Taxonomy of Hymenoxys Subgenus Rydbergia (Asteraceae: Helenieae: Tetraneurinae)

Author: Mark W. Bierner
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Taxonomy of Hymenoxys subgenus Rydbergia (Asteraceae: Helenieae: Tetraneurinae)

Mark W. Bierner

School of Biological Sciences and Plant Resources Center, The University of Texas, Austin, Texas 78712
Present address: Boyce Thompson Arboretum, 37615 U.S. Highway 60, Superior, Arizona 85273

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 sinonimias, 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 (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. Phileozera (Bier- ner, 2001) and species now separated from Hymenoxys into Tetraneuris Greene (Bier- ner 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 conspecific 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*, *Philezera*, 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. pinitorum, 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. chrysanthenoides, respectively, of subg. Phileozera, but they had similar average chemical similarity indices to H. cooperi, H. russeyi, 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**

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

**Polycarpic Perennials. Caudices** unbranched or ± 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 dotted with impressed glands; basal leaf bases expanded, clasping, usually persistent. HEADS 1–35 per plant, borne singly or in paniculiform to corymbiform arrays. PENDUNCLES 1–10 cm, expanded apically, moderately to densely pubescent, often densely tomentose distally beneath the involucres, sparsely to moderately dotted with sessile glands. INVOLUCRES hemispheric to subglobose, 10–25 × 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 × 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 ob lanceolate, 5.2–12 × 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 × 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, ½–¾ the total length, limbs yellow, cylindric to cylindric-campanulate, 2.3–6 × 0.6–1 mm, lobes 5, glabrous or sparsely pubescent, eglandular. RECEPTACLES hemispheric to globose, paleae none. CYPSELAE obpyramidal to narrowly obpyramidal, 2.3–3.7 × 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, 0.8–5.3 × 0.4–0.8 mm.

CHROMOSOME NUMBER. All three species of *Hymenoxys* subg. *Rydergia* 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 ± 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; involucres 13–16 × 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; involucres 15–25 × 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*


CAUDICES ± 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 tormentose distally beneath the involucres. INVOLUCRES 13–16 × 19–23 mm. PHYLARIES: outer phyllaries 10–20, usually basally connate 1/5–1/3 their lengths, sometimes
free, rarely purple-red-tinted on margins, 10–13.5 × 2–3.5 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 oblong-lanceolate, 6–10 × 1.5–3 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; inner phyllaries 16–24+.

**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.


**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 involucres. **INVOLUCRES** 15–25 × 18–30 mm. **PHYLLARES:** outer phyllaries 16–24, free or basally connate 1/5–1/4 their lengths, 9–15 × 1–2 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 dotted with sessile 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.

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 Pahsimeroriver, 3140 m, 14 Aug 1944, "Hitchcock & Muhlick 11104" (GH, NY, UTC); Ridge 0.75 mi NW of Garfield Peak, 3355 m, 27 Jul 1919, "Thompson 1938" (MONTU).


**Actinella insignis** A. Gray, Proc. Amer. Acad. Arts 19: 31. 1883. **TYPE:** MEXICO. Coahuila: "Coahuila, Mexico, at Lerios, in the mountains east of Saltillo, at 10,000 feet, July, 1880" (protologue), "Lerios, 15 leagues E. of Saltillo, 10,000 feet, July, 1880" (holotype label), "Lerios E. of Saltillo, 10,000 ft., February to October, 1880" (K isotype label), "Lerios, 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 Fl!, NY!], NY!, PH!, US-47375]).


**CAUDICES** ± 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 pinnatiligniform to corymbose arrays. **PEDUNCLES** 3–10 cm, densely pubescent to tomen-
LUNDELLIA

tose distally beneath the involucres. INVOLUCRES 10–15 × 15–20(–25) mm. PHYL­LARIES: 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 Pi3573 (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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LITERATURE CITED


Bierner: Taxonomy of Hymenoxys Subg. Rydbergia


