jct with Hwy 4 (jct in Palo Pinto), 10 Apr 1988, *Biernner 88-9* (TEX). Parker Co.: Weatherford, 27 May 1902, *Tracy 7905* (NEB, TEX). Pecos Co.: Mesa tops and occasionally in valleys, 6 Jul 1943, *Tharp 43-972* (MONTU, OKLA, TEX). Presidio Co.: 20 mi W of Marfa, 1400 m, 2 May 1947, *Warnock 5297* (TEX). Randall Co.: 5 mi E of Canyon near jct of Amarillo and Palo Duro Canyon Hwys, 23 Apr 1983, *Higgins 13108* (UT). Real Co.: Hwy 41, 13.4 mi W of Hwy 83 (jct in NE Real County), 16 Apr 1988, *Biernner 88-49* (TEX). Refugio Co.: Hwy 2441, ca 4 mi NW of Woodsboro, 7 May 1978, *Hill 7038* (TEX). Robertson Co.: Ca 1 mi S of Wheelock, 16 Apr 1978, *Fryxell 2974* (TEX). San Patricio Co.: Lake Corpus Christi State Park, 7 May 1959, *Traverse 1293* (TEX). San Saba Co.: Hwy 16, 2.9 mi N of Hwy 501 (jct in Cherokee), 8 Apr 1988, *Biernner 88-2* (TEX). Schleicher Co.: Southmost part of county along Hwy 864 where it crosses into Sutton Co., 1 Jun 2000, *Turner 20-304* (TEX). Shackelford Co.: Hwy 351, ca 6 mi NE of the Jones County line, 20 Apr 1963, *Henderson 63-433* (TEX). Starr Co.: N of El Sauz, 22 Dec 1967, *Wood 852* (TEX). Sterling Co.: N of Sterling City, 19 May 1899, *Bray 388* (TEX). Sutton Co.: 1 mi W of Sonora, 19 Jun 1961, *Johnston 6403* (LL). Tarrant Co.: On dry waste ground, 15 May 1922, *Ruth 62* (KSC). Terrell Co.: Sanderson, 11 Mar 1919, *Hanson s.n.* (KSC, RM, TEX). Travis Co.: NW Austin, W of intersection of W Duval Rd and W Cow Path, W of Hwy 183 ca 2 mi N of Loop 360, 23 Apr 1983, *Ertter 4753* (TEX). Trinity Co.: 1 mi SW of Trinity, 12 Apr 1958, *Turner 4389* (TEX). Uvalde Co.: Hwy 83, 15.4 mi N of

Uvalde, 2n = 14II, 27 Mar 1972, *Urbatsch 939.5* (LL). Val Verde Co.: Hwy 1024 to Pandale from Comstock, ca 19 mi N of Hwy 90, 14 Mar 1985, *Ertter & Bear 5607* (RM, TEX); 10–12 mi N of Del Rio toward Alta, 22 Jun 1957, *Warnock 15041* (LL). Van Zandt Co.: 3 mi E of Wills Point, 4 May 1945, *Lundell & Lundell 13739* (LL). Victoria Co.: Hwy 57, 10.5 mi NE of Goliad, 17 May 1972, *Biernner 359* (TEX). Walker Co.: Hwy 980, 6.5–7.5 mi NE of Huntsville, 15 Apr 1966, *Correll 32454* (LL). Ward Co.: 2 mi W of Pyote near old Hwy 80, 16 Apr 1970, *Powell et al. 1872* (TEX). Webb Co.: Apache Ranch, ca 2 mi above mouth of Espada Creek, on Rio Grande, ca 40 (airline) mi SW of Catarina, 6 Mar 1949, *Blair et al. 48-493* (TEX). Wichita Co.: Red River above Burkburnett, 21 Jul 1921, *Tharp 523* (TEX). Wise Co.: 5 mi E of Decatur, 1 Jun 1957, *Correll 16509* (LL). Zapata Co.: Upper part of county, 22 Mar 1933, *Clover 692* (TEX).

5b. *TETRANEURIS LINEARIFOLIA* (Hook.) Greene var. *ARENICOLA* Bierner.

Tetranneuris linearifolia (Hook.) Greene var. *arenicola* Bierner, *Sida* 15: 237. 1992. TYPE: UNITED STATES. Texas. Brooks Co.: "Hwy 3066, 14.3 mi W of Hwy 281 (jct S of Falfurrias)" (protologue and holotype label), 20 Mar 1991, *M. W. Bierner 91-13* (HOLOTYPE: TEX!; ISOTYPES: NY!, US!).

STEMS (1–)4–10, erect or \pm decumbent, unbranched or branched distally, 20–50 cm, densely pubescent. LEAVES usually densely pubescent, sparsely to moderately dotted with impressed glands, sessile glands sometimes present; basal blades usually spatulate in outline, usually with 2–6 lateral teeth or lobes, bases densely woolly or long-pubescent; proximal cauline blades usually oblanceolate in outline, usually with 2(–6) lateral teeth or lobes; mid blades usually oblanceolate in outline, (2.5–)3.9–9.5(–16) mm wide, entire or with 2 lateral teeth or

lobes; distal blades usually narrowly oblanceolate, usually entire or, sometimes, with 1–2 lateral teeth or lobes. HEADS 8–50 per plant, borne singly or in corymbiform arrays. PEDUNCLES (10–)13.2–22.4(–29) cm, densely pubescent proximally, very densely pubescent distally. INVOLUCRES 8–10 × 12–15 mm. PHYLLARIES: outer phyllaries 13–21, oblanceolate to lanceolate, (3–)3.9–4.9(–5.5) × (0.5–)0.7–1.1(–1.4) mm, margins usually not scarious, abaxial faces densely pubescent, eglandular or sparsely dotted with sessile glands; mid phyllaries (2.5–)3.5–4.2(–5) × 0.9–1.5 mm, margins often scarious, abaxial faces moderately to densely pubescent, eglandular or sparsely dotted with sessile glands; inner phyllaries 3–4 × 0.8–1.3 mm, abaxial faces moderately to densely pubescent. RAY FLORETS 14–25; corollas (9–)10.4–14.4(–16.8) × (2.8–)3.5–5.5(–7.1) mm. DISC FLORETS 75–200+; corollas 2.1–3 × 0.5–1 mm, glabrous proximally, sparsely to moderately pubescent distally. CYPSELAE 1.9–2.6 × 0.5–0.9 mm, surfaces white, moderately dotted with sessile and impressed glands; pappi 5–8, obovate scales, not aristate, 1–1.7 × 0.5–1 mm.

CHROMOSOME NUMBER: $2n = 30$.

DISTRIBUTION (Fig. 5) AND HABITAT: South Texas in the vicinity of Brooks, Hidalgo, Jim Hogg, and Zapata counties. Growing in sand at roadsides and in pastures, 50–170 m.

FLOWERING AND FRUITING: February through June (also December), mainly March and April.

REPRESENTATIVE SPECIMENS: **UNITED STATES.** **Texas.** Brooks Co.: Hwy 281, 10.7 mi S of Hwy 285 (jct in Falfurrias), $2n = 15II$, 15 Apr 1988, *Bierner 88-35* (SWT, TEX); Hwy 285, 5.2 mi E of Hwy 1329 (jct ca 9 mi W of Falfurrias), $2n = 15II$, 20 Mar 1991, *Bierner 91-12* (SWT, TEX). Hidalgo Co.: Hwy 490, 5.7 mi W of Hwy 281, 20 Mar 1991, *Bierner 91-14* (SWT, TEX). Jim Hogg Co.: Hwy 285, 5 mi E of Hebbbronville, *Fowler & Vergara 70* (TEX). Zapata

Co.: 5.5 mi NE of San Ygnacio on rd to Aguilares, 16 Mar 1966, *Correll 32248* (LL).

6. *TETRANEURIS SCAPOSA* (DC.) Greene, *Pittonia* 3: 266. 1898.

PERENNIALS. CAUDICES often highly branched, not thickened distally. AERIAL STEMS 1–50, erect, sometimes branched near bases, sometimes densely woolly between proximal leaves. LEAVES all basal-proximal, new leaves not tightly clustered, arising at various levels near bases of stems, blades spatulate to oblanceolate to linear-oblanceolate to linear, entire or, often, with 2 lateral teeth or lobes, sparsely to densely pubescent, moderately to densely dotted with impressed glands, bases sparsely pubescent to densely woolly or long-pubescent, bases of proximal leaves usually expanded, not necessarily clasping. HEADS 1–50 per plant, radiate, borne singly or in fastigiate arrays. PEDUNCLES green throughout to purple-red-tinted throughout, 12–40 cm, moderately to densely pubescent, sparsely to densely dotted with sessile glands. INVOLUCRES 5–10 × 7–12 mm. PHYLLARIES: outer phyllaries 8–16, often purple-red-tinted on apices and margins, sometimes purple-red-tinted throughout, obovate to oblanceolate to lanceolate to linear-lanceolate, 3.8–6.6 × 0.7–2.2 mm, margins sometimes to often slightly scarious, abaxial faces moderately to densely pubescent, sparsely to densely dotted with sessile and/or impressed glands; mid phyllaries sometimes to often purple-red-tinted on apices and margins, obovate to oblanceolate to lanceolate, 3.2–6.5 × 0.7–1.8 mm, margins scarious, abaxial faces moderately to densely pubescent, sparsely to moderately to, rarely, densely dotted with sessile glands; inner phyllaries sometimes purple-red-tinted on apices, 2.5–5.2 × 0.7–1.8 mm, abaxial faces sparsely to moderately pubescent, eglandular or sparsely to moderately dotted with sessile glands. RAY FLORETS 12–26; corollas 7.4–22 × 2.3–8 mm, abaxial faces gla-

brous or sparsely to moderately pubescent, sparsely to moderately dotted with sessile glands. DISC FLORETS 25–180+; corollas yellow, $2.5\text{--}3.5 \times 0.7\text{--}1$ mm, glabrous or sparsely to moderately pubescent, sparsely to moderately dotted with sessile glands. CYPSELAE $2\text{--}3 \times 0.7\text{--}1$ mm, surfaces white, sparsely to densely pubescent, eglandular or sparsely dotted with sessile glands; pappi 5–7, obovate- to oblanceolate-aristate scales, $1.6\text{--}2.3 \times 0.6\text{--}1$ mm.

Tetraneris scaposa var. *scaposa* and *T. acaulis* var. *acaulis* overlap in distribution over a wide geographic area (Fig. 2 and 6), but they do not seem to grow together often. The junior author has observed intermixed populations in Palo Duro Canyon, south of Amarillo, Texas, including putative hybrids or hybrid derivatives (Turner 4847, TEX), and the senior author has observed intermixed populations in Torrance County, New Mexico, (Bierner 89-28 and 89-29, TEX), with no evidence of hybridization. Our general impression is that the two taxa are genetically well separated from one another. Past hybridization may account for the populations of *T. acaulis* var. *acaulis* in Colorado and Wyoming that have more glandular and/or less pubescent leaves.

Tetraneris scaposa, like *T. acaulis*, is highly variable. When originally described, Candolle noted the leaves to be either entire or somewhat pinnately lobed. The latter condition occurs but rarely in *T. scaposa* var. *scaposa*, being more common in the southern portion of its distribution. Vestiture also varies greatly, some plants glabrous, others quite pubescent, even in the same population. Shinnery applied the varietal name *villosa* to plants of westernmost Texas that tend to be somewhat more villose than ones from central Texas; such plants otherwise seem to differ but little from *T. scaposa* var. *scaposa*. Many floristic works (e.g., Barkley, 1986) have applied the varietal name *glabra* to forms with glabrous leaves; the glabrous plants seem to have little populational or biological valid-

ity and seem best treated as but glabrous forms of a variable species. Varietal names, most notably *linearis*, *stenophylla*, and *fastigiata*, have been applied to plants with linear-lanceolate to linear leaves and highly branched caudices. Such plants are widespread in the more northern part of the range of *T. scaposa* var. *scaposa* from New Mexico to Kansas and Nebraska; plants with very narrow leaves and highly branched caudices can also be found throughout the central and southern parts of the range.

Variation in *Tetraneris scaposa* is especially complex in Mexico. Populations centered in Tamaulipan scrublands (500–900 m) of northcentral Nuevo León and adjacent Tamaulipas are distinguished by their short, broad, frequently lobed leaves, broad heads (3–5 cm across the extended rays), and tetraploid condition ($2n = 30$ pairs, Whalen 325, LL). The populations concerned (8 collections, LL, TEX) stand somewhat between *T. scaposa* var. *argyrocaulon* and *T. turneri*, the former a diploid and the latter a hexaploid.

Another unusual group of variant collections occurs at higher elevations (1500–2000 m) in the vicinity of Saltillo, Coahuila, and probably closely adjacent Nuevo León. All (representing 10 populations) have eglandular or very sparsely glandular leaves and are otherwise rather typical of *Tetraneris scaposa* var. *scaposa*. Occasional specimens from that area may show purplish disc corollas (Seigler DS-9308, LL), as well as weakly pubescent cypselae (Hinton 22775, TEX).

Tetraneris scaposa var. *argyrocaulon* is consistently distinguished from *T. scaposa* var. *scaposa* by its spaced-out basal-proximal leaves and densely woolly lower stems. As shown in Fig. 6, *T. scaposa* var. *argyrocaulon* has a distinctive distribution, although it appears to intergrade to the south into *T. scaposa* var. *scaposa*. In describing *T. scaposa* var. *argyrocaulon*, Parker (1970) thought the linear-lanceolate leaves might further distinguish it from *T. scaposa* var.

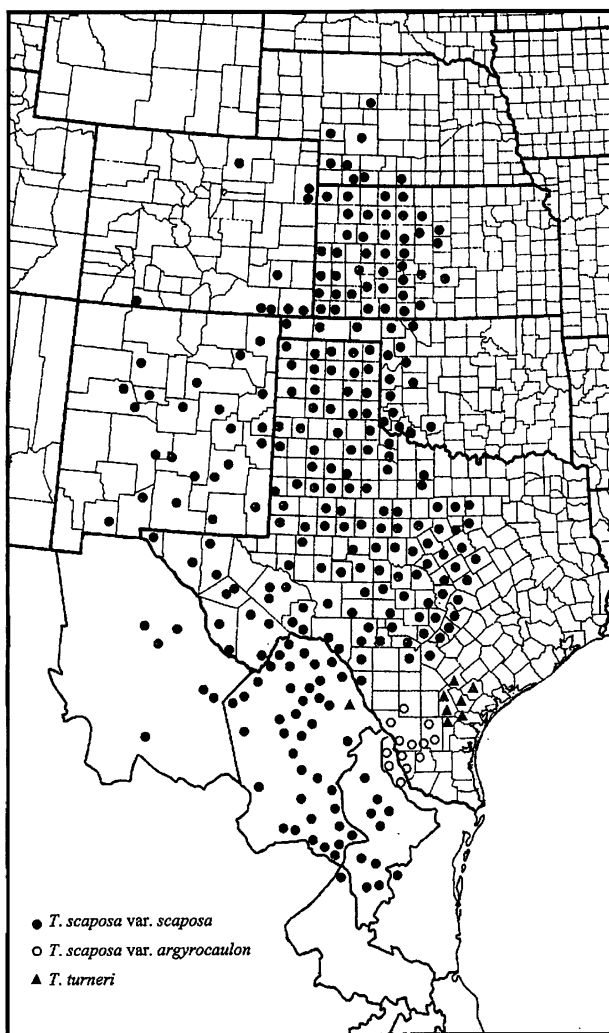


FIG. 6. Distribution of *Tetraneuris scaposa* var. *scaposa*, *T. scaposa* var. *argyrocaulon*, and *T. turneri*.

scaposa; additional material, assembled since her study, shows the leaves of the two taxa to be essentially the same, both having a wide variety of sizes and shapes (*T. scaposa* var. *argyrocaulon* more often possesses lobed leaves).

Oklahoma, eastern Colorado, western Kansas, and southwestern Nebraska

. 6a. *T. scaposa* var. *scaposa*

1. Stems densely woolly between proximal leaves; leaves not close together, internodes distinct; south Texas and adjacent Mexico

. 6b. *T. scaposa* var. *argyrocaulon*

KEY TO THE VARIETIES

1. Stems not densely woolly between proximal leaves; leaves close together, distinct internodes not obvious; northeastern Mexico through central, west, and north Texas to New Mexico, western

6a. *TETRANEURIS SCAPOSA* (DC.) GREENE var. *SCAPOSA*.

Cephalophora scaposa DC. in A. P. de Candolle and A. L. P. de Candolle, Prodr. 5: 663. 1836. TYPE: UNITED STATES. Tex-

as. Bexar Co.(?): "in Mexicanae prov. Texas district. orientalibus" (protologue), Nov–Dec 1828, *J. L. Berlandier* pl. exsic. 1882 (LECTOTYPE here designated: G-DC!, photograph GH!, microfiche TEX!; ISOLECTOTYPES: BM!, GH!, US-63712!; possible ISOLECTOTYPE: US-2515374!). Candolle cited two sheets in his protologue, *Berlandier* 1867 and 1882, both mounted on the same sheet (1867 to the left, which is devoid of a head; 1882 to the right, which possesses a head). We have selected 1882 as the lectotype because most of Candolle's description apparently came from that plant. *Tetraneuris scaposa* is exceedingly common along the Edwards Plateau escarpment of southcentral Texas, and it is likely that Berlandier first collected the plant concerned in this region, perhaps in northern Bexar County.

Actinella scaposa (DC.) Nutt., Trans. Amer. Philos. Soc. 7: 379. 1841.

Actinea scaposa (DC.) Kuntze, Revis. Gen. Pl. 1: 303. 1891.

Ptilepida scaposa (DC.) Britton, Mem. Torrey Bot. Club 5: 340. 1894.

Tetraneuris scaposa (DC.) Greene, Pittonia 3: 266. 1898.

Picradenia scaposa (DC.) Britton in N. L. Britton and A. Brown, Ill. Fl. N. U.S. 3: 449. 1898.

Hymenoxys scaposa (DC.) K. L. Parker, Madroño 10: 159. 1950.

Actinella glabra Nutt., Trans. Amer. Philos. Soc. 7: 379. 1841. TYPE: UNITED STATES. Missouri. Jackson Co.(?): "Missouri (near the Shawnee villages.)" (protologue), "Shawnee villages, Missouri" (holotype label), *T. Nuttall* s.n. (HOLOTYPE: BM!). Original material was not located at PH. Not *Actinella scaposa* var. *glabra* A. Gray (= *Tetraneuris herbacea* Greene).

Actinella acaulis (Pursh) Nutt. var. *glabra* (Nutt.) A. Gray, Proc. Amer. Acad. Arts 19: 32. 1883.

Tetraneuris glabra (Nutt.) Greene, Pittonia 3: 268. 1898.

Hymenoxys glabra (Nutt.) Shinnery, Field & Lab. 19: 80. 1951.

Actinella scaposa (DC.) Nutt. β. *linearis* Nutt., Trans. Amer. Philos. Soc. 7: 379. 1841. TYPE: UNITED STATES. "Texas" (protologue), without date, *J. L. Riddell* s.n. (LECTOTYPE here designated: NY-00149934—as database image!). Original material was not located at PH.

Tetraneuris linearis (Nutt.) Greene, Pittonia 3: 267. 1898.

Actinella linearis (Nutt.) A. Nelson, New Man. Centr. Rocky Mts. 560. 1909.

Actinea scaposa (DC.) Kuntze var. *linearis* (Nutt.) B. L. Rob., Proc. Amer. Acad. Arts 49: 506. 1913.

Actinea linearis (Nutt.) A. Nelson, Univ. Wyoming Publ. Sci., Bot. 1: 61. 1924.

Hymenoxys scaposa (DC.) K. L. Parker var. *linearis* (Nutt.) K. L. Parker, Madroño 10: 159. 1950.

Tetraneuris scaposa (DC.) Greene var. *linearis* (Nutt.) K. L. Parker, Phytologia 45: 467. 1980.

Gaillardia roemeriana Scheele, Linnaea 22: 161. 1849. TYPE: UNITED STATES. Texas. Comal Co.: "Prope Neubraunfels" (protologue), 1845–1847, *F. Roemer* s.n. (HOLOTYPE: LZ destroyed). NEOTYPE here designated: UNITED STATES. Texas. Comal Co.: Old Bear Creek Rd near jct Rt. 2722, 0.2 mi N of Rt. 46 ca 3 mi NW of New Braunfels; roadside vegetation, shallow soil on limestone; cedar-oak woodland, ca 1000 ft. Common, scape, rays and disk yellow, 22 Mar 1987, *B. Ertter & L. Woodruff* 6755 (TEX!).

Actinella scaposa (DC.) Nutt. var. *mutica* A. Gray, Mem. Amer. Acad. Arts (Series 2) 4: 101. 1849. TYPE: UNITED STATES. New Mexico. San Miguel Co.: "Woodlands from Pecos to San Miguel" (protologue and MO isotype, latter reads "the Pecos"), 11 Aug 1847, *A. Fendler*

466 (HOLOTYPE: GH!; ISOTYPES: BM!, MO-208169!).

Actinella lanuginosa Buckley, Proc. Acad. Nat. Sci. Philadelphia 1861: 459. 1862. TYPE: UNITED STATES. Texas. Burnet Co.: "Prairies, Burnet County" (protologue), April (HOLOTYPE: PH!).

Tetraneuris angustata [as *augustata*] Greene, Pittonia 3: 267. 1898. TYPE: MEXICO. Chihuahua. "Santa Eulalia Mountains" (lectotype label), 15 Nov 1886, C. G. Pringle 953 (LECTOTYPE here designated NY!; ISOLECTOTYPES: MO-208170!, MO-208173!, UC-89938!). In his protologue, Greene did not cite a collector; he listed the number 953 [of Pringle]. Original material was not located at NDG.

Tetraneuris fastigiata Greene, Pittonia 3: 268. 1898. TYPE: UNITED STATES. Kansas. Hamilton Co.: "Dry hills ... Coolidge" (holotype label), 22 Aug 1890, B. B. Smyth 206 (HOLOTYPE: NY!; probable ISOTYPE: US-47636!).

Actinella fastigiata (Greene) A. Nelson, New Man. Centr. Rocky Mts. 560. 1909.

Tetraneuris stenophylla Rydb. in N. L. Britton, Man. Fl. N. U.S. 1009. 1901. TYPE: UNITED STATES. Kansas. Ford Co.: "Ford Co. Kans." (holotype label), May 1891, L. D. Ellis s.n. (HOLOTYPE: NY!; probable ISOTYPE: MO-208198!).

Tetraneuris angustifolia Rydb., Bull. Torrey Bot. Club 32: 128. 1905. TYPE: UNITED STATES. New Mexico. Lincoln Co.: "White Mountains" (protologue and holotype label), 21 Aug 1897, E. O. Wooton 374 (HOLOTYPE: NY!; ISOTYPES: GH!, K!, MO-208140!, NDG-061656!, NDG-061668!, NY!, RM-17852!, UC-134200!, US-330599!).

Actinea angustifolia (Rydb.) A. Nelson, Univ. Wyoming Publ. Sci., Bot. 1: 61. 1924.

Actinea scaposa (DC.) Kuntze [var.] *angus-*

tifolia (Rydb.) Kittell, Fl. Ariz. New Mex. 470. 1941.

Hymenoxys scaposa (DC.) K. L. Parker var. *villosa* Shinnars, Field & Lab. 19: 79. 1951. TYPE: UNITED STATES. Texas. Brewster Co.: "just north of campus of Sul Ross State Teachers College, Alpine" (protologue and holotype label), 17 May 1946, V. L. Cory 53129 (HOLOTYPE: BRIT-SMU!).

Tetraneuris scaposa (DC.) Greene var. *villosa* (Shinnars) Shinnars, Spring Fl. Dallas-Ft. Worth Texas 410. 1958.

AERIAL STEMS 1–30(–50), not densely woolly between proximal leaves. LEAVES close together, distinct internodes not obvious, blades spatulate to oblanceolate to linear-oblanceolate to linear, sparsely to densely pubescent, usually densely dotted with impressed glands, bases sparsely pubescent to densely woolly or long-pubescent. HEADS 1–30(–50) per plant. PEDUNCLES 12–40 cm. INVOLUCRES 5–10 × 7–12 mm. PHYLLARIES: outer phyllaries 8–12, often purple-red-tinted on apices and margins, sometimes purple-red-tinted throughout, (4–)4.7–5.5(–6.5) × (0.7–)1–2.2 mm, margins often slightly scarious; mid phyllaries often purple-red-tinted on apices and margins, obovate to oblanceolate, (3.2–)4–5.6 × 0.7–1.8 mm, sparsely to moderately to, rarely, densely dotted with sessile glands; inner phyllaries 3.3–5 × 0.7–1.8 mm, eglandular or sparsely to moderately dotted with sessile glands. RAY FLORETS 13–25; corollas 9.5–22 × 2.3–6.3(–8) mm. DISC FLORETS (25–)70–180+; corollas 2.8–3.5 × 0.7–1 mm, sparsely to moderately pubescent. CYPSELAE 2.3–3 × 0.7–1 mm, sparsely to moderately pubescent; pappus scales 5–6, 1.6–2.3 × 0.7–1 mm.

CHROMOSOME NUMBERS: $2n = 30, 60$.

DISTRIBUTION (Fig. 6) AND HABITAT: Northeastern Mexico through central, west, and north Texas to New Mexico, western Oklahoma, eastern Colorado, western Kansas, and southwestern Nebraska. Growing at

roadsides, on hillsides, in pastures and other open areas, and at edges of woods, 300–2380 m.

FLOWERING AND FRUITING: Throughout the year, mainly March through June.

REPRESENTATIVE SPECIMENS: **MEXICO. Chihuahua.** N of Chihuahua, 10–19 Oct 1935, *LeSueur* 59 (LL); Slopes of Sierra de la Cueva 10.7 km SW of Coyame on the Chihuahua Hwy, 1250 m, 22 Oct 1972, *Wendt et al.* 9828 (LL); 4 mi SE of Organos, 5–6 Oct 1941, *Stewart & Johnston* 2039 (LL); Vicinity of Fierro, 8–9 Jul 1941, *Stewart* 758 (LL); Sierra Rica, 1800 m, 25 Jul 1997, *Estrada* 7532 (TEX); 8 mi N of Parral on Hwy 45, 1890 m, 4 Sep 1960, *Ellison* 133 (TEX). **Coahuila.** 1.5 mi S of Muralla, 2n = 30II, 5 Aug 1965, *Strother* 485 (OKL, TEX); ca 20 mi N of Sabinas, 23 Oct 1966, *Strother* 582 (TEX); ca 24 km N of Castillón, 13 Jun 1941, *Stewart* 493 (LL); 22 km ESE of La Cuesta del Plomo on the Múzquiz-Boquillas Hwy near the intersection of the Hwy from V. Acuña, 1000 m, 7 Jun 1972, *Chiang et al.* 7551J (LL); Aguaje El Pajarito, a spring in N part of Puerto Colorado ("El Sombrero"), a pass between Sa. de la Fragua to E and Sa. Colorada to W, 1360 m, 19 Mar 1977, *Wendt et al.* 1958 (LL); ca 12.5 air mi ESE of Boquillas, 6 mi W of Rancho El Jardín towards Mina Popo, 1650 m, 27 Jul 1973, *Henrickson* 11464 (LL); ca 35 air km N of Cuatro Ciénegas, 1435 m, 4 Aug 1973, *Henrickson & Wendt* 11866 (LL); Múzquiz, 1935, *Marsh* 210 (TEX); Mina El Aguirreño, N side of Sierra de la Paila, 1700–2200 m, 5 Jul 1973, *Johnston et al.* 11688 (LL); Sierra de La Rata, 14 Mar 1973, *Johnston et al.* 10161G (LL); Municipio de Múzquiz, Sierra Hermosa, Rancho La Morada of Mr. and Mrs. Aldan McKellar, ca 100 mi NW of Múzquiz, 1400 m, 12 May 1968, *Latorre s.n.* (TEX); Sierra de Parras, foot trail from W part of town of Parras up to highest part of the sierra, 14 May 1973, *Johnston et al.* 10997 (LL); Sierra del Pino, vicinity of La Noria, 20–26 Aug 1940, *Johnston & Muller* 678 (LL); Cañón

del Cuervo Chico ca 16 km N of Cuesta Zozaya, 27 Aug 1941, *Johnston* 8528 (LL); ca 78 air mi S of Big Bend Nat'l Park basin, in S central Valle de Pinos (Vacas) of Sierra Santa Fé del Pino, 1600 m, 8 Aug 1976, *Henrickson & Prigge* 15103 (LL); Sierra de Parras, N slope and top, approached from Ejido Cerro Colorado ca 10 km W of Parras de la Fuente, 4 Nov 1972, *Chiang et al.* 10077 (LL); 16 km due N of Ejido Piedritas, E face of the sierra which trends SSE from Cañón de San Vicente, 1050–1100 m, 17 Sep 1972, *Chiang et al.* 9366B (LL); Derramadero, on rd to Jame, 22 Jul 1981, *Poole et al.* 2355 (TEX); Sierra de la Madera, vicinity of "La Cueva" in Corte Blanco fork of Charretera Canyon, 11–15 Sep 1941, *Johnston* 9088 (LL); Rancho El Tunal ca 25 km a de Parras de la Fuente, 2050 m, 7 May 1983, *Rodríguez & Hernández* 887 (TEX); ca 54 mi SE of Big Bend Nat'l Park basin in the S end of the Sierra Maderas del Carmen in Cañón del Alamo, 1500–2000 m, 5 Aug 1976, *Henrickson & Prigge* 14948 (LL); Sierra La Madera, lower Cañada Desiderio (7 km W of Cerro de la Madera), 1750 m, 18 Mar 1983, *Thompson et al.* 568 (TEX); Puerta de San Lázaro, Sierra de San Lázaro, 31 Aug 1939, *Muller* 3094 (LL); 1 km N of Rancho de la Gavia on N side of Sierra de la Gavia, 1200 m, 18 Mar 1973, *Johnston et al.* 10277C (LL); ca 30 air mi WNW of Cuatro Ciénegas, Cañón los Pozos, ca 3–4 mi W of Rancho Cerro de la Madera along trail to Cañon Desiderio, 1400 m, 1 May 1977, *Henrickson & Lee* 15944 (TEX); 1 km W of Rancho Lagunitas, ca 900 m, 10 Apr 1976, *Riskind et al.* 1906 (TEX); Above Chorro de Agua, Hwy 75, 2 May 1959, *Correll & Johnston* 21365 (LL); 2.5 mi W of Mineral Padilla, 16 mi E and 18 mi N of Ocampo, 14 Jun 1956, *Graber* 143 (TEX); Between Melchor Múzquiz and Nacimiento de los Kikapos, 27 Jun 1963, *Latorre* 44 (TEX); Las Vigas, Cañón de la Carera, Sierra de Arteaga, no date, *Villarreal & Carranza* 3788 (TEX); Buenavista, 15 Jul 1975, *Seigler & Holstein* DS-9308 (LL); 7 mi S of Saltillo on Hwy 54, 2n = 15II, 2 Aug 1965, *Strother*

468 (OKL, TEX); 17 mi SE of Saltillo along Hwy 57, 22 Jul 1969, *Bierner & Turner* 85 (TEX); 24 km al S de Saltillo, 1920 m, 25 Sep 1978, *García* 696 (TEX); Buenavista, Saltillo, 1800 m, 19 May 1987, *Cabral* 848 (TEX); 1 km N de Estación Carneros, Hwy Saltillo-Concepción del Oro, 7 Jun 1989, *Martínez* 1878 (TEX); Sierra S. J. de los Nuncios, 1540 m, 2 Apr 1993, *Hinton et al.* 22775 (TEX); ca 6 km air W of Saltillo, E extremity of the Sierra de la Vega, 1800–2000 m, 30 Mar 1973, *Johnston et al.* 10499 (LL); ca 130 km NW of Múzquiz on Hwy 2A, 1250 m, 3 Jun 1992, *Nesom & Mayfield* 7384 (TEX); 30 km W of General Cepeda, 1948 m, 31 Mar 1992, *Neff* 92-2-31-2 (TEX). **Nuevo León.** Mts E of Hwy 34, 1.4 km N of jct to Bustamante, dirt rd 16.3 km E of Hwy, ca 1000 m, 15 Mar 1983, *Cowan & Nixon* 3818 (TEX); Mamulique Pass, 20 mi S of Sabinas Hidalgo on rd from Nuevo Laredo to Monterrey, 2n = 30II, 16 Mar 1976, *Whalen* 325 (LL); ca 5 mi S of Sabinas Hidalgo on Hwy 85, 13 Mar 1971, *Sanderson* 199 (TEX); N of Santa Rita, 2300 m, 14 May 1981, *Hinton* 18252 (TEX); Dr. Arroyo, 25 Nov 1967, *Hernández* 455 (LL); Hwy 51, 4.0 mi S of Pablillo, 2225 m, 26 Oct 1981, *Dorr et al.* 2115 (TEX); 10.5 km W of Tokio on San Roberto-Galeana Hwy, 2100 m, 17 May 1973, *Johnston et al.* 11059 (LL); 26.1 mi NE of Dr. Arroyo, 10 mi SW of La Escondida along Hwy 29, 1800 m, 9 Sep 1971, *Henrickson* 6596 (LL); 4 mi N of La Ascensión on Hwy 68, 15 Jul 1971, *Sanderson* 269 (TEX). **San Luis Potosí.** Charcas, Jul–Aug 1934, *Lundell* 5364 (TEX). **Tamaulipas.** Ca 5 mi S of San Carlos, N side of Bufa El Diente, 1080–1200 m, 15 Apr 1988, *Nesom et al.* 6304 (TEX). **Zacatecas.** San Juan del Alamo, 7 km de Villa Insurgentes, 19 km E of Sombrerete, 2380 m, 6 Nov 1978, *García & Delgado* 870 (TEX). **UNITED STATES. Colorado.** Archuleta Co.: Arboles, 31 May 1906, *Ferril s.n.* (CS). Baca Co.: 23 mi S of Pritchett, 1370 m, 4 May 1947, *Weber* 3285 (COLO, TEX, UTC); Spring Canyon, breaks of Cimarron River 2 mi S of Midway, 5 May 1949, *Weber*

4596 (COLO, OKL, TEX, UTC). Bent Co.: Rule Creek, 22 May 1913, *Osterhout* 4870 (COLO). Las Animas Co.: Mesa de Maya Region, Jesus Mesa, 1585 m, 18 May 1993, *Clark et al.* 3 (COLO); 12 mi W of Kenton, OK, 25 Apr 1948, *Rogers* 5640 (COLO). Weld Co.: Greeley Waterworks, 19 Aug 1934, *Smith s.n.* (CS). Yuma Co.: Bonny Prairie State Natural Area, Bonny Lake State Park, near N Cove of reservoir, 27 Jun 1999, *Lederer & Murphy* 99-58 (COLO); Along Arikaree River 1.5 mi NE of Beecher Island Nat'l Historical Monument, 10 Jun 1988, *Neely* 5104 (TEX). **Kansas.** Barber Co.: 2 mi S of Sun City, 28 May 1967, *Stephens* 11168 (OKLA). Cheyenne Co.: On plains, 17 May 1932, *Jacobs s.n.* (KSC). Clark Co.: N rim of Little Basin and St. Jacob's Well, 17 Jun 1957, *Hulbert* 2762 (KSC). Comanche Co.: 17 Aug 1896, *Hitchcock s.n.* (KSC). Decatur Co.: 27 Jun 1897, *Hitchcock s.n.* (KSC). Edwards Co.: May 1932, *Finch* 289 (KSC). Ellis Co.: Hays, 30 May 1931, *Savage s.n.* (LL). Ellsworth Co.: Wilson, 1928, *Weber* 34 (KSC). Finney Co.: 20 mi NE of Garden City, 18 May 1937, *Tolstead s.n.* (NEB). Ford Co.: Dodge City, 1891, *Ellis s.n.* (KSC). Gove Co.: Monument Rocks area, 10 May 1939, *Gates* 20954 (KSC). Graham Co.: 20 Jun 1897, *Hitchcock s.n.* (KSC). Grant Co.: Ulysses, 24 Jun 1893, *Thompson* 11 (KSC). Gray Co.: 1 Sep 1897, *Hitchcock s.n.* (KSC). Greely Co.: 14 mi N of Tribune, 5 Jun 1971, *Stephens* 47975 (OKL). Hamilton Co.: Syracuse, 12 May 1951, *Duvall s.n.* (KSC). Haskell Co.: Aug 1895, *Hitchcock s.n.* (KSC). Hodgeman Co.: Aug 1895, *Hitchcock s.n.* (KSC). Kearney Co.: 29 Aug 1897, *Hitchcock s.n.* (KSC). Kiowa Co.: Greensburg, 28 Jun 1888, *Kellerman s.n.* (KSC). Lane Co.: Aug 1895, *Hitchcock s.n.* (KSC). Lincoln Co.: 5 mi S, 3.5 mi E Sylvan Grove, 18 May 1969, *Stephens* 30695 (OKLA). Logan Co.: 10 mi SE of Russell Springs, 20 Jun 1957, *Hulbert* 2958 (KSC). Meade Co.: 1 Sep 1897, *Hitchcock s.n.* (KSC). Morton Co.: Aug 1895, *Hitchcock s.n.* (KSC). Ness Co.: Aug 1895, *Hitchcock s.n.* (KSC). Norton Co.: 1 mi NE of

Clayton, Nov 1952, *Keen s.n.* (KSC). Osborne Co.: Covert, 13 May 1933, *Neher 484* (KSC). Pawnee Co.: Hwy 156, 0.7 mi NE of the Hodgeman County line, 18 Jun 1981, *Freeman 1016* (KSC). Phillips Co.: Nov 1899, *Baker s.n.* (KSC). Rawlins Co.: Atwood, 2 Sep 1931, *Gates 16865* (KSC). Reno Co.: Spring 1937, *Brownlee s.n.* (KSC). Rooks Co.: Hwy 24, 1.5 mi W of Stockton, 15 May 1983, *Freeman & Wetter 1760* (KSC). Rush Co.: Aug 1895, *Hitchcock s.n.* (KSC). Russell Co.: 16 mi N of Russell, 8 Jun 1959, *Hulbert 3461* (KSC). Sheridan Co.: 16 Jul 1918, *Ikenberry s.n.* (KSC). Stafford Co.: Prairie near St. John, 31 Aug 1946, *Maupin s.n.* (KSC). Stanton Co.: W central Stanton County near Bear Creek, 19 Jul 1957, *Hulbert 2886* (KSC). Stevens Co.: Aug 1895, *Hitchcock s.n.* (KSC). Thomas Co.: 27 Jun 1897, *Hitchcock s.n.* (KSC). Trego Co.: Jun 1888, *Bodin 1397* (KSC). Wichita Co.: Jul 1895, *Hitchcock s.n.* (KSC). **Nebraska.** Chase Co.: 5.5 mi S of Imperial, 20 Jun 1992, *Rolfmeier 10414* (NEB). Franklin Co.: Franklin, 23 May 1932, *Hapeman s.n.* (UTC). Hayes Co.: E of rd 3 mi N, 1 mi E of Hamlet, 19 Jul 1990, *Rolfmeier 7067* (NEB). Hitchcock Co.: SE corner of county, 9 Aug 1941, *Tolstead 411585* (NEB). Keith Co.: Cedar Point Biological Station, 14 Jun 1983, *Sutherland 5625* (NEB). Lincoln Co.: S of North Platte, 15 May 1949, *Kiener 24531* (NEB). Red Willow Co.: S side of Red Willow Reservoir, 0.25 mi W of dam, 10 mi N, 2 mi W of McCook, 27 Jun 1992, *Rolfmeier 10483* (NEB). Thomas Co.: Halsey, Jul 1912, *Pool s.n.* (NEB). **New Mexico.** Bernalillo Co.: Jemez Mts near the Univ. of New Mexico campus, 30 May 1931, *Castelleo 1183* (RM). Chaves Co.: Roswell, 1785 m, 14 May 1998, *Chauvin 98YC014* (UNM); Hwy 70, 45 mi SW of Elida, 14 May 1988, *Worthington 16548* (RM). Cibola Co.: E of Laguna Pueblo, 28 May 1935, *Nelson & Nelson 2180* (RM, UTC). Curry Co.: W of Clovis, 30 Apr 1960, *Smith s.n.* (OKLA). De Baca Co.: Fort Sumner, 1370 m, 20 Sep 1035, *Nisbet s.n.* (TEX). Doña Ana Co.: Ash Canyon, San Andreas Mts, 1650 m, 10 May

1934, *Parker & Parker 2469* (TEX). Eddy Co.: Sitting Bull Falls Recreation Area, 22 Aug 1998, *Worthington 27897* (TEX, UNM). Guadalupe Co.: 10 mi S of Santa Rosa, 28 Apr 1978, *Sylvester s.n.* (UNM). Harding Co.: Kiowa Grasslands, 1830 m, 18 May 1982, *Fletcher 6028* (UNM). Lea Co.: 13 mi W of Hobbs, 4 mi N of Hwy 180 at Arkansas Junction on Hwy 483, 24 Apr 1992, *Sivinski 1830* (UNM). Lincoln Co.: 5 mi NW of Carrizozo, 1610 m, 26 Apr 1969, *Hutchins 1816* (UNM); Sonoran Hill country 40 mi W of Roswell, 1525 m, $2n = 30II \pm 1$, 10 Jun 1965, *Strother 318* (TEX). Luna Co.: Florida Mts, Mahoney Park, 1540 m, 8 May 1983, *Worthington 10351* (COLO). Otero Co.: S of High Rolls, Sacramento Mts, 2135 m, 16 Jun 1935, *Parker 349* (LL, TEX). Quay Co.: Banks of Canadian River near Logan, 15 May 1952, *Dittmer 9449* (UNM). Roosevelt Co.: ENMU Natural History Preserve, Portales, 1220 m, 8 May 1970, *Secor 5* (TEX). San Miguel Co.: 12 mi S of Las Vegas, 1950 m, 29 Aug 1946, *Parker & McClintock 6493* (COLO, LL, OKLA, RM, UTC). Sandoval Co.: Hwy 44, 40 mi S of Cuba, 1920 m, $2n = 30II$, 25 Jun 1965, *Strother 410* (TEX). Socorro Co.: Dripping Springs House in Helm's Valley, 1800 m, 17 Apr 1996, *Anderson 6783* (TEX). Torrance Co.: Hwy 285, ca 20 mi N of Hwy 60 (jct just W of Encino), 23 May 1989, *Bierner 89-28* (TEX). Union Co.: 10 mi NE of Clayton on Hwy 18, $2n = 15II$, 27 Jun 1965, *Strother 419* (TEX). Valencia Co.: 6 mi E of Cubero, 1740 m, 1 Jul 1934, *Parker & Parker 2815* (TEX). **Oklahoma.** Beaver Co.: 12 mi E of Forgan, 5 May 1969, *Crook 898* (OKL). Beckham Co.: 8 mi N of Sayre on Hwy 283, 18 May 1959, *Wiedeman 149* (OKL). Cimarron Co.: Slopes of Black Mesa, ca 0.5 mi E and 4.0 mi N of Kenton Post Office, 19 Oct 1991, *Thomas 25* (OKLA). Comanche Co.: Wichita Mt Refuge, 16 May 1959, *Crockett 66* (OKL). Custer Co.: 4 mi N and 3 mi W of Foss, 28 May 1939, *Waterfall 1168* (OKLA). Dewey Co.: E edge of Vici, 18 May 1973, *Goodman & Lawson 8292* (OKL). Ellis Co.: Ca 3 mi

E of Hwy 283, and 5.5 mi N of Hwy 51, 19 Jun 1986, *Erteeb* 1608 (OKLA). Greer Co.: S edge of Magnum, 23 May 1948, *Robbins* 3050 (COLO, LL, OKL, RM). Harmon Co.: Ca 4 mi SW of Reed, 23 Apr 1970, *Taylor & Taylor* 10222B (OKL). Harper Co.: Hwy 183, N of Buffalo, 16 Jun 1975, *Bierner* 51304 (TEX). Jackson Co.: 7.8 mi W of the jct of Hwys 62 and 283, 445 m, 19 Apr 1975, *Barber* 654 (OKL, OKLA). Roger Mills Co.: 4.1 mi N of Cheyenne at jct of Hwys 283 and 33, 10 May 1969, *Perino & Perino* 434 (TEX). Texas Co.: Hwy 95 where it crosses Big Goff Creek S of Elkhart, Kansas, 11 May 1974, *Taylor & Taylor* 16178 (OKL). Tillman Co.: 7 mi N of Tipton, 30 Apr 1970, *Black JB-100* (OKL). Wood Co.: 12 mi N of Freedom, 4 mi S of the Kansas line, 7 Jun 1973, *Nighswonger & Shedden* 1154 (OKL). Woodward Co.: 2 mi W, 2 mi S of Woodward, 28 Apr 1979, *Springer* 248 (OKL). **Texas.** Andrews Co.: Ca 13 mi NE of Andrews, Hwy 115, 9 May 1966, *Correll* 32783 (LL). Archer Co.: 4 mi N of Olney, 1 Apr 1966, *Siegler* 883 (OKL, OKLA). Bailey Co.: Just S of Muleshoe, Hwy 214, 28 Oct 1962, *Correll* 26488 (LL). Bandera Co.: Hwy 173, 6.4 mi N of the Bandera-Medina county line, 1.2 mi N of Julian Creek, 18 May 1975, *Bierner* 51195 (TEX). Bell Co.: Morgans Point, Dam Rd, 8.6 mi N of Belton, 19 Mar 1966, *Cope* 10 (TEX). Bexar Co.: Robinson Tuttle Ranch 5 mi NW of San Antonio, 3 May 1948, *Burr* 138 (TEX). Blanco Co.: Hwy 2766, 2.2 mi E of Hwy 281 (jct in Johnson City), 29 Apr 1989, *Bierner* 89-10 (TEX). Borden Co.: 10 mi W of Gail, 28 Mar 1963, *Adams* 8 (OKLA). Bosque Co.: Clifton, 20 Apr 1941, *Leuthold* 12 (COLO). Brewster Co.: Hwy 90, 21.0 mi E of Hwy 385 (Jct just E of Marathon), 9 May 1989, *Bierner* 89-13 (TEX); Hwy 90, 10 mi W of Hwy 385 (jct just E of Marathon), 9 May 1989, *Bierner* 89-14 (TEX); Boquillas Canyon, Big Bend Nat'l Park, 10 Aug 1955, *Warnock* 12895 (LL). Brisco Co.: 5 mi NW of Quitaque, 22 Apr 1962, *Melchert* 173-A (TEX). Brown Co.: Brownwood, 30 Mar 1966, *Zimmerman* 5 (LL). Burnet Co.: Hwy 281, 12.3 mi S of Lampasas, 15 Apr 1957, *Chambers* 1127 (LL). Callahan Co.: Hwy 36, ca 20 mi SE of Abilene, 30 Mar 1963, *Henderson* 63-120 (TEX). Castro Co.: Nazareth, 3 May 1946, *Rachaner* 5 (TEX). Childress Co.: Childress, Apr 1929, *bio class s.n.* (TEX). Coke Co.: Clark Ranch, SW portion of the county, 26 Nov 1994, *Turner* 94-126 (TEX). Coleman Co.: Hwy 84, 7.6 mi NW of Hwy 283 (jct N of Coleman), 10 Apr 1988, *Bierner* 88-15 (TEX). Collingsworth Co.: 12 mi NE of Memphis, 640 m, 21 Apr 1936, *Bennett* 24 (TEX). Comal Co.: Old Bear Creek Rd 2 near jct Rt 2722, 0.2 mi N of Rt 46 ca 3 mi NW of New Braunfels, 22 Mar 1987, *Ertter & Woodruff* 6755 (TEX). Comanche Co.: 1 mi W of Comanche, 26 Jun 1964, *Correll & Hanson* 29903 (LL). Concho Co.: Eden to San Angelo, 1 Sep 1929, *Whitehouse* 7772 (LL). Coryell Co.: 4 mi E of Gatesville, 9 Jul 1965, *Strother* 426 (TEX). Cottle Co.: 12 mi NW of Pakucuh, 29 Apr 1963, *Rowell* 8050 (OKLA). Crane Co.: 3-8 mi S of Crain, 1100 m, 24 May 1957, *Warnock* 14713 (LL). Crockett Co.: 30 mi N of Juno, 690 m, 5 Jun 1957, *Warnock* 15394 (LL). Crosby Co.: 4 mi E of Crosbyton, 24 Apr 1965, *Keeton* 36 (OKLA). Culberson Co.: Ca 3 mi N of Pine Springs, 27 Apr 1961, *Correll & Rollins* 23883 (LL); 7 mi W of Kent, 19 Jun 1963, *Correll & Wasshausen* 27911 (LL). Dallam Co.: 15 mi E of Texline, 3 Jun 1957, *Correll* 16637 (LL). Dickens Co.: Between Spur and Calgary, 28 Apr 1961, *Correll & Rollins* 23938 (LL). Donley Co.: Hwy 287, 5 mi N of Memphis, 2 Jun 1957, *Correll* 16558 (LL). Eastland Co.: Eastland, 2 Apr 1930, *Hall s.n.* (TEX). Edwards Co.: Hwy 41, 0.7 mi E of Hwy 377 (jct NE of Rocksprings), 16 Apr 1988, *Bierner* 88-48 (TEX); 4 mi N of Barksdale on Hwy 55, 15 May 1965, *Strother* 305 (TEX). El Paso Co.: West Well Canyon just up from Four Mile Draw, S Hueco Mts, 20 Aug 1976, *Butterwick & Lamb* 3160 (TEX). Erath Co.: Between Chalk Mt and Stephenville, 21 Jul 1941, *Sanders s.n.* (LL). Foard Co.: 7 mi N of Crowell, 11 Apr 1966, *Turner* 18 (LL). Gains Co.: Ca 3.8 mi S of Sem-

inole along Hwy 181, 16 May 2000, *Turner & Turner 20-264* (TEX). Garza Co.: 2.5 mi of Post, 25 Apr 1966, *Correll 32698* (LL). Gillespie Co.: Hwy 1, 5.1 mi E of its western jct with Hwy 290, 17 May 1975, *Bierner 51183* (TEX). Gray Co.: 8.7 mi W of McLean, 28 May 1964, *Rowell 10139* (OKLA). Hale Co.: 2 mi NE of Hale Corner, 28 Apr 1954, *Shinners 18634* (TEX). Hamilton Co.: Hwy 218, 1.0 mi E of Hwy 2486, W of Hamilton, 8 Apr 1988, *Bierner 88-7* (TEX). Hansford Co.: 1 mi E and 1 mi S of Gruver, 13 May 1955, *Cutter 10* (OKL). Hardeman Co.: 11 mi S of Quanah, 4 Apr 1966, *Turner 4* (LL). Hartley Co.: N side of Rita Blanca Lake, S side of Dalhart, 1195 m, 3 Jun 1991, *Carr 11204* (TEX). Hays Co.: Hwy 12, 10.5 mi SE of Wimberly, 17 May 1975, *Bierner 51177* (TEX). Hemphill Co.: 11 mi NE of Canadian, Jun 1957, *Parsons 5517* (TEX). Howard Co.: Big Spring, 1902, *Tracy 8149* (TEX). Hudspeth Co.: Sierra Diablo, ca 2 mi NW of J. V. McAdoo Ranch headquarters, 23 Apr 1961, *Correll & Rollins 23768* (LL). Hutchinson Co.: Near Stinnett, 21 Apr 1946, *McFarland 56* (OKL, RM, TEX). Irion Co.: Mertzon, 12 Apr 1929, *Cory 809* (LL). Jeff Davis Co.: Hwy 166, 7.8 mi W of Hwy 17 (jct S of Ft. Davis), 24 May 1975, *Bierner 51231* (TEX); Wild Rose Pass, Hwy 17 ca 22 mi S of Balmorhea city limits, 16 May 1989, *Woodruff & Mayfield 295* (TEX). Johnson Co.: Hwy 67, 1 mi S of Cleburne, 14 Apr 1957, *Chambers 1117* (LL). Jones Co.: Hwy 180, 1.6 mi W of Hwy 1226 (jct in Funston), 10 Apr 1988, *Bierner 88-11* (TEX). Kendall Co.: Spanish Pass, 29 Mar 1936, *Cory 18273* (LL). Kent Co.: 27 mi N of Snyder, 13 Jul 1963, *Courtney 137* (OKLA). Kerr Co.: Hwy 41, 1.3 mi NE of Hwy 83 (jct in Garvin), 16 Apr 1988, *Bierner 88-50* (TEX). Kimble Co.: Exit ramp to Hwy 290 from I-10, S side of 290, 13 Jun 1999, *Turner 99-373* (TEX). Kinney Co.: Ca 20 mi NE of Brackettville, $2n = 30 \pm 1$, 15 May 1965, *Strother 296* (COLO, TEX). Knox Co.: 5 mi E of Benjamin, 22 Apr 1962, *Melchert 169-A* (TEX). Lampasas Co.: 7 mi E of Lampasas on Hwy 190, 15 May

1955, *Johnston & McCart 5383* (RM, TEX). Lipscomb Co.: Ca 2 mi W of Darrouzett, 24 May 1961, *Correll 24048* (LL). Llano Co.: Along NE bank of Colorado River at Marble Falls, 31 Mar 1967, *Mears 1412* (TEX). Lubbock Co.: NW of Lubbock, 21 Apr 1930, *Demaree 7527* (TEX). Lynn Co.: 5 mi W of Tahoka, 24 Apr 1966, *Correll & Rollins 32696* (LL). Martin Co.: Campbell Ranch ca 30 mi N of Midland, 855 m, 1 May 1964, *Hodges 3* (NEB). Mason Co.: 10 mi N of Mason, 18 Apr 1940, *Hamby 912* (LL). Maverick Co.: Hwy 277, 14 mi N of Eagle Pass, 21 Mar 1994, *Helmkamp 51-15* (COLO). McCulloch Co.: 2 mi S of Brady, 11 Apr 1949, *Brown s.n.* (TEX). McLennan Co.: N of Lake Waco at gravel pit, Jul 1946, *Smith 13* (TEX). Medina Co.: Ca 12 mi N of Hondo, 28 Oct 1952, *Correll 15219* (LL). Menard Co.: Menard, 29 Apr 1933, *Mahony s.n.* (TEX). Midland Co.: 3 mi E of Midland, 4 Jun 1943, *Cory 42052* (LL). Mills Co.: Hwy 16, 5.2 mi N of the Mills-Comanche county line, 8 Apr 1988, *Bierner 88-6* (TEX). Mitchell Co.: Loraine, Spring 1927, *Finley 6528* (LL). Moore Co.: 7.5 mi S of Dumas, Hwy 287, 1100 m, 28 Apr 1945, *Jespersen & Jespersen 2663* (COLO, NEB, OKL, RM, UTC). Motley Co.: Hwy 70, 12 mi N of Matador, 22 Apr 1962, *Melchert 184* (TEX). Nolan Co.: Sweetwater, 27 Apr 1927, *Stanfield 6526* (TEX). Ochiltree Co.: 12 mi SE of Perryton on Hwy 83, 6 May 1960, *Wallis 8486* (OKLA, TEX). Oldham Co.: 3 mi W of Vega, 1 Jul 1936, *Howard 81* (LL). Palo Pinto Co.: S of Palo Pinto, 5 Jun 1952, *Gentry 1281* (TEX). Parker Co.: Hwy 180, 3.3 mi E of Hwy 113, between Weatherford and Mineral Wells, 10 Apr 1988, *Bierner 88-8* (TEX). Parmer Co.: 7.8 mi NE of Farwell, 30 May 1964, *Rowell 10035* (OKL, OKLA). Pecos Co.: Madera Mts, 25 mi S of Ft. Stockton, 15 Jun 1964, *Correll et al. 29701* (LL); 6.5 mi N of Ft. Stockton, 16 Apr 1941, *Lundell & Lundell 10240* (LL); 41.1 mi E of Ft. Stockton along I-10, 23 Mar 1997, *Turner & Turner 97-41* (TEX). Potter Co.: 20 mi N of Amarillo, 1150 m, 19 Apr 1991, *Simpson 914191*

(TEX). Presidio Co.: Just N of Solitario Peak in the Solitario on the Big Bend Ranch, 9 Jun 1975, *Butterwick & Strong* 785 (TEX); Thomas Ranch, 28 mi S of Marfa, 2 Apr 1929, *Ingram* 96259 (LL). Randall Co.: Hwy 217, 3.1 mi E of Hwy 87, 27 May 1972, *Biernier* 383 (TEX). Reagan Co.: Best, May 1931, *Ferguson s.n.* (TEX). Real Co.: 2–3 mi NE of Camp Wood, 22 Jun 1963, *Correll & Wasshausen* 28009 (LL). Roberts Co.: Miami, 16 Jun 1929, *Tharp* 7145 (LL). Runnels Co.: 5 mi N of Ballinger, 14 Apr 1949, *Warnock* 8385 (TEX). San Saba Co.: 10 mi S of Richland Springs, 26 Mar 1966, *Calhoun* 10 (LL). Schleicher Co.: Ft. McKavett, 21 Apr 1931, *Jones s.n.* (TEX). Scurry Co.: 17 mi SW of Snyder, 9 May 1964, *Robinson s.n.* (OKLA). Shackelford Co.: Hwy 351, ca 2 mi NE of the Jones County line, 27 Mar 1963, *Henderson* 63-94 (TEX). Sherman Co.: 1 mi N of Etter, 4 May 1951, *Creighton* 12 (COLO). Somervell Co.: 2 mi NE of Glen Rose, 25 Mar 1948, *Cory* 53974 (LL, NEB, OKLA). Stonewall Co.: Hwy 380 ca 8 mi W of Swenson, 22 Apr 1962, *Melchert* 192 (TEX). Sutton Co.: Hwy 277, 3.2 mi N of Hwy 55 (jct near Sutton-Edwards county line), 16 Apr 1988, *Biernier* 88-47 (TEX). Tarrant Co.: 1 mi SW of Benbrook, 14 May 1948, *Cory* 54445 (LL). Taylor Co.: Hwy 277, 2 mi SW of View, 10 Apr 1988, *Biernier* 88-14 (TEX). Terrell Co.: Hwy 90, 12.3 mi SE of Hwy 349 (jct in Dryden), 22 May 1975, *Biernier* 51221 (TEX); Hwy 90, 11.1 mi NW of Hwy 349 (jct in Dryden), 22 May 1975, *Biernier* 51223 (TEX); Blackstone Ranch, 13 mi S of Sheffield, 840 m, 7 Jun 1949, *Webster* 152 (TEX). Terry Co.: 15.2 mi NE of Brownfield, 23 Apr 1964, *Rowell* 8863a (OKLA). Tom Green Co.: 0.5 mi N of Red Creek on Hwy 277, 15 Apr 1951, *Johnson* 617 (TEX). Travis Co.: 2 mi W of Austin, 10 Apr 1948, *Cory* 54288 (LL, NEB). Val Verde Co.: 2 mi NW of Comstock, 15 Jun 1963, *Correll & Wasshausen* 27786 (LL); 8 mi NW of Del Rio, 1 Apr 1947, *McVaugh* 7742 (TEX). Wheeler Co.: Ca 3 mi SW of Shamrock, 23 May 1961, *Correll* 24008 (LL). Williamson Co.: Hwy 2338, ca 3.5 mi S of

Andice, 27 Dec 1964, *Strother* 45 (TEX). Yoakum Co.: Ca 1 mi N of intersection of Hwys 83 and 769, SW part of county, 16 May 2000, *Turner & Turner* 20-194 (TEX). Young Co.: 1 mi SW of Olney, 1 Apr 1939, *McCart* 850 (OKLA).

6b. *TETRANEURIS* *SCAPOS*A (DC.) Greene var. *ARGYROCAULON* (K. L. Parker) K. L. Parker.

Hymenoxys scaposa (DC.) K. L. Parker var. *argyrocaulon* K. L. Parker, *Phytologia* 20: 192. 1970. TYPE: UNITED STATES. Texas. Webb Co.: "Along highway 83 to Carrizo Springs, 15 mi. N of Laredo" (protologue and holotype label), 24 Mar 1960, *H. S. Gentry & A. S. Barclay* 18436 (HOLOTYPE: US-2608026!).

Tetraneuris scaposa (DC.) Greene var. *argyrocaulon* (K. L. Parker) K. L. Parker, *Phytologia* 45: 467. 1980.

AERIAL STEMS 1–20, densely woolly between proximal leaves. LEAVES not close together, internodes distinct, blades oblanceolate to linear-oblanceolate to, rarely, linear, moderately to densely pubescent, moderately to densely dotted with impressed glands, bases usually densely woolly or long-pubescent. HEADS 1–20 per plant. PEDUNCLES 15–40 cm. INVOLUCRES 6–10 × 9–12 mm. PHYLLARIES: outer phyllaries 8–16, sometimes purple-red-tinted on apices and margins, (3.8–)4.8–6(–6.6) × (0.7–)1.2–1.7 mm, margins sometimes slightly scarious; mid phyllaries sometimes purple-red-tinted on apices, obovate to oblanceolate to lanceolate, 3.8–5.5(–6.5) × 0.8–1.5 mm, sparsely to moderately dotted with sessile glands; inner phyllaries (2.5–)3–4.5(–5.2) × 0.7–1.8 mm, sparsely to moderately dotted with sessile glands. RAY FLORETS 12–26; corollas (7.4–)9.5–14 × 2.8–4.3(–5.2) mm. DISC FLORETS (40–)70–160+; corollas 2.5–3 × 0.7–1 mm, glabrous or sparsely pubescent. CYPSELAE 2–2.8 × 0.7–1 mm, sparsely to densely pubescent; pappus scales 5–7, 1.6–2.3 × 0.6–0.8 mm.

CHROMOSOME NUMBER: $2n = 30$.

DISTRIBUTION (Fig. 6) AND HABITAT: South Texas and adjacent Mexico (Tamaulipas). Growing at roadsides and in pastures, 100–200 m.

FLOWERING AND FRUITING: February through June (also November), mainly February through April.

REPRESENTATIVE SPECIMENS: **MEXICO. Tamaulipas.** 14 km S of Nuevo Laredo on rd to Monterrey, 17 Apr 1939, *Frye & Frye* 2398 (UTC); 50 mi SE of Nuevo Laredo, 28 Mar 1964, *Garcia* 52 (OKLA, TEX); 16 mi S of Nuevo Laredo on Hwy 85, 19 Mar 1967, *Wilson* 12166 (TEX). **UNITED STATES. Texas.** Duval Co.: Hwy 59, 4 mi E of Freer, 16 Feb 1963, *Bruno* 35 (TEX); Benavides facility, URI discharge arroyo NW of plant, N of Hwy 359 (between Bruni and Hebbronville), 7 May 1985, *Cowan* 5306 (TEX); 10 mi N of Concepcion, 25 Mar 1963, *Noyola* 20 (OKLA, TEX). Jim Hogg Co.: Hwy 649, 0.9 mi N of Hwy 3073 (jct in extreme NW part of county), 22 Apr 1989, *Biernier* 89-5 (TEX). La Salle Co.: Hwy 81, 5 mi N of Encinal, 23 March 1963, *Cabrera* 93 (TEX). Webb Co.: Hwy 649, 7.9 mi N of Hwy 3073 (jct in extreme NW Jim Hogg County), 15 Apr 1988, *Biernier* 88-37 (TEX); Hwy 83, 5.9 mi NW of I-35, 15 Apr 1988, *Biernier* 88-40 (TEX); Ca 6 mi S of Laredo, 20 Apr 1966, *Correll & Rollins* 32574 (LL). Zapata Co.: Hwy 83, 6.4 mi N of Hwy 16 (jct in Zapata), 15 Apr 1988, *Biernier* 88-39 (TEX); Hwy 83, ca 14.6 mi N of San Ygnacio city limits, $n = 15$, 26 Mar 1966, *Strother* 555 (TEX).

7. *TETRANEURIS TORREYANA* (Nutt.) Greene.

Actinea integrifolia Torr., Ann. Lyceum Nat. Hist. New York 2: 213. 1827, nom. illegit. Not *Actinea integrifolia* Kunth, Nov. Gen. Sp. 4:297. 1818.

Actinella torreyana Nutt., Trans. Amer. Philos. Soc. 7: 379. 1841. TYPE: UNITED

STATES. Wyoming. Natrona Co.: "On the lofty hills or mountains, called the 'Three Butes [sic]' of the upper Platte, on shelving rocks" (protologue), "Red Butes of Platte" (holotype label), "Red Butes of the Upper Platte" (BM isotype label), Jun 1834, *T. Nuttall s.n.* (HOLOTYPE: PH!; ISOTYPES: BM!, GH!, K!, NY!). A query for "Three Buttes" in Wyoming at the U.S. Department of the Interior National Atlas of the United States web site (<http://nationalatlas.gov>) produced a locality in Goshen County, which is nowhere near the Platte, and a locality in northern Natrona County, perhaps near the South Fork of the Powder River, but not near the North Platte. A query for "Red Buttes" produced two summit localities, one in Albany County, which is nowhere near the Platte, and another in Natrona County ca 2 mi south of the Oregon Trail southwest of Casper, Wyoming, which would be adjacent to the North Platte. We believe the latter to be the correct locality for this collection.

Tetraneuris torreyana (Nutt.) Greene, Pittonia 3: 265. 1898.

Actinea torreyana (Nutt.) J. F. Macbride, Contr. Gray Herb. 56: 44. 1918.

Hymenoxys torreyana (Nutt.) K. L. Parker, Madroño 10: 159. 1950.

Actinella depressa Torr. & A. Gray ex A. Gray, Mem. Amer. Acad. Arts (Series 2) 4: 100. 1849. TYPE: UNITED STATES. Utah. "Rocky Mountains, apparently at a great elevation, the locality unknown, Col. Fremont; collected in the second expedition" (protologue), "Fremont's 2nd Exped." (holotype packet), "Fremont's 2nd Jour. Rocky Mts." (K isotype label), 1843–1844, *J. C. Fremont s.n.* (HOLOTYPE: GH!; ISOTYPES: K!, NY!). According to Welsh (1998 p. 169), the type was collected in the Uinta Basin of north-eastern Utah during June 1844.

Actinea depressa (Torr. & A. Gray ex A. Gray) Kuntze, Revis. Gen. Pl. 1: 303. 1891.

Tetraneuris depressa (Torr. & A. Gray ex A. Gray) Greene, Pittonia 3: 266. 1898.

Hymenoxys depressa (Torr. & A. Gray ex A. Gray) S. L. Welsh & Reveal, Great Basin Naturalist 35: 336. 1975.

Hymenoxys lapidicola S. L. Welsh & Neese, Great Basin Naturalist 43: 373. 1983. TYPE: UNITED STATES. Utah. Uintah Co.: "T5S, R25E, Sec 20, Pt. of Pines camp area, S edge of Blue Mtn. Plateau, 8150 ft elev." (holotype label), 12 Jun 1982, E. C. Neese & C. Fullmer 11734 (HOLOTYPE: BRY-237976!; ISOTYPE: NY!).

PERENNIALS. CAUDICES \pm branched, thickened distally. AERIAL STEMS 1–30(–40), erect, unbranched. LEAVES all basal, new leaves very tightly clustered, appearing to arise from the same level at bases of stems, blades spatulate to, usually, oblanceolate to linear-oblanceolate, entire, midribs usually very distinct (more so than in other taxa), glabrous or, usually, sparsely to, sometimes, moderately or densely pubescent, densely dotted with impressed glands, bases usually densely woolly or long-pubescent. HEADS 1–10(–40) per plant, radiate, borne singly. PEDUNCLES green throughout to, sometimes, purple-red-tinted distally, (0.5–)2–15 cm, moderately to, usually, densely pubescent, almost always densely lanate below involucre, eglandular or sparsely dotted with sessile glands. INVOLUCRES 10–12 \times 12–15 mm. PHYLLARIES: outer phyllaries 4–8, often purple-red-tinted on apices and margins, rarely purple-red-tinted throughout, obovate to oblanceolate to lanceolate, 6–8.5 \times (1.5–)2–4 mm, margins usually conspicuously scarios, abaxial faces sparsely to densely pubescent, sparsely to moderately dotted with sessile and/or impressed glands; mid phyllaries often purple-red-tinted on apices and margins, obovate to oblanceolate to lanceolate, 6–8.5 \times 2.5–4 mm, margins scarios, abaxial faces sparsely to moderately pubescent, sparsely to moderately dotted with

sessile glands; inner phyllaries sometimes purple-red-tinted on the apices, 5.3–7.3(–8) \times 2–3.5 mm, abaxial faces glabrous or sparsely pubescent, eglandular or sparsely dotted with sessile glands. RAY FLORETS 7–14; corollas 11–17 \times 4.5–7.5 mm, abaxial faces glabrous or sparsely pubescent, sparsely to moderately to, sometimes, densely dotted with sessile glands. DISC FLORETS 25–160+; corollas yellow, 4–4.7 \times 1–1.5 mm, glabrous or sparsely pubescent, eglandular or sparsely dotted with sessile glands. CYPSELAE 3–4 \times 1–1.5 mm, surfaces white, moderately to densely pubescent, eglandular or sparsely dotted with sessile glands; pappi 5–7, obovate- to oblanceolate-aristate scales, 3–4(–4.5) \times 0.9–1.5 mm.

CHROMOSOME NUMBER: $2n = 28$.

DISTRIBUTION (Fig. 3) AND HABITAT: Southern Montana, Wyoming, northeastern Utah, and northwestern Colorado. Growing at roadsides, on hillsides and slopes, in open treeless areas, and at edges of woods, (1310–)1700–3050 m.

FLOWERING AND FRUITING: May through September, mainly May and June.

REPRESENTATIVE SPECIMENS: **UNITED STATES. Colorado.** Jackson Co.: Along County Rd, 3 mi S of Delaney Buttes Reservoir and 0.25 mi E of Beaver Creek, 2500 m, 23 May 1978, Wilken & Painter 13287 (CSU, UTC). Mesa Co.: 12 mi S of White-water, 2100 m, 21 May 1988, Dorn 4937 (COLO, RM). Moffat Co.: Dinosaur Nat'l Monument, adjacent to Haystack Rock, 1950 m, 14 May 1987, O'Kane 2661 (COLO, RM). Rio Blanco Co.: 3.5 mi SW of jct of Middle Fork Greasewood Creek and North Fork of Greasewood Creek, 2316 m, 20 May 1982, Walker & Sigstedt 82-39 (CSU). **Montana.** Carbon Co.: Along Crooked Creek Rd, ca 13 mi N of Lovell, WY, 1310 m, 16 Jun 1990, Evert 18956 (COLO, RM); Ridge N of the N Fork Grove Creek ca 6 mi SW of Red Lodge, 2135 m, 24 Jun 1986, Shelly & Leica 3895 (MONTU). **Utah.** Daggett Co.: Hwy 44, 10.0 mi S of Hwy 43 (jct in Manilla), 12 Jun 1975,

Biernier 51289 (TEX). Duchesne Co.: S of Starvation Lake along Hwy 40 ca 3.3 mi W of Strawberry River bridge at W edge of Duchesne, 1775 m, 19 May 1995, *Windham 95-66* (UT). Rich Co.: ESE of Bear Lake along tributary of North Fork of Sixmile Creek ca 2.64 km S of Shirley Spring, 2020 m, 21 May 1996, *Windham 96-136* (UT). Uintah Co.: ESE of Vernal on Blue Mt at S edge of Cliff Ridge ca 6.19 km NE of Davis Spring, 2440 m, collected as *T. lapidicola*, $n = 14$, $2n = 28$, 7 May 1999, *Windham 99-061* (TEX, UT). **Wyoming.** Albany Co.: Medicine Bow National Forest in NE corner of T15NR71W, 8 Jun 1972, *Asplund 72-4* (TEX); IH-80, just E of Laramie and 4.5 mi W of Happy Jack Rd (Lincoln Monument exit), 13 Jun 1975, *Biernier 51292* (TEX). Big Horn Co.: Medicine Mt top and upper slopes, ca 3050 m, 14 Jul 1978, *Hartman et al.* 7899 (RM). Carbon Co.: S side of Shirley Mts, adj to BLM Rd 3111 along Upper Austin Creek, ca 10 air mi SW of Hwy 77, 2620–2650 m, 12 Jun 1996, *Fertig 16602* (RM); Hwy 287, 1.2 mi N of Hwy 30 (jct in Rawlins), 12 Jun 1975, *Biernier 51291* (TEX). Fremont Co.: West slope of Wind River Range, Pine Creek, 0.5 mi W of Hwy 28, ca 3.5 air mi W of South Pass City, 2440 m, 13 Jun 1991, *Fertig 7662* (RM); E Gas Hills, NE of Jeffrey City, 26 May 1976, *Schreibeis GH-3121* (RM). Johnson Co.: Big Horn Mts, North Fork Crazy Woman Creek, ca 13 air mi SW of Buffalo, 2010 m, 28 Jun 1979, *Hartman 9680* (RM); Big Horn Mts, rim above Beartrap Meadows, ca 11.5 air mi NW of Mayoworth, ca 22.5 air mi NW of Kaycee, 2470 m, 9 Jun 1980, *Nelson 5248* (RM). Lincoln Co.: Green River Basin, just W of the Green River at the far north end of Fontenelle Reservoir, ca 5.5 air mi S of La Barge, 2010–2040 m, 26 May 1995, *Cramer 5029* (RM); South Salt River Range and vicinity, Wheat Creek to Windy Gap and Oyster Ridge, ca 14 air mi N of Kemmerer, 2255–2440 m, 28 May 1994, *Hartman 45616* (RM); SSE of Kemmerer on W slope of Oyster Ridge ca 0.38 km NE of the Hams Fork bridge on Hwy 30, 2125 m,

$n = 14$, 22 May 1996, *Windham 96-140* (UT). Natrona Co.: N Platte River Valley, NW rim of Benton Basin, ca 0.25 mi N of Hwy 220, ca 5.5 air mi W of Alcova, 1935 m, 21 May 1993, *Fertig 3528* (RM); E-K Creek, ca 7.5 air mi NNE of Arminto, 1990–2010 m, 1 Jun 1986, *Haines 6034A* (RM); Casper Mt area, summit of the first ridge E of Elkhorn Creek, 2440m, 14 Jun 1962, *Jozwik 106* (RM). Park Co.: SW end of Rattlesnake Mts, ca 6 mi W of Cody, 2560–2620 m, 25 Jun 1989, *Evert 17153* (RM). Sheridan Co.: Big Horn Mts, Ice Creek, ca 8.8 air mi W of Burgess Junction, 2745–2805 m, 23 Jun 1979, *Hartman 9252* (RM). Sublette Co.: Green River Basin, ca 4 air mi WNW of Boulder, 2165 m, 19 Jun 1995, *Cramer 6394* (RM); Upper Green River Basin, Cretaceous Mt/Hogsback Ridge area, 2 air mi NNW of Calpet, 2165–2180 m, 16 May 1993, *Hartman 37012* (RM). Sweetwater Co.: Ca 19 air mi SW of Green River, 1970 m, 14 Jun 1995, *Rafsdal 3950* (RM); Point of Rocks, 15 Jun 1898, *Nelson 4747* (RM). Uinta Co.: 8 mi NW of Milburne, 2100 m, 28 Jun 1947, *Parker & McClintock 6971* (COLO, RM, TEX, UTC).

Tetraneuris torreyana appears be closely related to *T. acaulis*. Like the latter, it has distally thickened caudices and tightly clustered basal leaves. The blades are very densely glandular, more so than *T. acaulis* var. *arizonica*, and the midribs tend to be much more distinct than in any of the other *Tetraneuris* taxa. The outer phyllaries usually have markedly scarious margins; those of other taxa have weakly or not at all scarious margins.

Tetraneuris torreyana is morphologically variable throughout its range, and it is not uncommon to find populations that contain dwarf-form plants. The extreme is represented by dwarf-form/pincushion plants in Uintah County, Utah, in the vicinity of Blue Mountain (e.g., *Windham 99-061*, TEX), which have been described as *Hymenoxys lapidicola*. They are quite distinctive given their diminutive size and oth-

er features such as outer phyllaries with red, recurved tips, but we do not believe that they warrant formal taxonomic recognition. We base our decision not only on the very restricted range of the Blue Mountain forms and the existence of other dwarf forms within *T. torreyana*, some of which also have outer phyllaries with red, recurved tips, but on our observations of similar dwarf forms of other taxa in other areas. For example, dwarf-form/pincushion plants at Raton Pass on the border of New Mexico and Colorado that were described as *Actinella depressa* var. *pygmaea* (e.g., Gordon s.n., GH, MO), are clearly *T. acaulis* var. *acaulis*, as are dwarf-form/pincushion plants (which also have a few outer phyllaries with reflexed tips) that grow on Sandia Crest in Bernalillo County, New Mexico (e.g., Martin 4186, UNM). We have also examined dwarf-form/pincushion plants with some outer phyllaries with reflexed tips from Carbon County, Wyoming (e.g., Degener 16115, RM), that are referable to *T. acaulis* var. *caespitosa*. The existence of dwarf-form/pincushion plants, some of which have outer phyllaries with recurved tips, in *Tetraneuris* seems not to be unusual.

8. *TETRANEURIS TURNERI* (K. L. Parker) K. L. Parker.

Hymenoxys turneri K. L. Parker, Phytologia 20: 192. 1970. TYPE: UNITED STATES. Texas. Karnes Co.: "2 mi N of Karnes City" (protologue and type labels), 21 Apr 1965, B. L. Turner 5154 (HOLOTYPE: US-3215707!; ISOTYPES: GH!, MO-3818692!, NY 2 specimens—as database images!, TEX!). The collection label of the specimen at US carries the notation "ISOTYPE"; however, the protologue indicates that the holotype is at US and this is the only type specimen at US. We feel confident that this specimen was intended to be the holotype.

Tetraneuris turneri (K. L. Parker) K. L. Parker, Phytologia 45: 467. 1980.

PERENNIALS. CAUDICES \pm branched, not thickened distally. AERIAL STEMS 1–20, erect or \pm decumbent, sometimes branched near bases, usually densely woolly or long-pubescent between proximal leaves. LEAVES all basal-proximal, new leaves not tightly clustered, arising at various levels near bases of stems, blades spatulate to oblanceolate to linear-oblanceolate, entire or the basal and more proximal often with 2(–4) lateral teeth or lobes, moderately to, usually, densely pubescent, sparsely to, usually, densely dotted with impressed glands, bases moderately to densely woolly or long-pubescent, bases of proximal leaves weakly or not expanded, weakly or not clasping. HEADS 1–20 per plant, radiate, borne singly. PEDUNCLES green throughout to purple-red-tinted throughout, 20–50 cm, moderately to densely pubescent distal from the leaves, sparsely to moderately dotted with sessile glands. INVOLUCRES 8–15 \times 12–20 mm. PHYLLARIES: outer phyllaries 12–16, often purple-red-tinted on apices and margins, sometimes purple-red-tinted throughout, obovate to oblanceolate to lanceolate, 5.2–7.8(–10) \times 1.5–2.3 mm, margins sometimes slightly scarious, abaxial faces sparsely to moderately pubescent, sparsely dotted with sessile and/or impressed glands; mid phyllaries often purple-red-tinted on apices, obovate to oblanceolate to lanceolate, 5–6.5(–8) \times 1.5–2 mm, margins usually scarious, abaxial faces moderately to densely pubescent, sparsely dotted with sessile glands; inner phyllaries sometimes purple-red-tinted on apices, 4–5(–6.2) \times 1–2 mm, abaxial faces sparsely to moderately pubescent, eglandular or sparsely dotted with sessile glands. RAY FLORETS 12–24; corollas 14–20 \times 3.8–6 mm, abaxial faces glabrous or sparsely pubescent, eglandular or sparsely dotted with sessile glands. DISC FLORETS 100–250+; corollas yellow proximally, yellow to sometimes purple-red-tinted distally, 3.5–3.8 \times 1–1.2 mm, glabrous or sparsely pubescent, eglandular or sparsely dotted with sessile glands. CYPSELAE 2.6–3.4 \times 1–1.2 mm, surfaces white, moderately pubes-

cent, sparsely to moderately dotted with sessile glands; pappi 6–7, lanceolate- to obovate- to oblanceolate-aristate scales, 3–4 × 0.9–1.1 mm.

CHROMOSOME NUMBER: $2n = 90$.

DISTRIBUTION (Fig. 6) AND HABITAT: South Texas and somewhat disjunct to adjacent Mexico (Coahuila). Growing at roadsides and in pastures, 50–130 m.

FLOWERING AND FRUITING: February through June, mainly March and April.

REPRESENTATIVE SPECIMENS: **MEXICO. Coahuila.** Municipio Allende. Hwy 57, 0.4 mi S of El Infante, 15 May 1982, *Dorr 2222* (TEX). **UNITED STATES. Texas.** Bee Co.: Hwy 59, 2.7 mi NE of Hwy 796 (jct SW of Beeville), 19 Mar 1991, *Biernner 91-3* (TEX). Goliad Co.: Hwy 59, 12.5 mi SW of Hwy 239 (jct just W of Goliad) and ca 1.5 mi NE of Berclair, 19 Mar 1991, *Biernner 91-2* (TEX). Jim Wells Co.: 4.5 mi S of Orange Grove between Hwy 359 and railroad, $2n = 45II$, 27 Mar 1966, *Strother 564* (TEX). Karnes Co.: 3 mi N of Karnes City along Hwy 123, 16 Apr 1980, *Turner 80-42A* (TEX). Live Oak Co.: Hwy 281, 13.8 mi S of Hwy 59 (jct in George West), 14 Apr 1988, *Biernner 88-30* (TEX); Hwy 72, 0.5 mi NE of I-37 (jct NE of Three Rivers), 14 Apr 1988, *Biernner 88-26* (TEX). San Patricio Co.: 2.5 mi NW of Mathis, 20 May 1980, *Turner 80-92M* (RM, TEX).

This hexaploid ($2n = 90$) taxon is closely related to *Tetraneuris scaposa*. It is confined to southern Texas and northeastern Mexico as localized or patchy colonies along roadsides in mostly calcareous soils with a distribution adjacent to that of *T. scaposa* var. *argyrocaulon*. Different from *T. scaposa*, *T. turneri* tends to have stems that are more or less decumbent and leaves that are densely woolly.

9. *TETRANEURIS VERDIENSIS* R. A. Denham & B. L. Turner.

Tetraneuris verdiensis R. A. Denham & B. L.

Turner, *Phytologia* 81: 5. 1996. TYPE: UNITED STATES. Arizona. Yavapai Co.: "5 mi E of Camp Verde" (protologue and holotype label), 3300 ft, 14 May 1995, R. A. Denham *et al.* 1840 (HOLOTYPE: TEX!).

PERENNIALS. CAUDICES \pm branched, thickened distally. AERIAL STEMS 1–15, erect, unbranched. LEAVES all basal, new leaves very tightly clustered, appearing to arise from the same level at bases of stems, blades obovate to oblanceolate to linear-oblanceolate, entire, densely pubescent, sparsely to, usually, moderately to densely dotted with impressed glands, bases densely woolly or long-pubescent. HEADS 1–15 per plant, discoid, borne singly. PEDUNCLES green throughout to purple-red-tinted throughout, 4–15 cm, moderately to densely pubescent, sparsely dotted with sessile glands. INVOLUCRES 5–9 × 6–10 mm. PHYLLARIES: outer phyllaries 8–10, often purple-red-tinted on apices and margins, sometimes purple-red-tinted throughout, obovate to ovate to lanceolate, 4–5(–6) × 1.5–2.5 mm, margins sometimes slightly scarious, abaxial faces densely pubescent, sparsely to moderately dotted with sessile and/or impressed glands; mid phyllaries often purple-red-tinted on apices and margins, obovate to ovate, 5–6 × 2.2–3.5 mm, margins scarious, abaxial faces sparsely to moderately pubescent, sparsely to moderately dotted with sessile glands; inner phyllaries often purple-red-tinted on apices, 4.5–5.2(–6) × 1.7–2.5 mm, abaxial faces sparsely to moderately pubescent, eglandular or sparsely dotted with sessile glands. RAY FLORETS none. DISC FLORETS 20–40; corollas yellow, 2.5–4 × 1–1.5 mm, glabrous or sparsely pubescent, eglandular or sparsely dotted with sessile glands. CYPSELAE 2.8–4 × 1–1.4 mm, surfaces white, moderately to densely pubescent, eglandular or sparsely dotted with sessile glands; pappi 5–6, ovate- to lanceolate-aristate or obovate- to oblanceolate-aristate scales, 2.5–3.5 × 1–1.3 mm.

CHROMOSOME NUMBER: Unknown.

DISTRIBUTION (Fig. 3) AND HABITAT: Known only from the Verde Valley area of Yavapai County, Arizona. Growing on low, gypsum hills, ca 1000 m.

FLOWERING AND FRUITING: Mainly May.

REPRESENTATIVE SPECIMENS: **UNITED STATES. Arizona.** Yavapai Co.: Verde Valley, ca 5 mi E of Camp Verde, small white knoll W of FS 618 (Beaver Creek Rd), 1025 m, 26 May 1999, *Anderson & Godec 99-15* (TEX — 2 sheets with 5 plants total).

Tetraneuris verdiensis is closely related to *T. acaulis* var. *arizonica* and is confined to low, gypsum hills of the late Tertiary Verde Formation near Camp Verde, Arizona (Denham and Turner, 1996; Daniel J. Godec, SWCA Inc., Environmental Consultants, Phoenix, AZ, personal communication). There are other discoid populations in *Tetraneuris* to which the name *T. eradiata* has been applied; such populations do not occupy a distinct geographic area and are found scattered in Texas, Colorado, and Wyoming. We include those populations in *T. acaulis* var. *acaulis*.

EXCLUDED NAMES

Tetraneuris brandegeei (Porter ex A. Gray) K. L. Parker, *Phytologia* 45: 467. 1980. = *Hymenoxys brandegeei* (Porter ex A. Gray) K. L. Parker, *Madroño* 10: 159. 1950. Basionym: *Actinella brandegeei* Porter ex A. Gray, *Proc. Amer. Acad. Arts* 13: 373. 1878 (as *brandegei*).

Tetraneuris glabriuscula Rydb., *Bull. Torrey Bot. Club* 33: 155. 1906. Nomen ambiguum. Based by Rydberg on *T. glabra* Greene, in part, which was a combination by Greene on *Actinella glabra* Nutt. At the same time Rydberg wrote, "Not *Actinella glabra* Nutt."

Tetraneuris grandiflora (Torr. & A. Gray) K.

L. Parker, *Phytologia* 45: 467. 1980. = *Hymenoxys grandiflora* (Torr. & A. Gray) K. L. Parker, *Madroño* 10: 159. 1950. Basionym: *Actinella grandiflora* Torr. & A. Gray, *Boston J. Nat. Hist.* 5: 109. 1845.

Actinella linearifolia (Hook.) Torr. & A. Gray var. *caule elatiore* A. Gray, *Plantae Wrightianae* 2: 97. 1852. In *Plantae Wrightianae*, Gray cited Wright specimens of *Actinella linearifolia* (= *Tetraneuris linearifolia*) from "Prairies of the Leona, Western Texas; May" to which he assigned the number 1264 and for which he provided the designation and descriptor "var. *caule elatiore* (*ultrapedali*) *strictiore*." Gray, however, never provided a legitimate name for this "entity" and never published it as a new variety.

Hymenoxys scaposa (DC.) K. L. Parker var. *glabra* (Nutt.) K. L. Parker. This name does not appear to have ever been published by Parker. Rather, she made the combination *Hymenoxys acaulis* (Pursh) K. L. Parker var. *glabra* (A. Gray) K. L. Parker based on *Actinella scaposa* (DC.) Nutt. var. *glabra* A. Gray, which she mistakenly called *Actinea scaposa* Nutt. var. *glabra* A. Gray (Parker, 1950).

ACKNOWLEDGMENTS

We are grateful to the institutions cited for loans of specimens. We also thank the following individuals for their help with type specimen information: Emily Wood and Kanchi Gandhi (GH), Thomas Zanoni and Melissa Tulig (NY), James Macklin and James Lendemer (PH), Ron Hartman (RM), and Rusty Russell (US). A special thanks to Barbara Hellenthal at NDG for an exhaustive search for what appear to be missing types at that institution. We also thank John Strother for his help with the manuscript in general and the descriptions in particular, and José Panero and Tom Wendt for their help with preparation of the Spanish abstract.

LITERATURE CITED

- Baldwin, B. G. and B. L. Wessa. 2000. Phylogenetic placement of *Pelucha* and new subtribes in Helenieae sensu stricto (Compositae). *Syst. Bot.* 25: 522–538.
- Barkley, T. M. 1986. *Hymenoxys*, Pp. 962–964 in *Flora of the Great Plains*, eds. T. M. Barkley, R. E. Brooks, and E. K. Schofield. Lawrence, Kansas: University of Kansas Press.
- Biernier, M. W. 1994. Submersion of *Dugaldia* and *Plummera* in *Hymenoxys* (Asteraceae: Heliantheae: Gaillardiiinae). *Sida* 16: 1–8.
- Biernier, M. W. 2001. Taxonomy of *Hymenoxys* subgenus *Picradenia* and a conspectus of the subgenera of *Hymenoxys* (Asteraceae: Helenieae: Tetraneurinae). *Lundellia* 4: 37–63.
- Biernier, M. W., J. G. Díaz, B. Barba, and W. Herz. 1992. *Tetraneuris linearifolia* var. *arenicola* (Asteraceae: Heliantheae): a new variety from south Texas. *Sida* 15: 231–239.
- Biernier, M. W. and R. K. Jansen. 1998. Systematic implications of DNA restriction site variation in *Hymenoxys* and *Tetraneuris* (Asteraceae, Helenieae, Gaillardiiinae). *Lundellia* 1: 17–26.
- Cronquist, A. 1994. *Hymenoxys*. Pp. 78–86 in *Intermountain Flora. Vascular Plants of the Intermountain West, U.S.A. Volume 5. Asterales*, eds. A. Cronquist, A. H. Holmgren, N. H. Holmgren, J. L. Reveal, and P. K. Holmgren. Bronx, New York: The New York Botanical Garden.
- Cusick, A. W. 1991. *Hymenoxys herbacea* (Asteraceae): an endemic species of the Great Lakes Region. *Rhodora* 93: 238–241.
- Denham, D. and B. L. Turner. 1996. A new species of *Tetraneuris* (Asteraceae, Helenieae) from the late Tertiary Verde Formation of central Arizona. *Phytologia* 81: 5–9.
- Greene, E. 1898. *Tetraneuris*. *Pittonia* 3: 264–270.
- Johnston, M. A. and E. K. Bonde. 1969. IOPB chromosome number reports XXII. *Taxon* 18: 433–442.
- Karis, P. O. and O. Ryding. 1994. Tribe Helenieae. Pp. 521–558 in *Asteraceae: Cladistics & Classification*, ed. K. Bremer. Portland, Oregon: Timber Press.
- Moran-Palma, P. and A. A. Snow. 1997. The effect of interplant distance on mating success in federally threatened, self-incompatible *Hymenoxys herbacea* = *H. acaulis* var. *glabra* (Asteraceae). *Amer. J. Bot.* 84: 233–238.
- Parker, K. F. 1950. New combinations in *Hymenoxys*. *Madroño* 10: 159.
- Parker, K. F. 1970. Two new taxa in Texas *Hymenoxys* (Compositae). *Phytologia* 20: 192.
- Parker, K. F. 1980. New combinations in *Tetraneuris* Greene (Heliantheae, Asteraceae). *Phytologia* 45: 467.
- Powell, A. M. and B. L. Turner. 1963. Chromosome numbers in the Compositae. VII. Additional species from the southwestern United States and Mexico. *Madroño* 17: 128–140.
- Robinson, H. 1981. A revision of the tribal and subtribal limits of the Heliantheae (Asteraceae). *Smithsonian Contr. Bot.* 51: 1–102.
- Sanderson, S. C. and J. L. Strother. 1973. The origin of aneuploidy in *Hymenoxys odorata*. *Nature, New Biol.* 242: 220–221.
- Spring, O., B. Zitterell-Haid, M. W. Bierner, and T. J. Mabry. 1994. Chemistry of glandular trichomes in *Hymenoxys* and related genera. *Biochem. Syst. Ecol.* 22: 171–195.
- Strother, J. L. 1966. Chromosome numbers in *Hymenoxys* (Compositae). *Southw. Naturalist* 11: 223–227.
- Strother, J. L. 1983. More chromosome studies in Compositae. *Amer. J. Bot.* 70: 1217–1224.
- Strother, J. L. and L. E. Brown. 1988. Dysploidy in *Hymenoxys texana* (Compositae). *Amer. J. Bot.* 75: 1097–1098.
- Turner, B. L. 1972. Chemosystematic data: their use in the study of disjunctions. *Ann. Missouri Bot. Gard.* 59: 152–164.
- Turner, B. L. and A. M. Powell. 1977. Helenieae—systematic review. Pp. 699–737 in *The Biology and Chemistry of the Compositae*, eds. V. H. Heywood, J. B. Harborne, and B. L. Turner. London: Academic Press.
- Welsh, S. L. 1983. Utah Flora: Compositae (Asteraceae). *Great Basin Naturalist* 43: 179–357.
- Welsh, S. L. 1987. Compositae. *Great Basin Naturalist Mem.* 9: 131–240.
- Welsh, S. L. 1998. *John Charles Frémont Botanical Explorer*. St. Louis, Missouri: Missouri Botanical Garden Press.
- Zhao, Z. 1996. Documented chromosome numbers 1996: 2. Miscellaneous U.S.A. and Mexican species, mostly Asteraceae. *Sida* 17: 259–263.