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TAXONOMY OF *HYMENOXYS* SUBGENUS *RYDBERGIA* (ASTERACEAE: HELENIEAE: TETRANEURINAE)

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Abstract: *Hymenoxys* subg. *Rydbergia* comprises *H. brandegeei*, *H. grandiflora*, and *H. insignis*. The treatment includes a discussion of the original circumscription of the taxa, the description of the genus *Rydbergia* to accommodate *H. brandegeei* and *H. grandiflora*, the eventual placement of *Rydbergia* within *Hymenoxys* as a subgenus, and relationships of the three taxa to one another and to other taxa of *Hymenoxys*. The treatment also includes synonymies, descriptions, and range maps for each of the species, and lectotypification of *Actinella brandegeei*.

Resumen: *Hymenoxys* subg. *Rydbergia* incluye *H. brandegeei*, *H. grandiflora*, y *H. insignis*. El tratamiento incluye una discusión de la circunscripción original de los taxones, la descripción del género *Rydbergia* para acomodar *H. brandegeei* y *H. grandiflora*, la colocación eventual de *Rydbergia* en *Hymenoxys* como un subgénero, y las relaciones filogenéticas de los tres taxones entre ellos y la de éstos con los otros taxones de *Hymenoxys*. El tratamiento incluye también sinónimias, descripciones, mapas de distribución para cada una de las especies, y lectotipificación de *Actinella brandegeei*.

Keywords: Asteraceae, Helenieae, Tetraneurinae, *Hymenoxys*, *Rydbergia*

Hymenoxys Cass. subg. *Rydbergia* (Greene) Bierner comprises *H. grandiflora* (Torr. & A. Gray) K. L. Parker, originally described as *Actinella grandiflora* (Torrey and Gray, 1845), *H. brandegeei* (Porter ex A. Gray) K. L. Parker, originally described at the varietal level as *Actinella grandiflora* var. *glabrata* (Porter, 1874) and later at the specific level as *Actinella brandegeei* Porter ex A. Gray (Gray, 1878), and *H. insignis* (A. Gray) Cockerell, originally described as *Actinella insignis* (Gray, 1883). *Actinella* Pers. was the generic name commonly used at that time (e.g., Torrey and Gray, 1842; Gray, 1883) for taxa now placed in *Hymenoxys* and *Tetraneuris* Greene.

When Gray (1883) described *Actinella insignis*, he placed it along with *A. brandegeei* and *A. grandiflora* in *Actinella* sect. *Euactinella* rather than in sect. *Hymenoxys*, based mainly on the morphology of the involucre. The phyllaries of taxa in sect. *Euactinella* are in two or three subequal series; those of taxa in sect. *Hymenoxys* are in two unequal series. *Actinella brandegeei*, *A. grandiflora*,

and *A. insignis* were thereby placed next to *A. chrysanthemoides* (= *Hymenoxys chrysanthemoides*) of subg. *Phileozeroa* (Bierner, 2001) and species now separated from *Hymenoxys* into *Tetraneuris* Greene (Bierner and Turner, 2003).

Greene (1898) was clearly dissatisfied with this arrangement. He placed most of the taxa of Gray's sect. *Euactinella* in *Tetraneuris*, and most of the taxa of Gray's sect. *Hymenoxys* in *Picradenia* Hook. *Tetraneuris* is now recognized as a genus separate from *Hymenoxys* (Bierner and Turner, 2003), and *Picradenia* is now recognized as a subgenus of *Hymenoxys* (Bierner, 2001). Greene (1898) then described *Rydbergia* to accommodate *Actinella brandegeei* and *A. grandiflora* (Mexican species were not treated), a circumscription followed by Cockerell (1904), Rydberg (1906, 1915), Coulter and Nelson (1909), and Robinson (1981). Other workers, such as Blake (1925), Parker (1950), Turner and Powell (1977), and Karis and Ryding (1994), felt there was no

clear basis on morphological grounds for maintaining *Rydbergia* as a separate genus.

The submersion of *Rydbergia* in *Hymenoxys* is supported by cytological and chemical evidence. All three taxa have chromosome numbers of $2n = 30$ (Turner et al., 1961; Speese and Baldwin, 1963), which is the predominant chromosome number among the diverse taxa of *Hymenoxys* (e.g., Speese and Baldwin, 1952; Beaman and Turner, 1962; Strother 1966; Sanderson, 1973; Turner et al., 1973).

Hymenoxys grandiflora produces a group of flavonoid compounds (notably flavone aglycones that are methoxylated at the 6-position of the A-ring but not at the 8-position) that are identical to ones produced by other species of *Hymenoxys* (Sanderson, 1975). In contrast, taxa that have been separated into *Tetraneuris* (Bierner and Turner, 2003) have a different flavonoid profile and produce flavone aglycones that are methoxylated at both the 6- and 8-positions of the A-ring (e.g., Bierner, 1978; Bierner and Turner, 2003).

Studies of sesquiterpene lactones and monoterpene glycosides of *Hymenoxys* and related genera by Spring et al. (1994) also support the notion that *Rydbergia* is congeneric with *Hymenoxys*. *Hymenoxys brandegeei*, *H. grandiflora*, and *H. insignis*, like the other taxa of *Hymenoxys* examined (except *H. texana*), were found to produce seco-pseudoguaianolides; these compounds are not produced by taxa of *Tetraneuris*. Furthermore, like the other taxa of *Hymenoxys* examined (except *H. texana*), they did not produce monoterpene glycosides; these compounds are produced by all of the *Tetraneuris* taxa examined. In 2001, Bierner formally recognized *Rydbergia* as a subgenus of *Hymenoxys*.

Hymenoxys insignis is geographically distant from the other two taxa (Fig. 1); yet, the morphological similarities are striking. All three have phyllaries in two or three subequal series and leaves that are usually dissected to some extent. The disc and ray florets are very similar, differing mainly in size

(although the pappus scales of *H. insignis* are very small compared to those of the other two taxa). At the macro-morphological level, *H. insignis* looks something like a taller, branched version of *H. grandiflora* with heads about the size of those of *H. brandegeei*. The three taxa clearly form a morphological trio similar to one another and different from other taxa of *Hymenoxys*.

The close relationship of *Hymenoxys brandegeei*, *H. grandiflora*, and *H. insignis* to one another is supported by chemical data presented by Spring et al. (1994). Chemical similarity indices (the proportion of shared to total compounds expressed as percentage) among the species pairs of *H. brandegeei*—*H. grandiflora*, *H. brandegeei*—*H. insignis*, and *H. grandiflora*—*H. insignis* were 72%, 90%, and 63%, respectively. The highest similarity index of any subg. *Rydbergia* species to any other taxon of *Hymenoxys* was 44% for *H. grandiflora* and *H. bigelovii*. In addition, the phenogram prepared by Spring et al. (1994) from sesquiterpene lactone data placed these three species in the same clade with an infragroup average chemical similarity index of 75%. The reliability of this analysis is supported by other groupings in the phenogram. For example, the species of subgenera *Hymenoxys*, *Phileozeroa*, and *Plummera* were grouped into separate clades with infragroup average chemical similarity indices of 76%, 80%, and 82%, respectively. The similarity index of 90% for the *H. brandegeei*—*H. insignis* pair suggests that the connection of *H. insignis* of Mexico is probably to the more southern *H. brandegeei*. This contention is supported by work documenting floristic similarities between the northern Sierra Madre Oriental of Mexico, where *H. insignis* is found, and the White Mountains of New Mexico, the southernmost edge of the distribution of *H. brandegeei* (McDonald, 1993).

The relationship of *Hymenoxys brandegeei*, *H. grandiflora*, and *H. insignis* to other taxa of *Hymenoxys* is not at all clear. Morphologically, they are somewhat similar

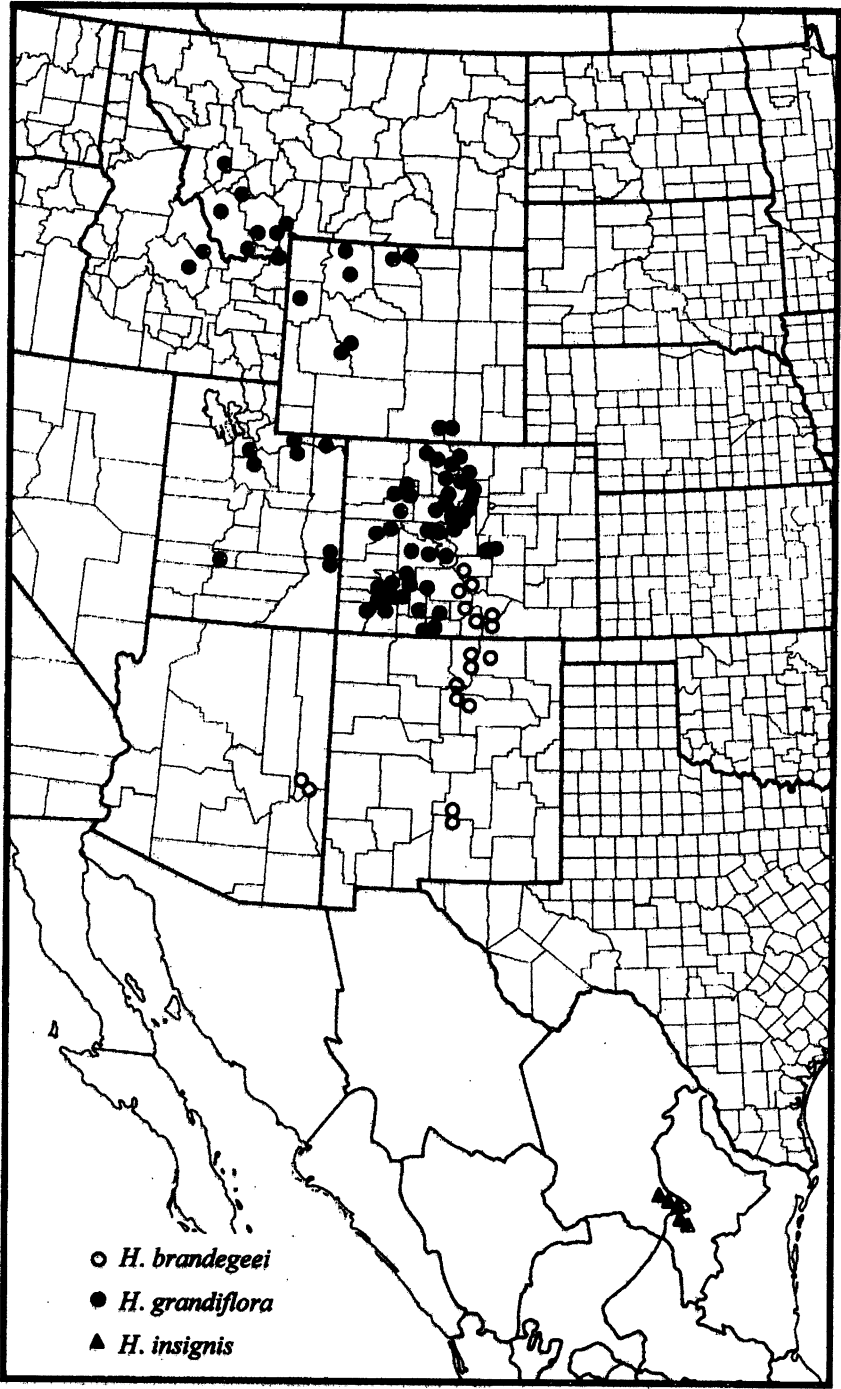


FIG. 1. Distribution of *Hymenoxys brandegeei*, *H. grandiflora*, and *H. insignis*.

to the taxa of subgenus *Dugaldia*, all having phyllaries in subequal series rather than in two unequal series (Bierner, 2001). The average chemical similarity index (Spring et al., 1994) of *H. brandegeei*, *H. grandiflora*, and *H. insignis* to *H. hoopesii* was relatively high at 32.7%, but their average chemical similarity indices to the other two taxa of subg. *Dugaldia*, *H. integrifolia* and *H. pincetorum*, were relatively low at 24% and 23.3%, respectively. *Hymenoxys brandegeei*, *H. grandiflora*, and *H. insignis* had relatively high average chemical similarity indices of 34% and 35% to *H. odorata* and *H. chrysanthemoides*, respectively, of subg. *Phileozeria*, but they had similar average chemical similarity indices to *H. cooperi*, *H. rusbyi*, and *H. subintegra* of subg. *Picradenia* (30.7%, 33.7%, and 36%, respectively). The highest average chemical similarity index of *H. brandegeei*, *H. grandiflora*, and *H. insignis* to any other *Hymenoxys* taxon was 39% to *H. bigelovii*, the lone species of subg. *Macdougalia*. In fact, the similarity index between *H. grandiflora* and *H. bigelovii* was 44%, the highest of any subg. *Rydbergia* species to any other taxon of *Hymenoxys*.

TAXONOMIC TREATMENT

Hymenoxys subg. *Rydbergia* (Greene)

Bierner, *Lundellia* 4: 37–63. 2001.

Rydbergia Greene, *Pittonia* 3: 270. 1898.

TYPE SPECIES: *Actinella grandiflora* Torr.

& A. Gray, *Boston J. Nat. Hist.* 5: 109, 1845. (= *Hymenoxys grandiflora*)

POLYCARPIC PERENNIALS. CAUDICES unbranched or \pm branched, AERIAL STEMS 1–10, erect, unbranched or branched distally, green throughout to purple-red-tinted proximally or distally to purple-red-tinted throughout, 8–80 cm, sparsely to densely pubescent, eglandular or sparsely dotted with sessile glands. LEAVES basal and cauline, alternate, blades simple and entire or pinnately or bipinnately divided into 3–41+ segments, glabrous or sparsely to densely pubescent, sparsely to densely dot-

ted with impressed glands; basal leaf bases expanded, clasping, usually persistent. HEADS 1–35 per plant, borne singly or in paniculiform to corymbiform arrays. PEDUNCLES 1–10 cm, expanded apically, moderately to densely pubescent, often densely tomentose distally beneath the involucre, sparsely to moderately dotted with sessile glands. INVOLUCRES hemispheric to subglobose, 10–25 \times 15–30 mm. PHYLLARIES in 2 or 3 subequal series, herbaceous; outer phyllaries 10–24, free or basally connate 1/5 to 1/3 their lengths, green throughout or yellow to yellow-green proximally and green distally, sometimes purple-red tinted on margins, lanceolate to narrowly lanceolate, 7–15 \times 1–4 mm, apices rounded to acute to acuminate, abaxial faces sparsely to densely pubescent, sparsely to moderately dotted with sessile and impressed glands, adaxial faces sparsely to densely pubescent, eglandular or sparsely to moderately dotted with sessile glands; inner phyllaries 12–24+, free, usually yellow to yellow-green proximally and green distally, sometimes green throughout, lanceolate to elliptic to obovate to oblanceolate, 5.2–12 \times 0.8–3 mm, apices acute to acuminate, abaxial faces sparsely to densely pubescent, eglandular or sparsely to moderately dotted with sessile and impressed glands, adaxial faces sparsely to moderately pubescent, eglandular or sparsely dotted with sessile glands. RAY FLORETS 14–44, pistillate, fertile; corollas yellow, 14–30 \times 3.5–8 mm, lobes 3, abaxial faces glabrous or sparsely pubescent, sparsely to moderately dotted with sessile glands, adaxial faces glabrous, eglandular. DISC FLORETS 150–400+, bisexual, fertile; corolla tubes yellow to yellow-brown, $\frac{1}{4}$ – $\frac{1}{3}$ the total length, limbs yellow, cylindric to cylindric-campanulate, 2.3–6 \times 0.6–1 mm, lobes 5, glabrous or sparsely pubescent, eglandular. RECEPTACLES hemispheric to globoid, paleae none. CYPSELAE obpyramidal to narrowly obpyramidal, 2.3–3.7 \times 0.7–1.1 mm, densely pubescent, hairs straight, forked, antrorse, eglandular or sparsely dotted with

sessile glands; pappi of 5–7 obovate- to lanceolate-aristate scales, $0.8\text{--}5.3 \times 0.4\text{--}0.8$ mm.

CHROMOSOME NUMBER. All three species of *Hymenoxys* subg. *Rydbergia* have $2n = 30$.

DISTRIBUTION. Mexico, the northern Sierra Madre Oriental in southeastern Coahuila and mid-western Nuevo León; United States from Arizona and New Mexico to Colorado, Utah, Wyoming, Idaho, and Montana (Fig. 1)

KEY TO THE SPECIES OF *HYMENOXYS* SUBG. *RYDBERGIA*

1. Aerial stems 8–30 cm tall, usually not branched distally; heads 1–10 per plant, usually borne singly; pappi of lanceolate-aristate scales (2.7–)4.1–5.3 mm long, nearly as long as the disc corollas; United States, widespread, Arizona and New Mexico to Colorado, Utah, Wyoming, Idaho, and Montana.
2. Caudices \pm branched; aerial stems arising singly from branches of caudices; basal leaf blades simple or pinnately divided into 3–5(–7) segments, mid leaf blades simple or divided into 3 segments, distal leaf blades simple; involucre 13–16 \times 19–23 mm; outer phyllaries 2–3.5 mm wide; pappi (2.7–)4.1–4.3 mm long; east-central Arizona, south-central New Mexico, north-central New Mexico, and south-central Colorado mainly along the Sangre de Cristo range 1. *H. brandegeei*
2. Caudices not branched or only moderately branched; aerial stems arising multiply from caudices; basal leaf blades pinnately or bipinnately divided into 3–15 segments, mid leaf blades simple or divided into 3–7 segments, distal leaf blades simple or divided into 3 segments; involucre 15–25 \times 18–30 mm; outer phyllaries 1–2 mm wide; pappi 4.5–5.3 mm long; western and central Colorado (not in Sangre de Cristo range) to Utah, Wyoming, Idaho, and Montana 2. *H. grandiflora*
1. Aerial stems 30–80 cm tall, usually branched distally; heads 5–35 per plant, usually borne in paniculiform to corymbiform arrays; pappi of ovate-aristate scales, 0.8–1.3 mm long, shorter than disc corollas; Mexico, known only from northern Sierra Madre Oriental in southeastern Coahuila and mid-western Nuevo León 3. *H. insignis*

1. *HYMENOXYS BRANDEGEEI* (Porter ex A. Gray) K. L. Parker, Madroño 10: 159. 1950.

Actinella brandegeei Porter ex A. Gray, Proc. Amer. Acad. Arts 13: 373. 1878, as *brandegei*. TYPE: UNITED STATES. Colorado: Huerfano Co.: “Sierra Blanca” (lectotype label), 1877, J. D. Hooker & A. Gray s.n. (LECTOTYPE here designated: GH!)

Actinea brandegeei (Porter ex A. Gray) Kuntze, Revis. gen. pl. 1: 303. 1891.

Rydbergia brandegeei (Porter ex A. Gray) Rydb., Bull. Torrey Bot. Club 33: 156. 1906.

Tetranneuris brandegeei (Porter ex A. Gray) K. L. Parker, Phytologia 45: 467. 1980.

Actinella grandiflora Torr. & A. Gray var. *glabrata* Porter, Synopsis of the Flora of Colorado (Misc. Publ. No. 4, U. S. Geol. & Geog. Survey of the Territories). 1874. TYPE: UNITED STATES. Colorado: Costilla Co.: “Alpine. Sangre de Cristo Pass.”

(protologue and holotype label), Aug 1873, T. S. Brandege 722 (HOLOTYPE: PH!; ISOTYPE: MO-208046!; probable ISOTYPE: PH!; possible ISOTYPES: GH—two collections on same sheet!, NY—two collections!, US-1415883!).

Rydbergia glabrata (Porter) Greene, Pittonia 3: 270. 1898.

CAUDICES \pm branched. AERIAL STEMS 1–3(–10) arising singly from branches of caudices, not branched distally, 8–24 cm. LEAVES: blades simple or pinnately divided into 3–5(–7) segments; basal leaf blades simple or divided into 3–5(–7) segments; mid leaf blades simple or sometimes divided into 3 segments; distal leaf blades simple. HEADS 1–3(–10) per plant, borne singly. PEDUNCLES 2–5 cm, usually densely tomentose distally beneath the involucre. INVOLUCRES 13–16 \times 19–23 mm. PHYLLARIES: outer phyllaries 10–20, usually basally connate 1/5–1/3 their lengths, sometimes

free, rarely purple-red-tinted on margins, $10\text{--}13.5 \times 2\text{--}3.5$ mm, apices rounded to acute, abaxial faces usually densely to sometimes moderately pubescent, adaxial faces sparsely to moderately pubescent, eglandular or sparsely to moderately dotted with sessile glands; inner phyllaries 12–20+, lanceolate to elliptic to obovate to oblanceolate, $6\text{--}10 \times 1.5\text{--}3$ mm, apices acuminate, abaxial faces sparsely to moderately dotted with sessile and impressed glands, adaxial faces sparsely pubescent, eglandular or sparsely dotted with sessile glands. RAY FLORETS 14–23; corollas $14\text{--}23 \times 3.5\text{--}7.5$ mm. DISC FLORETS 150–250+; corollas $4.1\text{--}5.2 \times 0.8\text{--}1$ mm. CYPSELAE $2.8\text{--}3.1 \times 1\text{--}1.1$ mm; pappi of 5–6 lanceolate-aristate scales, $(2.7\text{--})4.1\text{--}4.3 \times 0.4\text{--}0.8$ mm.

DISTRIBUTION (Fig. 1) AND HABITAT. Arizona, Colorado, and New Mexico; in north-central New Mexico and south-central Colorado, mainly along the Sangre de Cristo range. Meadows, often above timberline, 3612 ± 225 m (range 2800–4115 m; N = 52).

FLOWERING AND FRUITING. June through September, mainly July and August.

REPRESENTATIVE SPECIMENS (OF 75 SPECIMENS EXAMINED). UNITED STATES. ARIZONA. Apache Co.: Summit of Thomas Peak, White Mts, 3500 m, 18 Aug 1935, *Peebles & Smith 12546* (ARIZ, US); Exposed summit of Mt Baldy, White Mts, 3505 m, 3 Sep 1949, *Phillips & Phillips 3341* (ARIZ, NY, TEX, US). COLORADO. Alamosa Co.: Rio Grande National Forest, Sangre de Cristo Range, vicinity of S Zapata Lake, ca 3660 m, 15 Jul 1998, *Hogan 3427* (COLO). Costillo Co.: On divide of Culebra Range, head of N fork of Whiskey Creek, ca $\frac{1}{4}$ mi W of Las Animas Co, 3935 m, 14 Aug 1987, *Neely 4684* (COLO, CS). Custer Co.: San Isabel National Forest, Sangre de Cristo Range, North Colony Lakes basin, ca 3505 m, 30 Jul 1995, *Hogan 2790* (COLO, RM, UNM). Fremont Co.: 1874, *Brandeggee s.n.* (MO). Huerfano Co.: W Spanish Peak, 3000–3800 m, 9 Jul 1900, *Rydborg & Vreeland 5487* (NY). Las Animas Co.: Rocky S facing slopes on W Spanish Peak, 3720 m, 19 Jul 1995, *Scott 9317* (RM). Saguache Co.: Sangre de Cristo Range, 7.5 mi N of Crestone Peak, 3720 m, 25 Jul 1985, *Yeatts 2093* (COLO). NEW MEXICO. Colfax Co.: Ridges just S of Baldy Mt, 3600 m, 1 Jul 1968, *Hartman 2226* (RM, TEX). Lincoln Co.: White

Mts, 3050 m, 16 Aug 1897, *Wootton 492* (MO, NY, US). Otero Co.: White Mts, ca 0.5 mi N of top of Sierra Blanca, 3355 m, 5 Jul 1981, *Worthington 7217* (COLO). Rio Arriba Co.: Truchas Peak, 3810 m; 8 Aug 1908, *Standley 4791* (NY). San Miguel Co.: Top of Las Vegas Range, 3355 m, Jun 1901, *Cockerell 24* (RM). Santa Fe Co.: Santa Fe Baldy, 3780 m, 17 Jul 1954, *Hoff et al. 10417* (UNM). Taos Co.: Wheeler Peak, 3810 m, 8 Jul 1967, *Mackay 5T-328* (UNM); Carson National Forest, Goose Lake, 8 mi from Red River town, 3550 m, 23 Aug 1968, *Correll & Correll 36228* (LL).

2. HYMENOXYS GRANDIFLORA (Torr. & A. Gray) K. L. Parker, *Madroño* 10: 159. 1950. *Actinella grandiflora* Torr. & A. Gray, *Boston J. Nat. Hist.* 5: 109. 1845. TYPE: UNITED STATES. Wyoming: Fremont or Sublette Co.: "Wind River Chain of the Rocky Mts near snow line" (holotype label), J. C. Fremont s.n. (holotype: NY!).

Actinea grandiflora (Torr. & A. Gray) Kuntze, *Revis. gen. pl.* 1: 303. 1891.

Ptilepida grandiflora (Torr. & A. Gray) Rose, *Contr. U. S. Natl. Herb.* 3: 570. 1896.

Rydbergia grandiflora (Torr. & A. Gray) Greene, *Pittonia* 3: 270. 1898.

Tetraneuris grandiflora (Torr. & A. Gray) K. L. Parker, *Phytologia* 45: 467. 1980.

CAUDICES not branched or only moderately branched. AERIAL STEMS 1–10 arising multiply from caudices, usually not branched distally, 8–30 cm. LEAVES: blades simple or pinnately or bipinnately divided into 3–15 segments; basal leaf blades divided into 3–15 segments; mid leaf blades simple or divided into 3–7 segments; distal leaf blades simple or divided into 3 segments. HEADS 1–10 per plant, usually borne singly. PEDUNCLES 1–10 cm, usually densely tomentose distally beneath the involucre. INVOLUCRES $15\text{--}25 \times 18\text{--}30$ mm. PHYLLARIES: outer phyllaries 16–24, free or basally connate $1/5\text{--}1/4$ their lengths, $9\text{--}15 \times 1\text{--}2$ mm, apices acute, abaxial faces sparsely to densely pubescent, adaxial faces sparsely pubescent, eglandular or sparsely dotted with sessile glands; inner phyllaries 16–24+,

lanceolate to oblanceolate, 8–12 × 0.8–1.2 mm, apices acute to acuminate, abaxial faces eglandular or sparsely to moderately dotted with sessile and impressed glands, adaxial faces sparsely pubescent, eglandular or sparsely dotted with sessile glands. RAY FLORETS 15–34(–44); corollas 16–30 × 4–8 mm. DISC FLORETS 150–400+; corollas 5–6 × 0.6–1 mm. CYPSELAE 3.3–3.7 × 0.8–1 mm; pappi of 5–7 lanceolate-aristate scales, 4.5–5.3 × 0.4–0.8 mm.

DISTRIBUTION (Fig. 1) AND **HABITAT**. Colorado, Idaho, Montana, Utah, and Wyoming. Meadows, often above timberline, 3541 ± 279 m (range 2620–4270 m; N = 330).

FLOWERING AND FRUITING. June through September, mainly July and August.

REPRESENTATIVE SPECIMENS (OF 519 SPECIMENS EXAMINED). **UNITED STATES. COLORADO. Archuleta Co.:** S San Juans, ridge N of Green Lake, divide between the Navajo and S Conejos, 3750 m, 24 Aug 1972, *Willard 7284* (COLO). **Boulder Co.:** Niwot Ridge, Institute of Arctic and Alpine Research, ca 8 mi N of Nederland, 3660 m, *n* = 15, 16 Jun 1961, *Wiens 2872* (COLO). **Chaffee Co.:** Mt Princeton, 4115 m, 21 Jul 1940, *Livingston s.n.* (MO). **Clear Creek Co.:** Loveland Pass, 2*n* = 15II, 24 Jul 1988, *Bierner 88–68* (TEX). **Conejos Co.:** San Juan National Forest, just W of Continental Divide along trail to Crater Lake, 3720 m, 26 Jul 1998, *Heil 12374* (CS). **Dolores Co.:** San Juan National Forest, ca 2.5 air mi E of Rico, along the Colorado Trail at Black Hawk Basin, ca 3810 m, 15 Aug 1995, *Moore 8669* (RM). **Eagle Co.:** Gore Range, Eagles Nest Wilderness Area, S facing slopes near Deluge Lake, 3500 m, 17 Jun 1987, *Hogan & Arapkiles 188* (COLO). **El Paso Co.:** Pike's Peak, Glen Cove, 25 Jul 1935, *Christ 1211* (CS). **Garfield Co.:** Causeway Lake Basin, ca 36 air mi NNE of Glenwood Springs, ca 5 air mi NE of Trappers Lake, ca 3260 m, 12 Jul 1990, *Vanderhorst 1020* (RM); Mt Baxter, ca 7 air mi N of Glenwood Springs, ca 3385 m, 22 Jul 1990, *Vanderhorst 1249* (RM). **Gilpin Co.:** Rollins Pass, 3355 m, 17 Jul 1975, *Asplund 75–4* (RM). **Grand Co.:** Halfway up Ptarmigan Peak, FR 160.2 to FR 111 to unmarked trail off to the right just before the Bryer's Peak trailhead, 3476 m, 4 Jul 1999, *Owens & Ackerfield 389* (CS); Along SE ridge of Parkview Mt, 3500 m, 7 Aug 1995, *Tear 1823* (CS); Peak above Fall River Pass, Rocky Mt National Park, 3660 m, 30 Aug 1950, *Parker & Parker 7323* (TEX). **Gunnison Co.:** Vicinity of Cumberland Pass, 3690 m,

23 Jul 1964, *Gierisch 2867* (COLO, CS, RM); Southern Gunnison Basin, from level area on E side of saddle S of Sheep Mt to the top of Sheep Mt, 3780–4020 m, 29 Jul 1999, *Arnett & Taylor 5982* (RM); Robinson Basin, 30 mi N of Gunnison, 8 mi W of Crested Butte, 2 mi N of Kebler Pass, 3598 m, 9 Jul 1967, *Bathke 381* (CS). **Hinsdale Co.:** Ca 1 mi S of Slumgullion Pass and the head of Mill Creek, 3660 m, 28 Jun 1961, *Barrell 128–61* (US); Southern Gunnison Basin, San Juan Mts, along E Fork Alpine Gulch, ca 1.1–1.2 air mi WSW of Red Mt, ca 0.5–1.4 air mi NNW of Grassy Mt, 3230–3720 m, 30 Aug 1999, *Arnett 7917* (RM). **Jackson Co.:** Park Range, ca 23 air mi WSW of Walden, Mt Ethel and proximity, 3520 m, 25 Jul 1989, *Kastning et al. 2450* (RM); Medicine Bow Mts, to summit of Clark Peak, ca 6 air mi NE of Gould, 3870–3950 m, 21 Jul 2000, *Hartman & Nunn 68602* (RM). **Lake Co.:** Hwy 82, 0.8 mi E of Independence Pass, 19 Aug 1975, *Bierner 51398* (TEX). **La Plata Co.:** Little Kate Mine, La Plata Mts, 3505 m, 14 Jul 1893, *Baker et al. 516* (COLO, GH, NY, RM, US). **Larimer Co.:** Rocky Mts National Park, Ute Trail on Tombstone Ridge, ca 8–9 air mi W of Estes park, 3535 m, 26 Jul 1986, *Williams 342* (RM); Medicine Bow Mts, Clark Peak from Ruby Jewel Trailhead, ca 21 air mi SE of Walden, 3780–3935 m, 5 Aug 2001, *Nunn 4234* (RM). **Mesa Co.:** Mosquito Mt, 3810 m, Jul–Aug 1877, *McCosh & Greene s.n.* (NY); Side of highest spine of Crag Crest Trail, 17 Jul 1982, *Young 10* (COLO). **Mineral Co.:** ESE exposure above timberline on saddle between Sawtooth Mt and Table Mt, 3780 m, 23 Jun 1984, *Mooers & Berg 166* (CS, NY). **Montezuma Co.:** Mt Hesperus, W ridge, 6 Aug 1995, *Cyndie 726* (COLO). **Ouray Co.:** San Juan Mts, W slope of Engineer Mt, 3965 m, 26 Jun 1996, *Scott 10374* (RM). **Park Co.:** Pike National Forest, along rd 659, in tundra ca 10 mi N of Fairplay, 3665 m, 6 Aug 2002, *King & Garvey 12285* (NY); Summit of Georgia Pass, N of Jefferson, 3450 m, 20 Jul 1984, *Weber & Randolph 17359* (COLO). **Pitkin Co.:** Ca 13 mi ESE of Aspen, Independence Pass vicinity, 4035 m, 23 Jul 1990, *Brooks 20447* (RM). **Rio Blanco Co.:** Between Killarny Reservoir and old Jeep Trail on Little Flat Tops, ca 45 air mi ENE of Meeker, ca 9.5 air mi W of Yampa, 3295 m, 26 Jun 1990, *Nelson 19096* (RM); Big Marvin Peak, ca 30 air mi ESE of Meeker, 3565 m, 16 Aug 1990, *Vanderhorst 1833* (RM). **Rio Grande Co.:** Greyback Mt, summit and upper rocky slopes, 3840 m, 20 Aug 1978, *Hartman & Coffee 8029* (RM). **Routt Co.:** Park Range, 21 air mi WNW of Walden, at Red Dirt Pass and Mt Zirkel, 3565 m, 20 Jul 1989, *Kastning & Fraser 2352* (RM). **Saguache Co.:** La Garita Wilderness Area, head of Cochetopa Creek, 11–13 Aug 1971, *Willard 6882* (COLO). **San Juan Co.:** Peak above Red Mt Pass, San Juan Forest, 3963 m, 26 Aug 1946, *Parker et al. 6404* (GH, MO, NY, OKLA, US). **San Miguel Co.:** Near Trout Lake, 3505

m, 18 Aug 1924, *Payson & Payson* 4166 (RM). **Summit Co.:** Gore Range, Eagles Nest Wilderness Area, head of S Willow Creek between Eccles Pass and Red Buffalo Pass, 3500 m, 8 Jul 1986, *Hogan & Arapkiles* 85 (COLO); Loveland Pass, 3655 m, 25 Jun 1962, *Gillett & Taylor* 11504 (US). **Teller Co.:** N-facing slope, 3750 m, 10 Sep 1979, *Creel & Mijer* 74 (CS). **IDAHO. Custer Co.:** Lost River Mts, E fork Pahsimeroi River, 3140 m, 14 Aug 1944, *Hitchcock & Muhlick* 11104 (GH, NY, UTC). **Fremont Co.:** Mts NE of Henry Lake, 2805 m, 11 Jul 1920, *Payson & Payson* 1969 (GH, MO, NY). **Lemhi Co.:** E slope of Lemhi Range, Salmon National Forest, ca 1 mi NW of Meadow Lake, 5 mi W of Gilmore, 3020 m, 4 Jul 1973, *Henderson & Jackson* 964 (ASU, NY). **MON-TANA. Beaverhead Co.:** High limestone ridge connecting Sheep Mt and Black Lion Mt, Pioneer Range, 2835 m, 30 Jul 1945, *Hitchcock & Muhlick* 12984 (GH, NY, UTC); Ridge 0.75 mi NW of Garfield Peak, 2775 m, 2 Aug 1981, *Thompson* 1938 (MONTU). **Gallatin Co.:** Lone Mt, S of Bozeman, 1906, *Chesnut* 36 (US). **Granite Co.:** Flint Creek Mts, SE flank of Racetrack Peak, 2835 m, 22 Jul 1959, *Bamberg* 433 (COLO). **Madison Co.:** Talus Mt 0.5 mi N of Koch Peak, Taylor Mts, 2 Aug 1946, *Hitchcock & Muhlick* 15169 (NY); Top of Gravelly Range 13 mi S of Crockett Lake, 25 Jul 1947, *Hitchcock* 16813 (NY). **Silver Bow Co.:** Red Mt, 2850 m, 21 Jul 1981, *Lackschewitz* 9721 (NY). **UTAH. Daggett Co.:** Santiago Peak, Uinta Mts, 3355 m, Sep 1878, *Cosh s.n.* (NY). **Duchesne Co.:** Uinta Mts, head of Wedge Hollow, 2.9 mi due SW of Upper Stillwater Reservoir, 3385 m, 22 Jun 1994, *Huber* 1126 (MO, NY, RM). **Grand Co.:** Lower SSW ridge of Mans Peak, ca 18 mi ESE of Moab, 3535 m, 27 Jul 1984, *Tuhy* 1823 (NY, UTC). **Piute Co.:** Grassy tundra, above timberline, Delano Peak, above Puffer Lake, Tushar Mts, 3505 m, 22 Aug 1946, *Parker et al.* 6354 (ARIZ, TEX, US). **Salt Lake Co.:** Wasatch Range, Little Cottonwood Canyon, above Albion Basin, Devil's Castle Peak, 3340 m, 16 Aug 1981, *Arnold* 5833 (NY, UT, UTC). **San Juan Co.:** La Sal Mts, 3300–3600 m, 7 Jul 1911, *Rydborg & Garrett* 8682 (NY, RM, US, UT). **Summit Co.:** Divide between E fork of Bear River and Black's Fork, 3355 m, 9–13 Jul 1930, *Goodman & Hitchcock* 1541 (GH, MO, NY, RM). **Utah Co.:** Lone Peak Wilderness Area, along ridge E of Mt Pfeifferhorn, above Red Pine Fork & Maybird Gulch, ca 3320 m, 30 Jul 1983, *Franklin & Chandler* 325 (NY). **WYOMING. Albany Co.:** Medicine Bow National Forest, in tundra along hwy 130, ca 35 mi E of Saratoga, ca 3318 m, 18 Jul 2000, *King & Garvey* 11425 (MO, NY). **Big Horn Co.:** Big Horn Mts, SE of Hunt Mt, ca 33.5 air mi ESE of Lovell, ca 19 air mi WSW of Burgess Junction Meadow, 2990 m, 13 Jul 1980, *Nelson* 6352 (NY). **Carbon Co.:** Open mesic alpine meadow along hwy 130, high in the Medicine Bow Mts, 10 Jul 2000, *McNeilus* 00–833 (TEX). **Fremont Co.:** Popo Agie

Primitive Area, Wind River Mts, W of Lander, tundra area in cirque above Cathedral Lake, 3280 m, 6 Aug 1975, *Albee* 2748 (UT). **Park Co.:** Top of Carter Mt, at headwaters of N fork of Meeteetse Creek, ca 24–25 mi SW of Cody, ca 3200 m, 3 Jul 1987, *Evert* 12890 (NY); Beartooth Plateau, 3050–3325 m, 26 Aug 1959, *Bamberg* 483 (COLO). **Sheridan Co.:** Dome Lake, Elk Mt, 3505 m, 28 Jun 1897, *Pammel & Stanton s.n.* (NY). **Sublette Co.:** W Slope Wind River Range, W flank of Temple Peak, 4 air mi E of Big Sandy Lodge, ca 36.5 air mi ESE of Pinedale, ca 3350 m, 12 Jul 1991, *Fertig* 9136 (RM). **Teton Co.:** Teton Range, Grand Teton National Park, on talus just below the summit of Table Mt, ca 2.5 air mi WNW of the Grand Teton, 3300 m, 9 Aug 1988, *Halse* 3739 (ARIZ).

3. HYMENOXYS INSIGNIS (A. Gray) Cockrell, *Torreya* 4: 170. 1904.

Actinella insignis A. Gray, *Proc. Amer. Acad. Arts* 19: 31. 1883. TYPE: MEXICO. Coahuila: "Coahuila, Mexico, at Leries, in the mountains east of Saltillo, at 10,000 feet, July, 1880" (protologue), "Leries, 15 leagues E. of Saltillo, 10,000 feet, July, 1880" (holotype label), "Leries E. of Saltillo, 10,000 ft., February to October, 1880" (K isotype label), "Leries, Mexico, a mountain section 15 leagues east of Saltillo, supposed to be 10,000 feet above the level of the sea; July 10 to 13–1880" (NY and PH isotype labels), *E. Palmer* 632 (HOLOTYPE: GH!; ISOTYPES: K! [photograph of K isotype at F!, NY!], NY!, PH!, US-47375!).

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

CAUDICES \pm branched. AERIAL STEMS 1–10 arising singly or multiply from branches of caudices, usually branched distally, 30–80 cm. LEAVES: blades simple or pinnately or bipinnately divided into 3–41+ segments; basal leaf blades divided into 11–41+ segments; mid leaf blades divided into 9–25 segments; distal leaf blades simple or usually divided into 3–13 segments. HEADS 5–35 per plant, usually borne in paniculiform to corymbiform arrays. PEDUNCLES 3–10 cm, densely pubescent to tomen-

tose distally beneath the involucre. INVOLUCRES 10–15 × 15–20(–25) mm. PHYL-LARIES: outer phyllaries 14–23, free or only slightly basally connate, 7–12 × 1.5–4 mm, apices acute, abaxial faces moderately to densely pubescent, adaxial faces sparsely to moderately pubescent, eglandular or sparsely dotted with sessile glands; inner phyllaries 14–25+, lanceolate to elliptic to oblanceolate, 5.2–9 × 2–3 mm, apices acute to acuminate, abaxial faces eglandular, adaxial faces sparsely to moderately pubescent, eglandular. RAY FLORETS 15–33(–40); corollas 15–22 × 4–7 mm. DISC FLORETS 150–400+; corollas 2.3–3 × 0.7–1 mm. CYPSELAE 2.3–3 × 0.7–1 mm; pappi of 5–7 ovate-aristate scales, 0.8–1.3 × 0.4–0.7 mm.

DISTRIBUTION (Fig. 1) AND HABITAT. Mexico, known only from northern Sierra Madre Oriental in southeastern Coahuila and mid-western Nuevo León. Meadows and woodlands, sometimes above timberline, 3123 ± 427 m (range 2440–3650 m; N = 23).

FLOWERING AND FRUITING. May to October, mainly June to August.

REPRESENTATIVE SPECIMENS (OF 36 SPECIMENS EXAMINED). MEXICO. COAHUILA. Rd past San Antonio, ca 30 mi E of jct with hwy 57, Douglas fir and oak hillsides, 2650 m, 2n = 15II, 21 Jun 1976, *Pinkava* P13573 (ASU); Sierra El Coahuilón, 3040 m, 14 May 2000, *Hinton* 27534 (TEX); Cerro de la Viga, ca 4 mi E of Jamé on logging rd, 3050 m, 15 May 1981, *Poole & Nixon* 2275 (TEX). NUEVO LEÓN. Las Joyas, 2700 m, 30 Sep 1989, *Hinton* 19840 (TEX); Cerro Potosí, top of mt, ca 3650 m, n = 15, 1 Jul 1959, *Beaman* 2649 (GH, NY).

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