# *CUNICULOTINUS* AND *LORANDERSONIA*, TWO NEW GENERA OF ASTERACEAE: ASTEREAE AND NEW COMBINATIONS IN *CHRYSOTHAMNUS*

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ABSTRACT

***Cuniculotinus*** is described as a new monotypic genus from California and Nevada to accommodate *Chrysothamnus gramineus*, resulting in the new combination ***Cuniculotinus gramineus***. Sequence-based phylogenetic investigations clearly demonstrate its remoteness from *Chrysothamnus* and place it nearer *Sericocarpus*. Four additional species regarded as *Chrysothamnus* are likewise shown to be phyletically distinct and are accomodated in the proposed new genus ***Lorandersonia***. *Lorandersonia* also includes one species previously recognized in *Hesperodoria*, *H. salicina*, and two species previously treated as *Tonestus*, *T. microcephalus* and *T. peirsonii*. New combinations in *Lorandersonia* are ***L. baileyi***, ***L. linifolia***, ***L. microcephala***, ***L. peirsonii***, ***L. pulchella***, ***L. salicina***, and ***L. spathulata***. *Chrysothamnus* is further modified by the inclusion of *Hesperodoria scopulorum* and *Vanclevea stylosa*, necessitating the new specific combinations ***C. scopulorum*** and ***C. stylosus*** and the varietal combination ***C. scopulorum*** var. ***canonis***.

RESUMEN

Se describe el género ***Cuniculotinus***, como un género nuevo monotípico de California y Nevada para ubicar a *Chrysothamnus gramineus* H.M. Hall. Por lo tanto se realiza una nueva combinación, ***C. gramineus***. Investigaciones filogenéticas basadas en secuenciación de ADN demuestran claramente su lejanía con *Chrysothamnus* y la ubica cerca de *Sericocarpus*. Del mismo modo, cuatro especies adicionales consideradas como *Chrysothamnus* muestran ser filogenéticamente distintas, por lo cual se propone el género nuevo ***Lorandersonia***. Este nuevo género también incluye especies reconocidas previamente en *Hesperodoria*, *H. salicina*, y dos especies tratadas generalmente como *Tonestus*, *T. microcephalus* (Cronquist) G.L. Nesom & D.R. Morgan y *T. peirsonii* (D.D. Keck) G.L. Nesom & D.R. Morgan. Las combinaciones nuevas en *Lorandersonia* son: ***L. baileyi***, ***L. linifolia***, ***L. microcephala***, ***L. peirsonii***, ***L. pulchella***, ***L. salicina***, ***L. spathulata***. Además, se modifica *Chrysothamnus* con la inclusión de *Hesperodoria scopulorum* (M.E. Jones) Greene y *Vanclevea stylosa* (Eastwood) Greene lo cual hace necesarias las nuevas combinaciones específicas, ***C. scopulorum*** y ***C. stylosa***, y la combinación de variedad *C. scopulorum* var. ***canonis***.

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## INTRODUCTION

Phylogenetic investigations based on sequence data of the nuclear ribosomal DNA spacer region, the ITS 1 and 2, plus the 5.8S, and a portion of 3' ETS, used to test decades-old hypotheses of relationships for species of *Chrysothamnus*, readily demonstrate its non-monophyly (Roberts & Urbatsch 2004). Hall and Clements (1923) comprehensively monographed *Chrysothamnus*, and Anderson (1986a) provided an updated and inclusive synopsis, nomenclatural information, keys, and distribution maps. During the intervening years, five species unknown to earlier monographers were published or elevated to specific rank; *Chrysothamnus pyramidatus* Hall & Clements was transferred to *Baccharis* (Rzedowski 1972) and subsequently placed in *Aztecaster* (Nesom 1993). The treatments by Hall and Clements and Anderson also differed in species alignments at infrageneric levels.

The sixteen species accounted for by Anderson (1986a) are placed in four distantly related clades in our sequence-based gene tree shown in Figure 1 (Roberts & Urbatsch 2004). Except for *Chrysothamnus* sect. *Punctati*, infrasectional gene tree relationships compared to the five sections recognized by Anderson (1986a) are largely incongruous. *Chrysothamnus albidus* (M.E. Jones ex A. Gray) Greene (sect. *Chrysothamnus*), *C. paniculatus* (A. Gray) H.M. Hall and *C. teretifolius* (Durand & Hilgard) H.M. Hall (sect. *Punctati*), and *C. nauseosus* Pallas ex Pursh) G.L. Nesom & G.I. Baird and *C. parryi* (A. Gray) G.L. Nesom & G.I. Baird (sect. *Nauseosi*) were resolved within *Ericameria*, supporting the conclusions of Nesom and Baird (1993), whose decisions were partially influenced by cpDNA restriction enzyme investigations of Suh (1989) and Morgan (1990). Thus, two independent molecular data sets, one chloroplast and one nuclear, corroborate the generic disposition of sect. *Punctati* and sect. *Nauseosi*. *Chrysothamnus gramineus* (sect. *Gramini*), the next most divergent taxon, is positioned outside of *Sericocarpus* and is here segregated as the monospecific genus *Cuniculotinus*.

*Lorandersonia* is proposed to accommodate four other species of *Chrysothamnus*, resulting in the following new combinations: *L. baileyi* and *L. pulchella* (*Chrysothamnus* sect. *Pulchelli* sensu Anderson 1986a) and *L. linifolia* and *L. spathulata* (sect. *Chrysothamnus*). Three additional species are robustly supported within the *Lorandersonia* clade and new combinations are made for these: *L. microcephala* and *L. personii*, formerly regarded as *Tonestus*, and *L. salicina*, traditionally treated within *Hesperodoria*.

*Chrysothamnus* in the sense of Anderson (1986a) is left with seven species. Two additional taxa regarded as other genera are resolved within the *Chrysothamnus* clade and new combinations are proposed for them: *C. scopulorum* and *C. stylosus*, previously treated as *Hesperodoria scopulorum* and *Vancleva stylosa*, respectively. *Chrysothamnus* as newly constituted comprises 9 species (Fig. 1).

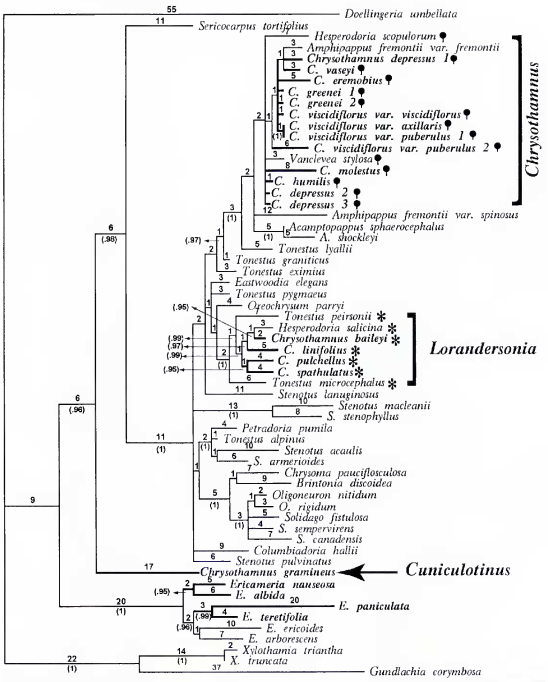


FIG. 1. Fifty percent majority rule consensus tree resulting from Bayesian analysis of combined ETS and ITS data sets is shown. This figure is modified from one published in Roberts & Urbatsch (2004). More details and a discussion of results from this and other analyses based on these sequence data are given. Bolded taxon names and wider branches highlight taxa treated as *Chrysothamnus* (Anderson 1986a). A large arrow indicates taxa treated herein as *Cuniculotinus*, the asterisk symbol * those considered *Lorandersonia*, and the ✝ symbol those taxa regarded as *Chrysothamnus*.

The primary purpose of the present paper is to provide formal nomenclatural changes reflecting the relationships discovered in our sequence-based phylogenetic studies. Taxa are also characterized and their relationships are discussed. A key to the taxa considered in this study is provided.

## NOMENCLATURAL TREATMENT

**Cuniculotinus** Urbatsch, R.P. Roberts, & Neubig, gen. nov. TYPE: *Chrysothamnus gramineus* H.M. Hall, Muhlenbergia 2:342. 1916. *Cuniculotinus gramineus* (H.M. Hall) Urbatsch, R.P. Roberts, & Neubig, combination made herein. *Chrysothamnus* sect. *Gramini* L.C. Anderson, in part, Proc. Symp. Biol. *Artemisia* and *Chrysothamnus*, 29. 1986. *Ericameria* sect. *Gramini* L.C. Anderson, Great Basin Naturalist 55:87. 1995, in part.

E radice perenne multicaulis; caules erecti ca. 1 dm alti glabri striati, basi frutescentes usque ad apices foliosi; folia alterna sessilia lanceolata acuminata 30–85 mm longa 3–9 mm lata e basi 3–5-nervia glabria, marginibus integris scabris; capitula pauca, laxe racemosa 1–2 bracteata; bracteae angustae acutae quam involucro brevioribus; pedunculi 0.5–8 cm longi ad axillas foliorum oriundis; involucra cylindracea 11–15 mm longa 3–4 mm lata; phyllaria valde imbricata ca. 3-seriata oblonga obtusissima chartacea, exterioribus mucronatis ciliatis apice viridescentibus; flosculi disci 4–7 consimiles, corollis glabris tenuibus infundibuliformibus 9–12 mm longis, dentibus 5 ovatis acutis, antheris basi minute auriculatis apice attenuatis, ramis stylorum acutis longe exsertis; cypselae fere exacte cylindraceis 5–6-striatae glabrae; pappi setae argentei corollae aequilongi.

Subshrubs from a branching, woody caudex to 1 dm. Stems annual, several, to 6 dm, green with tan ridges descending from leaf bases, glabrous. Leaves cauline, alternate, ascending, sessile, linear to lanceolate or oblong-oblanceolate, 30–85 × 3–9 mm, coriaceous, margins entire or edged with conic trichomes, glabrous to sparsely pubescent, often resin dotted, midvein and 2–4 collateral veins prominent; basal leaves ± persistent; cauline leaves reduced in size distally and becoming bract-like in the capitulescence. Capitulescences solitary to cymose at branch tips, branches racemose. Involucres tubinate to cylindric, 11–15(–17.5) × 3–4 mm. Phyllaries in 4–6 series, graduated, silvery to pale yellow, generally marked with green to brownish distal patch, not keeled, ±imbricate, ovate or oblong to obovate, 2–14 × 0.7–3 mm, mostly chartaceous, midvein and 2 collaterals evident, apices truncate, mucronate to caudate tipped. Capitula discoid, receptacles flat, finely alveolate. Disk flowers 4–7, yellow, corollas 9–12 mm, lobes acute, 1–1.3 mm; anthers 3.1–4.1 mm, appendages attenuate, 0.5–1.1 mm. Style branches 3.5–4.2 mm, appendages linear, 1.4–1.7 mm, apices acute. Cypselae tan-brownish, oblong, 7–9 mm, glabrous, 5–6 nerved. Pappi silvery-tan, ±80 minutely-setose bristles, 8–10 mm. $x = 9$.

*Etymology.*—The generic name is based on the Latin word *cuniculus*, a rabbit, + "tinus" as applied to laurustinus (*Viburnum tinus* L.), a shrubby plant," thus "rabbit brush" a commonly used name for species of *Chrysothamnus* in the traditional sense.

*Prominent features, distribution, and relationships.*—*Cuniculotinus* is distinguished by its herbaceous annual stems arising from a woody caudex; leaves relatively broad, nearly glabrous, with a prominent midvein and 1–2 pairs of collateral veins; capitula discoid, racemosely disposed; phyllaries multiseriate, imbricate, mostly chartaceous, often truncate to emarginate and mucronately-tipped that when fresh are marked with a conspicuous, green, apical patch. Its only known species, *C. gramineus*, occurs in Clark and Nye counties, Nevada,

and adjacent Inyo County, California, where it grows as an uncommon, understory element in yellow pine savanna communities at relatively high elevations. Sequence-based phylogenies show it in a relatively isolated position, with *Sericocarpus* as its closest kin; alternatively, it occupies a position between *Sericocarpus* and *Ericameria* (Roberts & Urbatsch 2004; Beck et al. 2004). *Sericocarpus*, with two species in the western United States and three in the east, also exhibits an herbaceous perennial life form and has coriaceous, green-tipped, multiseriate, phyllaries.

**Cuniculotinus gramineus** (H.M. Hall) Urbatsch, R.P. Roberts, & Neubig, comb. nov. BASIONYM: *Chrysothamnus gramineus* H.M. Hall, Muhlenbergia 2:342. 1916. *Ericameria graminea* (H.M. Hall) L.C. Anderson, Great Basin Naturalist 55:86. 1995. *Petradoria discoidea* L.C. Anderson, nom. nov., Trans. Kans. Acad. Sci. 65:676. 1964. [*non Petradoria graminea* Wooton & Standley, Contr. U.S. Natl. Herb. 16:183. 1913. *Petradoria pumila* Greene var. *graminea* (Wooton & Standley) S.L. Welsh, Great Basin Naturalist 43:324. 1983]. TYPE: U.S.A. NEVADA: Clark Co.: Charleston Mountains, head of Lee Canyon, alt. 2450 m, 4 Aug 1913, *A.A. Heller 11075* (HOLOTYPE: UC 175597).

*Discussion.*—The relationship of *Chrysothamnus gramineus* has puzzled systematists since its discovery and publication by Hall (1916). Hall and Clements (1923) noted the anomalous nature of the species relative to other *Chrysothamnus* but justified their placement of it by reference to its striate achenes, which are similarly seen in members of *Chrysothamnus* sect. *Pulchelli* and in *C. vaseyi*. Potential kinship with the monotypic *Petradoria* and with *Hesperodoria scopulorum* were also suggested but dismissed due to morphological discordance (Hall & Clements 1923). Anderson (1964a) concluded that anatomical and morphological evidence supported the placement of *C. gramineus* in *Petradoria*, a genus previously containing but one species, *P. pumila* (Nutt.) Greene. The published name *Petradoria graminea* Wooton & Standley for a different taxon necessitated creating the epithet *P. discoidea* L.C. Anderson for *C. gramineus*. Anderson (1983) noted similarities in habit and other features of *P. discoidea* to *C. eremobius* L.C. Anderson, also from Nevada, subsequent to the discovery and publication of the latter. Shortly thereafter, he re-evaluated the status of these species and reinstated *P. discoidea* within *Chrysothamnus*, accommodating both it and *C. eremobius* in his newly proposed *Chrysothamnus* sect. *Gramini* (Anderson 1986a). Molecular-based studies have shown *Cuniculotinus* to be distant from its earlier hypothesized congeners and its treatment as a distinct genus is warranted (Roberts & Urbatsch 2004).

**Lorandersonia** Urbatsch, R.P. Roberts, & Neubig, gen. nov. TYPE: *Linosyris pulchella* A. Gray, Pl. Wright. 1:96. 1852. *Lorandersonia pulchella* (A. Gray) Urbatsch, R.P. Roberts, & Neubig, combination made herein. *Chrysothamnus* Nutt., Trans. Amer. Philos. Soc. ser. 2, 7:323. 1840, in part. *Hesperodoria* Greene, Leafl. Bot. Observ. Crit. 1:173. 1906, in part. *Tonestus* A. Nelson, Bot. Gaz. 37:262. 1904, in part.

Plantae frutices vel suffrutices; caules erecti ad ascendentes; folia plerumque semper virentia linearia ad oblonga vel lanceolata ad anguste oblanceolata, costis prominentibus aliquando cum 1–2 nervae collaterales, involucri valde gradati vel subaequales 3–6-seriati; phyllaria imbricatia vel verticalia ordinata; capitula discoidea vel radiata, flosculi radii (1–)6–8 pistillati fertiles, corollis flavis, flosculi disci 4–15, corollis coloratis similibus flosculis radiis; pappi setae albidi 10–80+ subaequalis similes in flosculi radii et disci.

Plants suffrutescent or shrubs to 3.5 m. Stems erect to ascending, often fastigiately or intricately branched; bark typically tan, becoming white to gray when older; twigs usually greenish, glabrous to scabrous, often resinous, punctate in one species. Leaves mostly evergreen, cauline, often crowded, appressed or ascending to spreading, becoming deflexed in one species, laminar, linear to oblong or lanceolate to narrowly oblanceolate, 4–75 × 0.5–8 mm, sessile or short-petiolate, blades planar to concave, margins entire or edged with trichomes, apices acute, glabrous to scabrous, sometimes punctate, often ± resin-coated, sometimes resin-dotted; midvein prominent, 1–2 pairs of collateral veins sometimes present. Capitulescences usually congested, rounded compound cymes to corymbose, occasionally racemose. Involucres cylindric to obconic or hemispheric, 4–15 × 1.5–6 mm. Phyllaries in 3–6 series, imbricate to vertically aligned, strongly graduated or subequal, green to tan, ovate to oblong or lanceolate, to oblanceolate, 0.5–7 × 0.5–1.3 mm, apices acute, acuminate, cuspidate, obtuse, erect or slightly spreading, often resinous; midvein obscure to evident, sometimes enlarged subapically and glandular; lowermost sometimes herbaceous or herbaceous-tipped, otherwise mostly chartaceous. Capitula discoid or radiate in *L. microcephala* (rays have also been observed in *L. spathulata*), flowers 4–22. Ray flowers (1–)6–8, pistillate, fertile, ranging from pale to darker yellow; laminae elliptic to obovate, 3.5–5 × ±1 mm. Disc flowers 4–15, bisexual, corollas same color as ray corollas, 3.5–14 mm, lobes erect to spreading or reflexed, 0.5–2.2 mm. Style branches 1.7–4.6 mm, appendages lanceolate or attenuate to subulate, 0.7–2.2 mm. Cypselae mostly tan to brownish, usually prismatic, oblong to obconic, 1.5–7 mm, glabrous to densely pubescent. Pappi similar in ray and disk flowers, whitish-tan, 20–80+, subequal, setose bristles, 3–12 mm. $x = 9$.

*Etymology.*—*Lorandersonia* is named for Loran C. Anderson, Professor of Biological Sciences, Florida State University, Tallahassee, Florida, who has dedicated much of his professional career to the study of *Chrysothamnus* and related Astereae and has significantly increased our knowledge of these taxa.

*Prominent features, distribution, and relationships.*—Features diagnostic for the genus include the following: shrubs with leafy stems; stems annual in *L. microcephala* and *L. peirsonii* from a woody caudex; leaves ascending, often parallel to the stem but not appressed, sessile to subsessile, laminar, oblanceolate to narrowly so, margins entire to ciliate, remotely serrate in *L. peirsonii*, apices attenuate, obtuse in *L. peirsonii*, and blades relatively thin, midvein conspicuous, collateral veins arising proximally often evident; capitula usually numer-

ous, small, congested, organized into rounded cymes, forming corymboid capitulescences, monocephalous in *L. peirsonii*; phyllaries in 3–6 series, typically strongly graduated, chartaceous except for an apical or subapical, often narrow, diamond-shaped green patch, median vein mostly evident, sometimes somewhat thickened distally, phyllaries subequal in *L. peirsonii*; ray flowers absent except in *L. microcephala* and *L. peirsonii*, rarely present in *L. spathulata*. Evenly spaced gland-tipped hairs occur at least on young stems and emergent leaves, especially those transitional from leaves to phyllaries. The glandular portion is soon deciduous in most species but is persistent in *L. peirsonii*.

The southern Rocky Mountains is the center of diversity for this genus, but its entire range includes central Coahuila and northern Chihuahua, Mexico, northward to southwestern Kansas, southern Montana, and central Utah, with one outlyer in Inyo and Mono counties, California. Species in this genus occupy a considerable altitudinal range, 300–3600 meters, and are adapted to various arid habitats ranging from sand dunes to stony soils and rock crevices.

Basal to *Lorandersonia* in our gene trees are *Oreochrysum parryi* (A. Gray) Rydberg, *Tonestus pygmaeus* (Torrey & A. Gray) A. Nelson, and *Eastwoodia elegans* Brandegee. Sister to the just named taxa is a grade, although not always fully resolved, consisting of three species of *Tonestus*, *Acamptopappus*, and *Amphipappus fremontii* Torrey & A. Gray var. *spinosus* A. Nelson, crowned with *Chrysothamnus* sensu stricto. See Fig. 1 for more details and Roberts and Urbatsch (2004) for additional discussion.

**Lorandersonia baileyi** (Wooton & Standley) Urbatsch, R.P. Roberts, & Neubig, comb. nov. BASIONYM: *Chrysothamnus baileyi* Wooton & Standley, Contr. U.S. Natl. Herb. 16:181. 1913. *C. pulchellus* (A. Gray) Greene subsp. *baileyi* (Wooton & Standley) Hall & Clements, Phylog. Method Taxon., 194. 1923. *Chrysothamnus pulchellus* Greene var. *baileyi* (Wooton & Standley) S.F. Blake, J. Washington Acad. Sci. 30:467. 1940. *Ericameria pulchella* subsp. *baileyi* (Wooton & Standley) L.C. Anderson, Great Basin Naturalist 55:86. 1995. TYPE: U.S.A. NEW MEXICO: N end of Guadalupe Mountains, 4 Sep 1902, *V.O. Bailey 490* "number provided in protologue is 498 compared to 490 on specimen" (HOLOTYPE: US 00443565).

*Distribution, ecology, and relationships.*—This taxon has been documented for the states of Chihuahua and Coahuila, Mexico and for Arizona, Colorado, Kansas, New Mexico, Oklahoma, Texas, and Utah. It grows in open prairies typically in deep, sandy soils at elevations 1350–2350 m and flowers from late summer to fall. *Lorandersonia baileyi* is often treated as a subspecies of *L. pulchella*, and the two are very similar in habit, leaf form and in having involucres composed of relatively long, vertically aligned phyllaries. Ciliate leaf margins and young stems with evenly spaced trichomes distinguish *L. baileyi* from the glabrous *L. pulchella*. In our best resolved phylogenies, *L. baileyi* and *L. salicina* are sister taxa, with *L. linifolia* basal (Roberts & Urbatsch 2004). Presence of gland-tipped hairs on young stems and young leaves transitional to phyllaries is a

feature seen in *L. baileyi* and to a lesser extent in other taxa with the exception of *L. peirsonii*, which is covered throughout with similar appearing indumentum.

**Lorandersonia linifolia** (Greene) Urbatsch, R.P. Roberts, & Neubig, comb. nov. BASIONYM: *Chrysothamnus linifolius* Greene, Pittonia 3:24. 1896. *Bigelowia linifolia* A. Nelson, Wyoming Agric. Exp. Sta. Bull. 28:123. 1896. *Chrysothamnus viscidiflorus* (Hook.) Nutt. subsp. *linifolius* (Greene) Hall & Clements, Phylog. Method Taxon. 184. 1923. *Chrysothamnus viscidiflorus* var. *linifolius* (Greene) Kittell in Tidestrom & Kittell, Fl. Arizona and New Mexico, 395. 1941. *Ericameria linifolia* (Greene) L.C. Anderson, Great Basin Naturalist 55:86. 1995. TYPE: U.S.A. WYOMING: in moist, alkaline soil, plentiful along a streamlet near Rock Springs, 9 Aug 1895, *E.L. Greene s.n.* (HOLOTYPE: NDG).

*Distribution, ecology, and relationships.*—This species is often locally abundant and widespread, ranging from Arizona and New Mexico northward to Utah, Montana, and Wyoming. It occupies alkaline moist sites along rivers, stream banks, and drainage areas at elevations from 1200 to 2400 meters and flowers late summer and fall. Growing to over 3 meters tall, it is the largest member of the genus. It superficially resembles *L. spathulata* but may be distinguished from that species by its leaf shape, glabrous to glabrate shoots, and densely pubescent achenes. A population sampled in Mesa County, Colorado, differed from the norm in having numerous spreading trichomes on its young twigs and capitulescence branches, and trichome-edged leaves with more noticeable resin dots. *Lorandersonia linifolia* is basal to *L. baileyi* and *L. salicina* in our gene-based trees (Roberts & Urbatsch 2004) and combines some features of both species. This is especially true for the Mesa County population, whose foliage is conspicuously resin-dotted and which has pubescent achenes typical of *L. salicina*. Its pubescent stems and trichome-edged leaves, however, are characteristic of *L. baileyi*.

**Lorandersonia microcephala** (Cronquist) Urbatsch, R.P. Roberts, & Neubig, comb. nov. BASIONYM: *Haplopappus microcephalus* Cronquist, Madroño 11:186. 1951. *Tonestus microcephalus* (Cronquist) G.L. Nesom & D.R. Morgan, Phytologia 68:178. 1990. TYPE: U.S.A. NEW MEXICO: Taos Co: Tres Piedras, crevices of granitic rocks in open yellow pine forest, altitude 8200 ft., 8 Jul 1950, *Ripley & Barneby 10316* (HOLOTYPE: WS; ISOTYPE: CAS).

*Distribution, ecology, and relationships.*—*Lorandersonia microcephala* grows on thin soils and cracks in granite outcrops at elevations from 2400 to 2700 meters and flowers from July to September. Its distribution is restricted to a few sites in northern New Mexico and southern Colorado where it is uncommon and of special conservation concern. Cronquist (1951) discussed this species obscure affinities and regarded it as *Haplopappus* after considering *Petradoria* and *Hesperodoria* as possible congeners. The species was transferred to *Tonestus* by Nesom and Morgan (1990). Lane et al. (1996) based on limited sampling noted that *L. microcephalus* shared more DNA characters with their cpDNA constituted

*Petradoria* group than with *Tonestus*. In our ETS/ITS based trees this species is basal in *Lorandersonia* and quite remote from *Petradoria*. *Tonestus* as constituted by Nesom and Morgan (1990) is highly polyphyletic with *L. peirsonii* the only *Tonestus* placed in the *Lorandersonia* clade. As with *L. baileyi*, *L. microcephala* has glandular trichomes on its young stems and leaves, especially those transitional to phyllaries, as abundantly seen in on all aerial parts of *L. peirsonii*. Besides sharing similar trichomes types, the latter two taxa have herbaceous stems from woody caudices with persistent leaves and especially leaf bases, congested internodes, radiate capitula, and both grow on granite outcrops and at high elevations. *Lorandersonia microcephala* closely resembles other species in the genus in leaf form and capitulum size, shape, number, and arrangement.

**Lorandersonia peirsonii** (D.D. Keck) Urbatsch, R.P. Roberts, & Neubig, comb. nov. BASIONYM: *Haplopappus eximius* H.M. Hall subsp. *peirsonii* D.D. Keck, Madroño 5:169 1940. *Haplopappus* (*Aplopappus*) *peirsonii* (D.D. Keck) J.T. Howell, Leafl. Western Bot. 6:86. 1950. *Tonestus peirsonii* (D.D Keck) G.L. Nesom & D.R. Morgan, Phytologia 68:178. 1990. TYPE: U.S.A. CALIFORNIA. Inyo Co.: Transverse Ridge, Upper Rock Creek Lake Basin, NW corner of Inyo County, 3380 m, 5 Aug 1933, *F.W. Peirson* (HOLOTYPE: UC, ISOTYPE: JEPS).

*Distribution, ecology, and relationships.*—*Lorandersonia peirsonii* is a morphologically divergent species in an otherwise relatively uniform genus. It grows in the High Sierra Province in California rather than the Rocky Mountains and nearby plains. Its shoots are densely and uniformly covered with glandular trichomes, leaf margins are remotely and conspicuously serrate, and its capitulescence monocephalous. Nevertheless, as noted in the discussion of *L. baileyi* and *L. microcephala*, there are some similarities to other *Lorandersonia* species. That this species is convergent in DNA sequence for the ETS/ITS region is yet untested. All sequences for *L. peirsonii* taken from different specimens at different times with different stock reagents yielded identical results, except for one or two base pairs, but all samples were taken from herbarium specimens and the possibility of contamination needs to be unequivocally eliminated.

Even more puzzling than *Lorandersonia peirsonii*'s overall dissimilarity to other *Lorandersonia* is its great similarity to *Tonestus eximius* (H.M. Hall) A. Nelson & J.F. Macbride. Keck (1940) treated *L. peirsonii* as a subspecies of the latter in its original publication. Howell (1950) raised it to specific rank. In their reinstatement of *Tonestus*, Nesom & Morgan (1990) grouped the two species together, along with *T. alpinus* (L.C. Anderson & Goodrich) G.L.Nesom & D.R. Morgan, based on morphological similarities. The technical features that distinguish *T. eximius* include its narrower capitula, fewer phyllaries with more obtuse apices, fewer ray flowers, and shorter disk corollas. Yet the two species differ by several basepairs in their ETS/ITS sequences. *Tonestus eximius* is associated with a grade

of taxa just below *Chrysothamnus* sensu stricto, several nodes removed from *Lorandersonia* (Fig. 1). DNA sequences obtained from freshly collected leaves of *T. eximius* were virtually identical to samples obtained from herbarium specimens and reported by Roberts and Urbatsch (2004). Here, too, molecular variation unrelated to phylogeny is suspected. These two species and *Tonestus*, in general poses many questions for further investigation. Most species of *Tonestus* sensu Nesom and Morgan (1990) are generally restricted rocky outcrops at high elevations. Perhaps the genetic potential to converge into high elevation life forms exists in several lineages of Astereae. Brouillet et al. (2004) provided such evidence by demonstrating, based on ETS/ITS sequence data, that *T. kingii* and *T. aberrans* are allied to the phyletically distant Eurybioid/Machaerantherinae clade and that their similarity to other *Tonestus* is superficial.

**Lorandersonia pulchella** (A. Gray) Urbatsch, R.P. Roberts, & Neubig, comb. nov.
BASIONYM: *Linosyris pulchella* A. Gray, Pl. Wright. 1:96. 1852. *Chrysothamnus pulchellus* Greene, Erythea 3:93. 1895. *Chrysothamnus pulchellus* Greene subsp. *typicus* Hall & Clements, Phylog. Method Taxon. 194. 1923. *Ericameria pulchella* (A. Gray) L.C. Anderson, Great Basin Naturalist 55:86. 1995. TYPE: U.S.A. TEXAS: prairies below El Paso, Oct 1849, *Wright 287* (HOLOTYPE: GH; ISOTYPE: US).

*Chrysothamnus elatior* Standley, Proc. Biol. Soc. Washington 26:118. 1913. *Chrysothamnus pulchellus* (A. Gray) Greene subsp. *elatior* (Standley) H.M. Hall & Clements, Phylog. Method Taxon. 194. 1923. TYPE: U.S.A. NEW MEXICO. Dona Ana Co.: San Andreas Mountains, sandhills N of Goldenbergs Ranch, 12 Oct 1912, *E.O. Wooton s.n.* (HOLOTYPE: US).

*Distribution, ecology, and relationships.*—This species occurs in Chihuahua, Mexico, and in New Mexico and Texas, where it grows on dry hills and plains, often in sandy soils, at elevations from 1500–2000 meters. Its similarities and differences to *L. baileyi* are noted in the discussion of that species. In our sequence-based trees, *L. pulchellus* is sister to *L. spathulatus* (Roberts & Urbatsch 2004), from which it differs in several morphological characters, involucral features being the most notable.

**Lorandersonia salicina** (S.F. Blake) Urbatsch, R.P. Roberts, & Neubig, comb. nov.
BASIONYM: *Haplopappus salicinus* S.F. Blake, Proc. Biol. Soc. Washington 48:171. 1935. *Hesperodoria salicina* (S.F. Blake) G.L. Nesom, Phytologia 71:245. 1991. TYPE: U.S.A. ARIZONA. Coconino Co.: Grand Canyon, Bright Angel Trail, 22 Oct 1905, *A. Eastwood 10* (HOLOTYPE: US 00619950).

*Distribution, ecology, and relationships.*—This species is restricted to a few sites in northern Arizona and is of conservation concern. Its habitat consists of rocky cliff faces and stony soils from 300 to 950 meters. What became the type specimen for *Haplopappus salicinus* (*Eastwood 10*) was earlier considered by Hall (1928) to be *Haplopappus scopulorum* in sect. *Hesperodoria*. Blake (1935) noted its distinctive nature when describing it as a new species but still allied it to *H. scopulorum*. So did Nesom (1991), who further noted numerous similarities and

differences between the two species. Combining *Hesperodoria*, *Vancleveа*, and *Petradoria* into a single genus or broadening *Chrysothamnus* to encompass these species were also proposed (Nesom 2000). In our gene-trees *L. salicina* is sister to *L. baileyi*, with *L. linifolia* basal (Roberts & Urbatsch 2004). Among the lorandersonias, *L. salicina* is most like *L. linifolia* in often having resin-dotted leaves that are similar in size and form, relatively short involucres, and achenes pubescent with long ascending hairs. The adaxial, often copious resin coating of the emerging leaves of *L. salicina* is characteristic of *L. baileyi*, *L. linifolia*, and perhaps some of its other congeners as well. *Lorandersonia salicina* is differentiated from *L. linfolia* by its much smaller stature, resin-coated to resin-dotted stems, absence of the uniformly spaced, spreading trichomes, and its few-headed, loosely corymboid capitulescences.

**Lorandersonia spathulata** (L.C. Anderson) Urbatsch, R.P. Roberts, & Neubig, comb. nov. BASIONYM: *Chrysothamnus spathulatus* L.C. Anderson, Madroño 17:226. 1964. *Ericameria spathulata* (L.C. Anderson) L.C. Anderson, Great Basin Naturalist 55:86. 1995. TYPE: U.S.A. NEW MEXICO. Otero Co.: Upper Burro Flats, 6000 ft, between LaLuz and LaBorcita canyons, 7 mi NE by road from town of LaLuz, T15S, R19E, sec 14 & 15, 14 Oct 1961, *L.C. Anderson 2052* (HOLOTYPE: UC; ISOTYPES: KSC, MSC, NMC, US, UTC).

*Distribution, ecology, and relationships.*—*Lorandersonia spathulata* is known from south-central New Mexico and nearby areas in Texas, where it grows on loamy soils associated with piñon, juniper, and oak woodlands from around 1700 to 2200 meters. Anderson (1964b) noted its similarity to *C. viscidiflorus* (Hook.) Nutt. subsp. *lanceolatus* (Nutt.) Hall & Clements in corolla shape and style branch size, apparently regarding this as some measure of relatedness. He maintained *L. spathulata* in sect. *Chrysothamnus* in his (1986a) synopsis. This species is robustly supported within the *Lorandersonia* clade, and as noted previously, is sister to *L. pulchella*.

**Chrysothamnus** Nutt., Trans. Amer. Philos. Soc. ser. 2, 7:323. 1840. TYPE: *Chrysothamnus pumilus* Nutt. (typ. cons.). = *Chrysothamnus viscidiflorus* (Hook.) Nutt. *Chrysothamnus* sect. *Graminii* L.C. Anderson, Proc. Symp. Biol. *Artemisia* and *Chrysothamnus*. 29. 1986, in part. *Chrysothamnus* sect. *Pulchelli* Hall & Clements, Publ. Carnegie Inst. Washington 326:175. 1923, in part. *Hesperodoria* Greene, Leaf l. Bot. Observ. Crit. 1:173. 1906, in part.

*Vancleveа* Greene, Pittonia 4:50. 1899.

*Discussion.*—*Chrysothamnus* in the traditional sense has long been considered a difficult genus due to complex infraspecific variation in *Chrysothamnus nauseosa*, *C. parryi*, and *C. viscidiflorus* (Hook.) Nutt. and also because of uncertainty concerning its monophyly (Hall & Clements 1923; Anderson 1986b). Species in sect. *Punctati* and *C. albidus*, in particular, have been noted for their anomalies relative to others in the genus and for their similarities to species elsewhere in tribe Astereae (Hall & Clements 1923). Sequence-based phylogenetic investigations have been invaluable in addressing questions concerning

generic circumscription and interspecific species relationships, as discussed in the present paper and elsewhere (Roberts & Urbatsch 2004; Suh 1989; Morgan 1990). Such data also have added a new level of complexity and have posed new hypotheses concerning the circumscription of *Chrysothamnus*.

*Acamptopappus*, *Amphipappus*, and *Vancleveа* are closely associated with or are included in *Chrysothamnus* in our sequence-based clade (Fig. 1). *Acamptopappus* is supported as part of a polytomy that also includes *Amphipappus fremontii* var. *spinosus* and *Chrysothamnus* (Fig. 1). Three taxa traditionally regarded as other genera are supported within *Chrysothamnus* (Fig. 1). Among these, *Hesperodoria scopulorum* and *Vancleveа stylosa* can readily be placed in *Chrysothamnus* because they exhibit no morphologically incongruous characteristics. Their affinities to one another (Anderson & Weberg 1974) and to *Chrysothamnus* had been noted (Nesom 1997, 2000) and sequence data support these hypotheses (Roberts & Urbatsch 2004). The presence of *Amphipappus fremontii* within the *Chrysothamnus* clade is perplexing because *A. fremontii* var. *spinosus* is placed several nodes below. Functionally staminate disk florets and 1–2 pistillate ray florets, features unknown for other taxa in this investigation except in *Petradoria*, characterize *Amphipappus*. There is some evidence for intergradation between the two varieties of *A. fremontii* (Nesom 2005), and the pubescence characters, their major distinguishing feature, are regarded as technical and perhaps trivial. Although Nelson (1934) recognized *A. spinosus* as a distinct species, he noted its strong similarity to the typical taxon. Furthermore, some years earlier (Nelson 1909), he described the same variant as a variety of *A. fremontii* based on a different type.

Lane (1988) hypothesized that *Acamptopappus*, *Amphipappus*, *Chrysothamnus*, *Vancleveа*, *Ericameria*, and others share a common ancestral stock. Sequence data support certain aspects of her hypothesis and her generalized statement is brought to a finer focus. *Chrysothamnus* is paraphyletic since it includes typical *Amphipappus fremontii*. Because of its distinctive floret morphology, the possibility of convergence among ETS/ITS sequences, and possible analytic problems such as long branch attraction or sample contamination, incorporation of *Amphipappus* into *Chrysothamnus* should be delayed until hypotheses posed herein are tested further. *Acamptopappus* is also maintained as a distinct genus because of its morphological cohesiveness and monophyly robustly supported by sequence data (Roberts & Urbatsch 2004).

**Chrysothamnus scopulorum** (M.E. Jones) Urbatsch, R.P. Roberts, & Neubig, comb. nov. BASIONYM: *Bigelowia menziesii* var. *scopulorum* M.E. Jones, Proc. Calif. Acad. Sci. ser. 2, 5:692. 1895. *Haplopappus scopulorum* (M.E. Jones) S.F. Blake, Contr. U.S. Natl. Herb. 25:542, 546. 1925. *Hesperodoria scopulorum* (M.E. Jones) Greene, Leafl. Bot. Observ. Crit. 1:173. 1906. TYPE: U.S.A. UTAH. Canyon of the upper Virgin River above Springdale, 1219 m, 23 Sep 1894, *M.E. Jones 6074* (LECTOTYPE: US 00236810).

*Haplopappus scopulorum* var. *hirtellus* S.F. Blake, Proc. Biol. Soc. Washington 48:170. 1935. TYPE: U.S.A. UTAH: Iron Co.: Cedar Canyon, 2 Sep 1931. *A.O. Garrett 6051* (HOLOTYPE: US 01623835)

**Chrysothamnus scopulorum** var. **canonis** (S.L. Welch) Urbatsch, R.P. Roberts, & Neubig, comb. nov. BASIONYM: *Haplopappus scopulorum* (M.E. Jones) S.F. Blake var. *canonis* S.L. Welsh, Utah Flora (ed. 3), 200. 2003. TYPE: U.S.A. UTAH: Naturalist Cove, base of N facing cliffs, east of The Neck, Canyonlands National Park, n.d., *S.L. Welsh 8813* (HOLOTYPE: BRY).

*Distribution, ecology, and relationships.*—*Chrysothamnus scopulorum* grows on brushy mountain slopes and in the understory of ponderosa pine in Arizona and Utah between 1200 and 2200 m. Features diagnostic for this species include its compact clusters of 20± capitula on long peduncular branches bearing widely spaced, distally reduced leaves/bracts, 5–6 seriate involucres, imbricate phyllaries, relatively large capitula of 10–16(–20) florets, and pubescent achenes. In our gene tree (Fig. 1), it is one of seven basal polytomic branches, its sister relationships unresolved. Within *Chrysothamnus* it closely resembles *C. stylosus* but is readily differentiated from that taxon by its non-glutinous involucres, smaller capitula, and terete pappus bristles. It is the type for the ditypic *Hesperodoria*, earlier regarded as a section within *Haplopappus* (sensu Hall 1928). As noted in the discussion of *Lorandersonia*, similarities between *C. scopulorum* and *L. salicina* (*H. salicina*) are convergent.

**Chrysothamnus stylosus** (Eastwood) Urbatsch, R.P. Roberts, & Neubig, comb. nov. BASIONYM: *Grindelia stylosa* Eastwood, Proc. Calif. Acad. Sci. ser. 2, 6:293. 1896. *Vancleva stylosa* (Eastwood) Greene, Pittonia 4: 51. 1899. TYPE: U.S.A. UTAH: 13 Jul 1895, *A. Eastwood 36* (HOLOTYPE: CAS).

*Distribution, ecology, and relationships.*—*Chrysothamnus stylosus* is endemic to the Colorado Plateau and has been documented for at least six counties in southern Utah and in adjacent Arizona, where it inhabits dunes and sandy soil at elevations from 1100–1700 meters. It is readily diagnosed by its glutinous shoots and involucres, relatively broad, spreading to deflexed, falcate leaves with acute apices, 3–5-seriate involucres, graduated, acuminate-tipped phyllaries, 20 or more flowers per head, and numerous, flattened pappus bristles. Previously treated in the monotypic genus *Vanclevea*, its similarity to *Hesperodoria* (as suggested by Anderson and Weberg 1974) and to *Chrysothamnus* (Nesom 1997, 2000) is supported in part by ETS/ITS sequence data (Roberts & Urbatsch 2004). Within *Chrysothamnus*, it and five other taxa, plus a branch bearing several other species, form a basal polytomy (Fig. 1). As in other studies of this nature (Roberts & Urbatsch 2003, 2004), low levels of sequence variation provide little resolution within genera.

The following is key to taxa within and related to Cuniculotinus, *Chrysothamnus*, and *Lorandersonia* based ETS/ITS sequence data (Fig. 1). A key to the genera *Chrysothamnus*, and *Lorandersonia* is not possible due to appar-

ent convergence among various species. Therefore, taxa in these two genera appear at various places in the key.

KEY TO TAXA IN THE *CHRYSOTHAMNUS* AND *LORANDERSONIA* CLADES

1. Disk flowers 3–7, functionally staminate; ray flowers 1–2, pistillate, ligule apices distinctly 2–3 lobed; pappus of crinkly bristles, 2 to several fused at base _____ **Amphipappus**
1. Disk flowers hermaphroditic, often many more than 7 per capitulum; rays 0 to numerous; ligule apices rounded or irregularly notched or toothed, pappus of separate bristles or scales, not conspicuously contorted.
   2. Rays 0; florets, at least the outer several series, associated with readily deciduous paleae, much longer than achenes; pappus of 5–8 narrowly deltate scales; capitula with 30 or more florets _____ **Eastwoodia**
   2. Rays 0–several; palea lacking, relatively short, conic projections present in certain taxa, pappus of 10 or more bristles; capitula may contain fewer or more than 30 florets.
      3. Phyllaries graduated, mid-level ones obovate, more than 2 mm wide distally, apices retuse to emarginate, notch conspicuously cuspiate, lower or outermost chartaceous _____ **Cuniculotinus**
      3. Phyllaries graduated or subequal, rarely more than 2 mm wide distally, but if so, apices obtuse to rounded, never notched, lower or outermost often herbaceous.
         4. Receptacles with persistent, sharp, conic projections; phyllaries 2–3 seriate; involucres hemispheric to nearly spheric; desert shrubs of the southwestern U.S. with disk flowers 14 or more; rays present in one species, absent in another _____ **Acamptopappus**
         4. Receptacles without sharp, conic; phyllaries (2–)3–6+ seriate; involucres cylindric, turbinate, or campanulate; disk flowers 15 or fewer in most species except for certain low growing, montane, herbaceous-stemmed taxa with 15 or more ray florets per capitulum.
            5. Ray flowers 5 or more per capitulum.
               6. Capitula in compact corymbiform clusters; disk flowers 15 or fewer _____ **Lorandersonia microcephala**
               6. Capitula solitary; disk flowers 40 or more.
                  7. Leaf margins entire rarely with a few apical teeth; shoots and phyllaries pubescent with spreading and mostly gland-tipped hairs _____ **Tonestus lyallii**
                  7. Leaf margins saliently toothed; shoots and phyllaries pubescent with shaggy, crisped hairs, or with gland-tipped hairs.
                     8. Many-stemmed, tap-rooted perennial herbs from an underground, branching caudex; stems and involucres pubescence of eglandular, shaggy, crisped hairs; Rocky Mountain alpine meadows _____ **Tonestus pygmaeus**
                     8. Mat-forming herbaceous perennials from underground, branching caudices and deep-seated rhizomes; stems and involucres with abundant, gland-tipped hairs; mountains of east-central California and adjacent Nevada _____ **Lorandersonia eximius**
            5. Ray flowers 0; reported for *L. spathulata* but rare.
               9. Disk flowers 8 or more per capitulum.
                  10. Disk flowers 30 or more; involucres and often stems distally glutinous _____ **Chrysothamnus stylosa**

10. Disk flowers 20 or fewer; involucres and stems may be resin dotted but not glutinous.
    11. Basal leaves and lower cauline leaves bearing 1–3 pairs of salient teeth; shoots and involucres pubescent with relatively long gland-tipped hairs _____ **Tonestus graniticus**
    11. Leaf margins entire; shoots resin-dotted or pubescent with short, conic, eglandular hairs.
        12. Stems and leaves resin-dotted; involucres 3–6 seriate _____ **Lorandersonia salicina**
        12. Stems and leaves pubescent with spreading, eglandular hairs; involucres 6+–seriate _____ **Chrysothamnus scopulorum**
9. Disk flowers fewer than 8 per capitulum (the highly variable *C. viscidiflorus* subsp. *viscidiflorus* is known to have up to 14 flowers per head, but it may be distinguished by its leaves twisted on their long axes).
    13. Leaves 10 or more mm wide, strongly veined; stems annual _____ **Chrysothamnus eremobius**
    13. Leaves less than 10 mm wide, midvein often evident, collateral veins 0 or inconspicuous; stems perennial.
        14. Leaves twisted about long axis _____ **Chrysothamnus viscidiflorus**
        14. Leaves flat, not twisted.
            15. Achenes glabrous to sparsely pubescent throughout or distally only, sometimes with glistening atomiferous trichomes.
                16. Stems and leaves glabrous or uniformly pubescent with short, spreading conic trichomes; distal portion of achenes usually with glistening atomiferous trichomes and sometimes a few elongated hairs or glabrous throughout.
                    17. Stems and leaves uniformly and abundantly pubescent with short, spreading, conic trichomes; distal portion of achenes usually with glistening atomiferous trichomes and sometimes a few elongated hairs or glabrous throughout; disk corollas 7–11 mm long _____ **Chrysothamnus depressus**
                    17. Stems uniformly and abundantly pubescent with short, spreading, conic trichomes or glabrous; leaves glabrous or ciliolate margined; achenes glabrous; disk corollas 9 mm or more long.
                        18. Margins of leaves ciliolate; widespread in New Mexico and adjacent states ___ **Lorandersonia baileyi**
                        18. Margins of leaves glabrous; central New Mexico and adjacent Texas _____ **Lorandersonia pulchella**
                16. Stems and leaves uniformly predominantly pubescent with gland-tipped trichomes, short, spreading conic trichomes if present sparsely so;

achenes glabrous or distal portion with a few elongated hairs; disk corollas 7 or more mm long.
19. Stems and leaves mainly pubescent with gland-tipped trichomes, eglandular ones may also be present _____ **Chrysothamnus molesta**
19. Achene apices with a few elongated hairs or glabrous throughout; leaves resin dotted _____ **Chrysothamnus vaseyi**

15. Achenes pubescent to densely so with elongated trichomes; atomiferous spheres typically lacking.
20. Leaves or capitulescence bracts extending to apices of the involucres or far beyond; leaves often resin dotted _____ **Chrysothamnus humilis**
20. Leaves or capitulescence bracts not extending to the level of the involucres.
21. Leaves 1–2 mm wide or narrower, glabrous or remotely scaberulous; phyllary apices acuminate or cuspidate with a slender tip.
22. Leaves 1(–2) mm wide or narrower, glabrous or remotely scaberulous; phyllary apices acuminate or cuspidate with a slender tip _____ **Chrysothamnus greenei**
22. Leaves 1–2 mm wide, glabrous; phyllary apices acute to rounded, somewhat thickened apically _____ **Chrysothamnus viscidiflorus** subsp. **planifolius**
21. Leaves (2–)3 mm or more wide; phyllary apices acuminate, acute, or rounded.
23. Cypselae densely pubescent; twigs glabrous or nearly so; leaves lanceolate, widest point nearer the leaf base, glabrous, often resin dotted; northeastern New Mexico and northward _____ **Lorandersonia linifolia**
23. Cypselae sparsely pubescent; twigs scabrous; leaves oblanceolate to spatulate, widest point nearer the leaf apex, scabrous, lacking resin dots; southern New Mexico and adjacent Texas _____ **Lorandersonia spathulata**

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