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TAXONOMIC REVIEW OF *CHLORACANTHA* (ASTERACEAE, ASTEREAE)

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ABSTRACT

The four entities that comprise the North American genus *Chloracantha* are morphologically discrete, with little or no intergradation. Var. *spinosissima* (Baja California Sur) and var. *strictospinosa* (Central America, southern Mexico) do not overlap in distribution with other entities. Var. *spinosa* and var. *jaliscensis* are largely allopatric but they are sympatric along the Pacific slope in Chihuahua, Sonora, and Sinaloa. Each of the four is recognized here at specific rank: *Chloracantha spinosa* (Benth.) Nesom, **Chloracantha spinosissima** (Brandeg.) Nesom, **comb. et stat. nov.**, **Chloracantha ortegae** (Blake) Nesom, **comb. nov.** (= var. *jaliscensis*), and **Chloracantha australis** Nesom, **nom. et stat. nov.** (= var. *strictospinosa*).

The genus *Chloracantha* has been considered to comprise a single species with four varieties. (Nesom et al. 1991; Sundberg 1991; Nesom & Robinson 2007). The typical variety occurs from the south-central and southwestern USA through the northern two-thirds of Mexico; var. *spinosissima* and var. *jaliscensis* are endemic to western Mexico; var. *strictospinosa* is abundant from Central America (Panama to Guatemala) into southernmost Mexico. Sundberg (1991) provided a treatment of infraspecific taxonomy and discussions of typification.

The genus is recognized by its shrubby habit and green, usually leafless stems bearing scattered, small, white-rayed heads. All plants except those of var. *jaliscensis* usually produce spines (branch homologues, technically thorns). Although *Chloracantha spinosa* (all variants) produces no terminal resting buds and its permanently green stems without periderm are herbaceous in aspect, it behaves like a shrub in its perennial stems (alive for up to about four growing seasons) with a quickly developed vascular cambium and its production of axillary buds with bud scales (Nesom et al. 1991). The leaves are usually shed by flowering, except in var. *jaliscensis*. The plants occur in a variety of habitats, though most commonly near water and mostly at low elevations but at some sites up to nearly 2000 meters. Molecular studies indicate that *Chloracantha*, the monotypic genus *Batopilasia* of southern Chihuahua, and *Boltonia* of the eastern USA are closely related (Brouillet et al. 2009).

Perhaps because of the highly distinctive appearance of plants of the *Chloracantha* complex across its geographic distribution, most authors have chosen to recognize a single species with formal variants at varietal rank (Brandgee 1917; McVaugh 1972, 1984; Sundberg 1991), but none has provided an explicit rationale for choice of rank. In his treatment of Mesoamerican Astereae, Pruski (2018) regarded putative differences in thorniness, phyllary morphology, and pappus length as of no taxonomic significance and recognized only a single species, *C. spinosa*, with no infraspecific taxa.

In the review here, the existence of four entities is confirmed — each is morphologically discrete and intergrades little or none with the others. Morphological differences are consistent in vegetative, involucral, and fruit characters. Var. *spinosissima* and var. *strictospinosa* do not overlap in geography with other entities; var. *spinosa* and var. *jaliscensis* are largely allopatric but sympatric along the Pacific slope in Chihuahua, Sonora, and Sinaloa. Each of the four taxa has a discrete geographical range, non-intergrading with the others, and each is recognized here at specific rank.

CHLORACANTHA Nesom, Suh, Morgan, Sundberg, & Simpson, Phytologia 70: 378. 1991. **TYPE**: *Chloracantha spinosa* (Benth.) Nesom

Aster sp. group Spinosi Alexander in Small, Man. S.E. Fl., 1365, in clave. 1933. *Aster* sect. *Spinosi* (Alexander) A.G. Jones, Brittonia 32: 233. 1980. *Erigeron* sect. *Spinosi* (Alexander) Nesom & Sundberg, Phytologia 67: 85. 1989. **TYPE**: *Aster spinosus* Benth.

Perennial subshrubs, spreading by rhizomes, glabrous or glabrate. **Stems** strictly erect, 0.5–1.5(–2.5) m tall, lateral branches sharply ascending, the latter sometimes modified as thorns, axillary buds with scales, thorns commonly adnate to stems 0.5–2 mm. **Leaves** all cauline, alternate, 1-nerved, mostly 1–4 cm long, oblanceolate, entire or very rarely with 1–2 pairs of small teeth, early deciduous (except in *C. ortegae*), glabrous except the margins sometimes sparsely ciliate and the upper surface sometimes with scattered minute hairs. **Heads** produced singly in loose, corymboid panicles; buds erect; involucres broadly turbinate to hemispheric; phyllaries strongly graduated in (3–)4–5 series, the inner 4–7.5 mm long, each with (1–)3(–5), parallel, orange-resinous veins, oblong-elliptic to lanceolate, apices usually rounded but sometimes lanceolate, the margins (including the apex) hyaline. **Ray florets** 10–33 in a single series, pistillate, fertile, the corollas 4–8(–11) mm long, the ligules (0.5–)1–2 mm wide, white, sometimes bluish-tinged, coiling at maturity. **Disc florets** bisexual, fertile, the corollas yellow with orange-resinous veins, becoming purplish at maturity. **Achenes** glabrous, slightly compressed, 1.5–4 mm long, with 5(–6) nerves; pappus of 30–60 barbellate bristles in ca. 2 series, 2.5–6.5 mm long, usually with a few with much shorter outer setae. **Base chromosome number** $x=9$.

Key to species

1. Leaves often persisting, at least proximally, until flowering; stems usually without spines (spines 5-15 mm long if present, straight to recurved); phyllaries broadly oblong-elliptic to lanceolate-elliptic, apex of midportion rounded ..... **Chloracantha ortegae**

1. Leaves deciduous by flowering; stems sparsely spiny on proximal portions or densely spiny over all; phyllaries mostly lanceolate, apex of midportion acute.

2. Stems densely spiny, spines (6–)20–70 mm long; pappus bristles 3–4 mm long ..... **Chloracantha australis**

2. Stems densely or sparsely spiny, spines 3–20(–30) mm long or 20–70 mm long; pappus bristles 4.5–6.5 mm long.

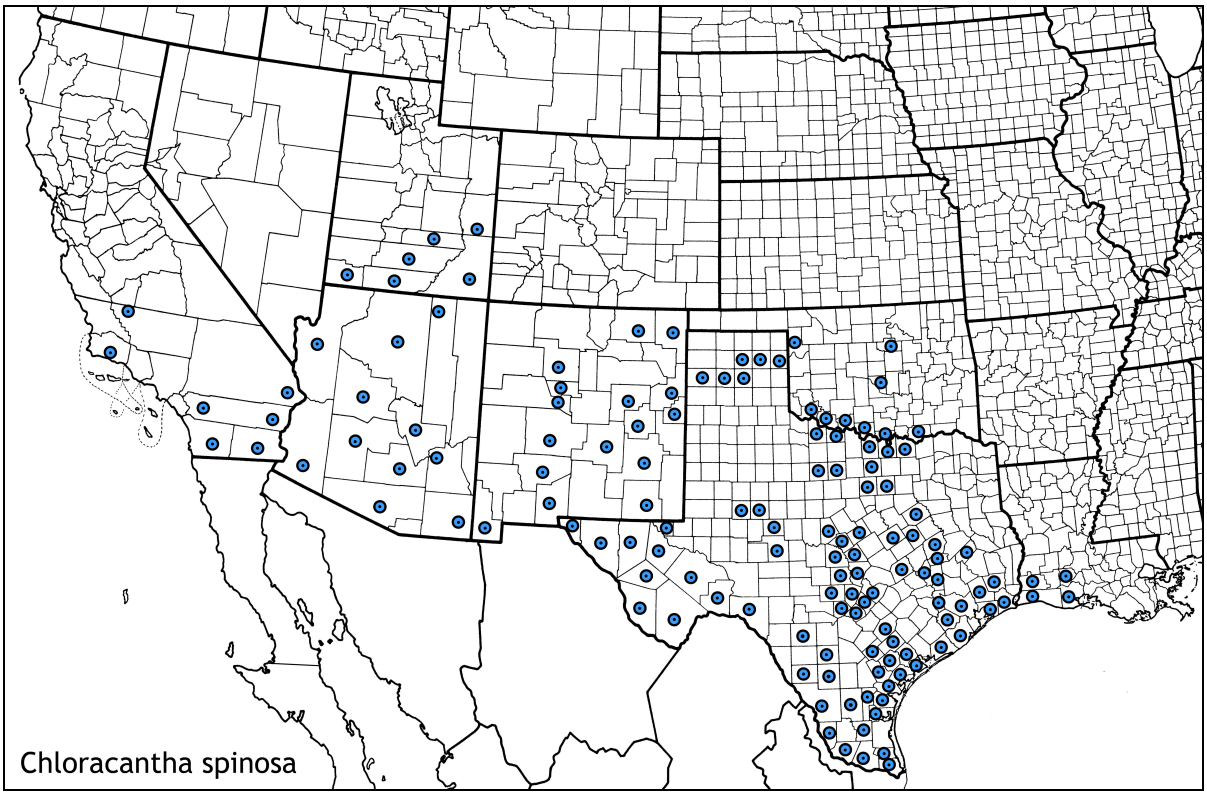
3. Stems sparsely to densely spiny proximally or sometimes without spines, distal branches spineless; spines 3–20(–30) mm long, straight to slightly recurved, spreading; involucres 4–5.5(–6) mm high; achenes 1.5–2.3 mm long ..... **Chloracantha spinosa**

3. Stems consistently densely spiny proximally and distally; spines 20–70 mm long, straight, ascending; involucres (5–)6.5–7.5 mm high; achenes 2.8–3.5 mm long **Chloracantha spinosissima**

1. **CHLORACANTHA SPINOSA** (Benth.) Nesom, Phytologia 70: 378. 1991. *Aster spinosus* Benth., Pl. Hartweg., 20. 1839. *Leucosyris spinosa* (Benth.) Greene, Pittonia 3: 244. 1897. **TYPE**: **MEXICO**. **Aguascalientes**. 1839, *K.T. Hartweg 148* (holotype: K image!; isotypes: BM, CGE, E image!, GH image!, LD image!).

USA (south-central and southwest), Mexico (broadly distributed; (Maps 1, 2). Along streams and ditches, lake shores, low areas in pastures and prairies, seepage, sometimes saline areas, 20–1250 (–1500) m; flowering mostly Sep–Feb, all year with moisture. Chromosome number $2n=18$.

As noted by Sundberg (1991), "collections from cultivated areas in the Valley of Oaxaca may be introductions from farther north": Valley of Oaxaca, fields along Route 190, ca. 10 mi NW of Oaxaca, locally abundant roadside weeds, 27 Jul 1960, King 3518 (TEX); ca. 6 mi N of city of Oaxaca on Rte 190, beside road in grassy field with occasional *Acacia* and other thorn scrub, 1700 m, 19 Jan 1990, *Soule 2182* (TEX).

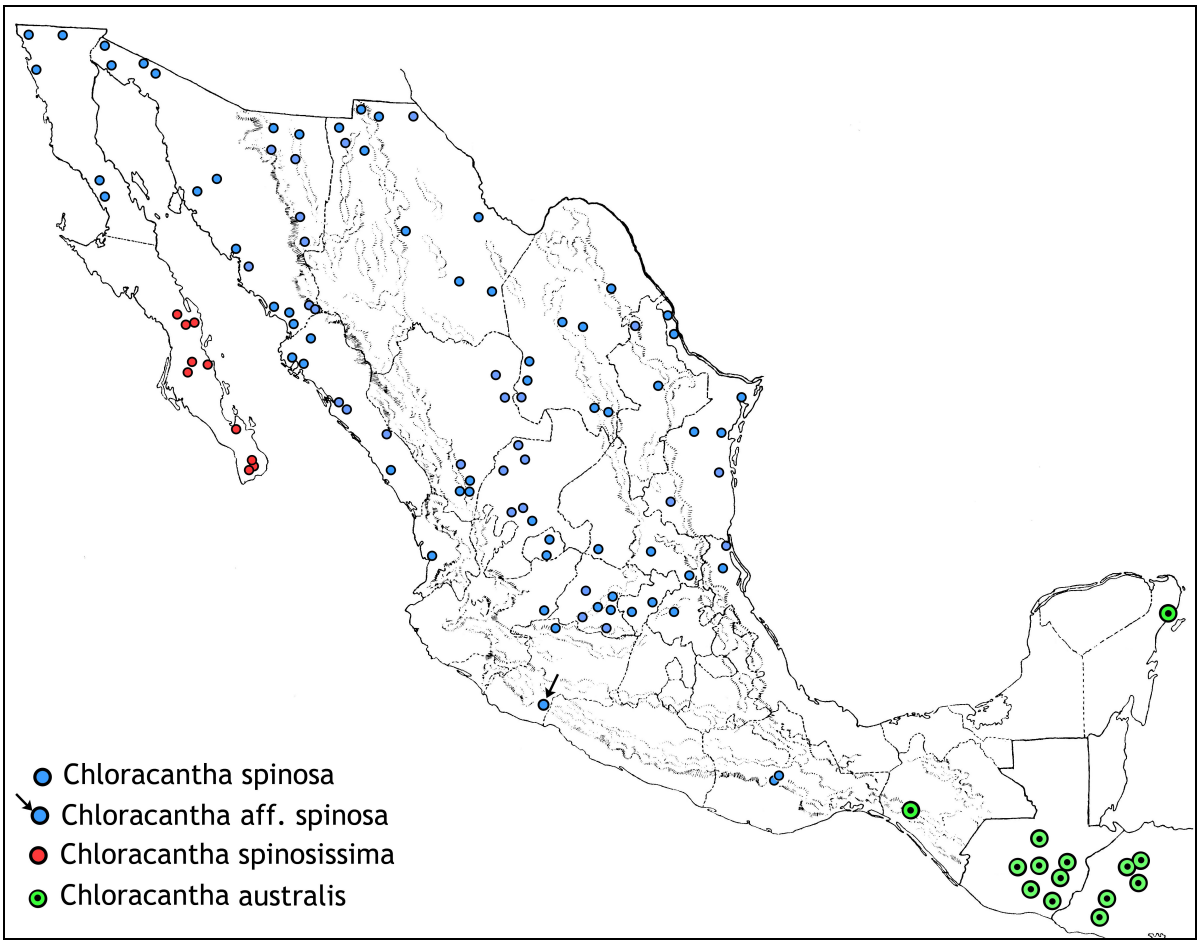


Map 1. Distribution of *Chloracantha spinosa* in the USA.

"Populations from the Imperial Valley and the lower Colorado River of southern California and Arizona are unusual in having fleshy stems, larger heads, and short branchlets in the capitulescence. In this area, the plants are often phreatophytic, growing in areas that are frequently flushed by of salt buildup" (Sundberg 1991, p. 386). Sundberg made numerous collections from this area in August 1983 and 1984, mostly from along irrigation ditches — chromosome counts from three populations were $2n = 18$. The specimens appear to be within the morphological range of typical *Chloracantha spinosa*.

A collection from along the coast near Guaymas, Sonora, was annotated by Sundberg as a typical *Chloracantha spinosa* influenced by genes of var. *spinosissima*: N of Guaymas along coast just S of Catch 22 airfield at Playa de los Algodones, *Maytenus*-dominated shrubland and tidal mudflat area, 5 Jan 1983, *Keil 16615* (TEX). The plants have relatively large heads, with pappus 6 mm long, and short, thick spines, but the phyllaries are mostly oblong-lanceolate, more like those of var. *jaliscensis* than either var. *spinosa* or var. *spinosissima*.

A collection from southern Michoacan was identified by Sundberg (1991) as var. *strictospinosa*: Distr. Huetamo, Tacupa, cliffs over Balsas River, 2 Dec 1934, *Hinton 5610* (MEXU image, Fig. 4, MO; also GH, NY, and US fide Sundberg 1991). As such, however, these plants would be long-disjunct (Map 2) and their morphology is mostly like typical *Chloracantha spinosa*. The plants are densely spiny and the pappus is short as in var. *strictospinosa* but the spines are relatively short and the phyllaries are mostly lanceolate. One of the branches has persistent cauline leaves. They are identified here as *Chloracantha* aff. *spinosa*.



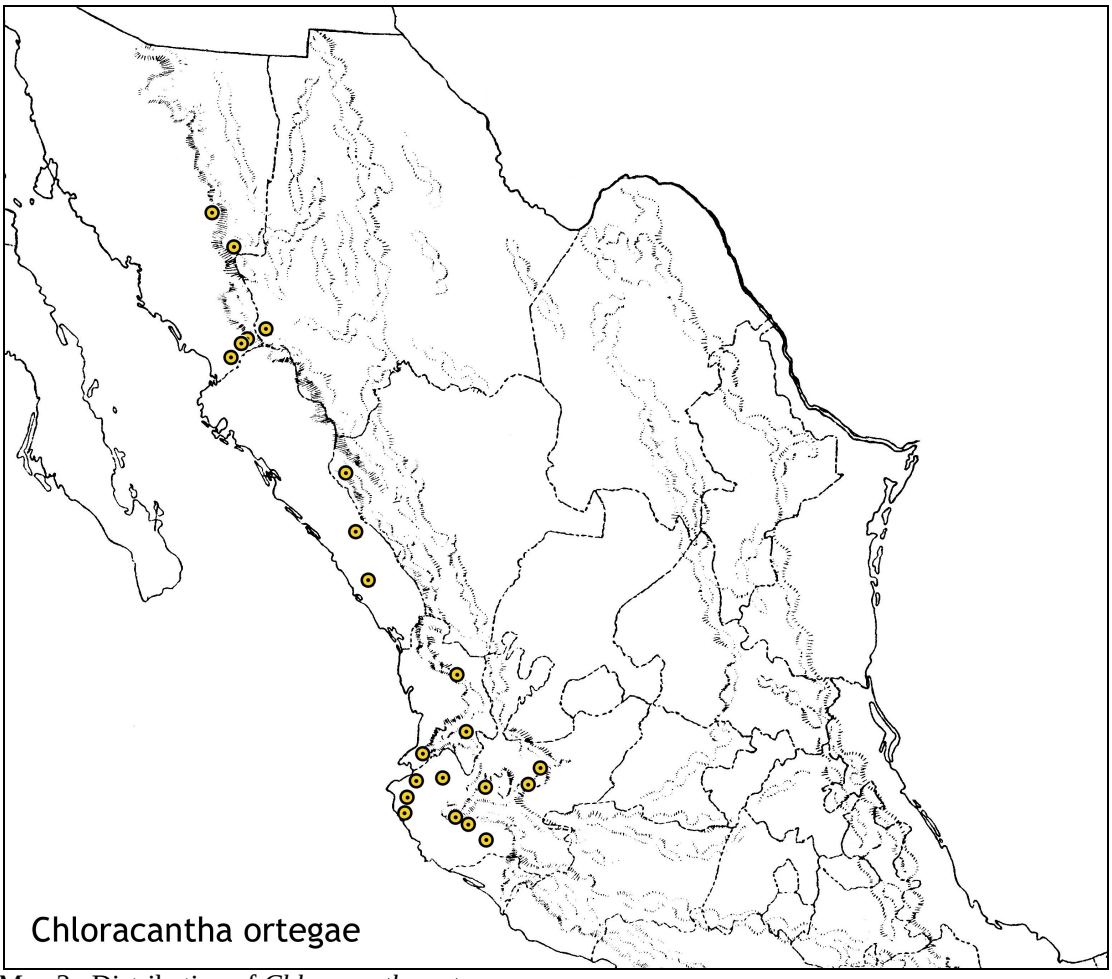
Map 2. Distribution of *Chloracantha spinosa* (Mexican localities), *C. spinosissima* (endemic to Baja California Sur), and *C. australis* (Map 4 for range through Central America). See text for comments on "*Chloracantha* aff. *spinosa*" in Michoacan.

2. **CHLORACANTHA SPINOSISSIMA** (Brandeg.) Nesom, **comb. et stat. nov.** *Aster spinosus* var. *spinosissimus* Brandeg., Univ. Calif. Publ. Bot. 6: 375. 1917. *Chloracantha spinosa* var. *spinosissima* (Brandeg.) Sundberg, Phytologia 70: 386. 1991. **TYPE**: **MEXICO**. **Baja California Sur**. San Gregorio, 1 Feb 1889, *T.S. Brandegee s.n.* (holotype: UC!; isotypes: PH image!, US image!).

Baja California Sur (Map 2). Arroyos and canyons, along rivers and around springs and ponds, fencelines; 10–900 (–1100) m; flowering (Apr–)Jun–Jan.

3. **CHLORACANTHA ORTEGAE** (Blake) Nesom, **comb. nov.** *Erigeron ortegae* Blake, Proc. Biol. Soc. Washington 37: 55. 1924. **TYPE**: **MEXICO**. **Sinaloa**. Mpio. San Ignacio: San Javier, terrenos de Balboa, Jan 1923, *J.G. Ortega 4974* (holotype: US!; isotype: K digital image!).

Aster spinosus var. *jaliscensis* McVaugh, Contr. Univ. Michigan Herb. 9: 363. 1972. *Chloracantha spinosa* var. *jaliscensis* (McVaugh) Sundberg, Phytologia 70: 388. 1991. **TYPE**: **MEXICO**. **Nayarit**. 2 mi NE of Santa María del Oro, steep mountainsides, in the basin of La Laguna, abundant among rocks in streambed, 800 m, oak forest near summits and tropical forest with *Ficus*, *Brosimum* below, 15-16 Sep 1960, *R. McVaugh 19049* (holotype: MICH digital image!; isotypes: DUKE image!, ENCB image!, LL!, NY image!, US image!).



Map 3. Distribution of *Chloracantha ortegae*.

Sonora, Chihuahua, Sinaloa, Nayarit, Jalisco (Map 3). Along rivers, streams, and ditches, arroyos, rocky and gravelly channels, riparian and gallery forests, disturbed oak-pine; 50–1900 m; flowering Sep–Jan. Chromosome number 2*n*=18.

Northern localities. **Chihuahua**. 6 km antes de Batopilas, intersection Arroyo de Santiago con el Rio Batopilas, 600-650 m, 14 Nov 1998, *Lebgue et al. 1726* (NMC). **Durango**. 10 mi N of Tamazula, rocky canyon bottom, climax short tree forest, 1500 ft, 18 Dec 1939, *Gentry 5260* (MEXU-2 sheets images). **Sinaloa**. Mpio. Concordia: La Tuna on Rio Magistral, 3 km by air NNE of Piedras Blancas, 12.5 km by air NE of Concordia, semideciduous forest, 843 ft, 0.3-0.6 m shrub on rocks near water, 5 Dec 2007, *Van Devender et al. 2007-1219* (ARIZ). Mpio. Cosalá: Vado Hondo, ca. 8.2 km W of Cosalá, tropical deciduous forest, 426 m, uncommon subshrub at edge of water, 4 Jan 2006, *Van Devender 2006-28* (USON). **Sonora**. Mpio. Alamos: Arroyo el Cobre, ca. 0.5 km S of Choquincahui, ca. 6.5 mi N of Guirocoba, 530 m, stream bottom in tropical deciduous forest with *Cyperus involucratus*, 16 Mar 1995, *Fishbein 2192* (USON); ca. 8 mi SE of Alamos on road to Guirocoba, lower crossing of Rio Cuchujaqui, edge of stream, 30 Dec 1983, *Van Devender 830153* (TEX); El Guayabo crossing of Río Cuchujaqui, 2.6 km NE of Sabinito Sur, 14 km (by air) ESE of Alamos, tropical deciduous forest on slopes and *Taxodium-Salix* gallery forest along stream, along stream, 350 m, 21 Nov 1993, *Van Devender 93-1221* (ASU); Rio Cuchujaqui at Arroyo El Mentidero, 11.3 km S of Alamos, 240 m, edge of river with *Taxodium*, 28 Oct 1995, *Van Devender 95-1162* (UCR). Mpio. Sahuaripa: 42.9 km (by air) NNW of Sahuaripa, Río Áros, Rancho El Refugio, 488 m, 30 Mar 2011, *Van Devender 2011-42* (USON). Mpio. Yecora: 3.9 km E of Yecora on Mex Hwy 16, Arroyo El Otro Lado, oak woodland, locally common in water at edge of stream,

1560 m, 25 May 1998, Van Devender 98-635 (TEX); Río Yepachic near jct with Arroyo Hondo, ca. 2 km by air W of Chihuahua border, 1380 m, oak woodland with canyon riparian forest with *Acer*, *Alnus*, *Cupressus*, and *Prunus gentryi*, in water, 27 Sep 1998, *Van Devender & Reina G. 98-1780* (NMC).

Chloracantha ortegae and *C. spinosa* are largely allopatric but the range of *C. ortegae* extends northward along the Pacific slope from its concentration in Jalisco and Nayarit to the Yecora area of east-central Sonora. Along this northward, linear extension, it is sympatric with *C. spinosa* (Maps 2, 3) apparently with little or no intergradation. The two entities are compared in the following couplet.

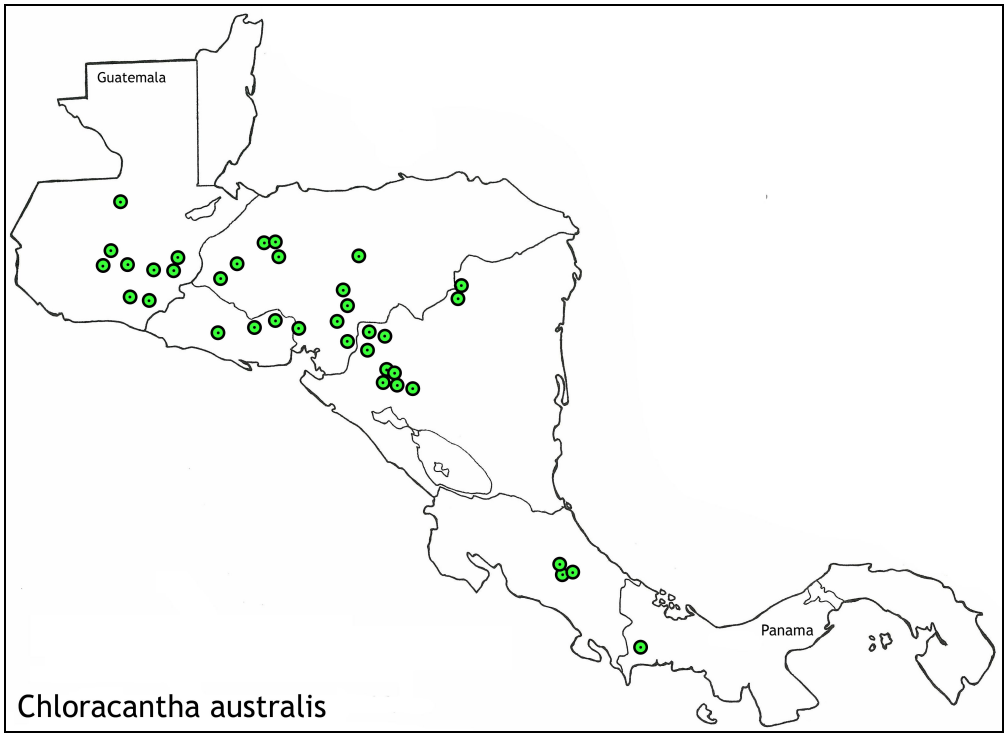
a. Leaves often persisting until flowering; stems usually without spines; phyllaries broadly oblong-elliptic to lanceolate-elliptic, apex rounded; achenes 2–3 mm long, pappus bristles 2.5–3.5 mm long ..... **Chloracantha ortegae**

a. Leaves consistently deciduous by flowering; stems usually sparsely spiny proximally, with many spineless branches above; phyllaries mostly lanceolate, apex acute; achenes 1.5–2.3 mm long, pappus bristles 4–6.5 mm long .....**Chloracantha spinosa**

4. **CHLORACANTHA AUSTRALIS** Nesom, **nom. et stat. nov.** *Chloracantha spinosa* var. *strictospinosa* Sundberg, Phytologia 70: 389. 1991. **TYPE**: **HONDURAS**. **Dept. Morazán**. Rocks in Río Caparosa, near Zamorano, 800 m, 1 Jan 1963, *L.O. Williams 23285* (holotype: LL!; isotypes: ARIZ image!, F image!, GH image!, MEXU image!, MO!, PH image!, US image!). Sundberg cited additional collections at DS, MICH, NY, and UC.

Mexico (Chiapas; the collection from Quintana Roo is out of range and probably adventive), Central America (Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama) (Maps 2, 4). Moist or marginally wet areas, river banks, 800–1200 m; flowering Jul–Jan.

Mexico localities (Map 2). **MEXICO**. **Chiapas**. Rancho La Aurora, *Sanchez 1078* (ENCB, UC). **Quintana Roo**. Playa Paraíso, grounds of Iberostar Paraíso Del Mar resort, along Carretera Chetumal-Cancún, km 309, 12 Dec 2005, *King & Garvey 14164* (ARIZ).



Map 4. Distribution of *Chloracantha australis* (Central American localities).

Figure 1. *Chloracantha spinosa*, Texas — variation in branching and spine production, I.

Figure 2. *Chloracantha spinosa*, Baja California — variation in branching and spine production, II.

Figure 3. *Chloracantha spinosa*, Coahuila — variation in branching and spine production, III.

Figure 4. *Chloracantha* aff. *spinosa*, Michoacan — unusual variant, out of geographical range.

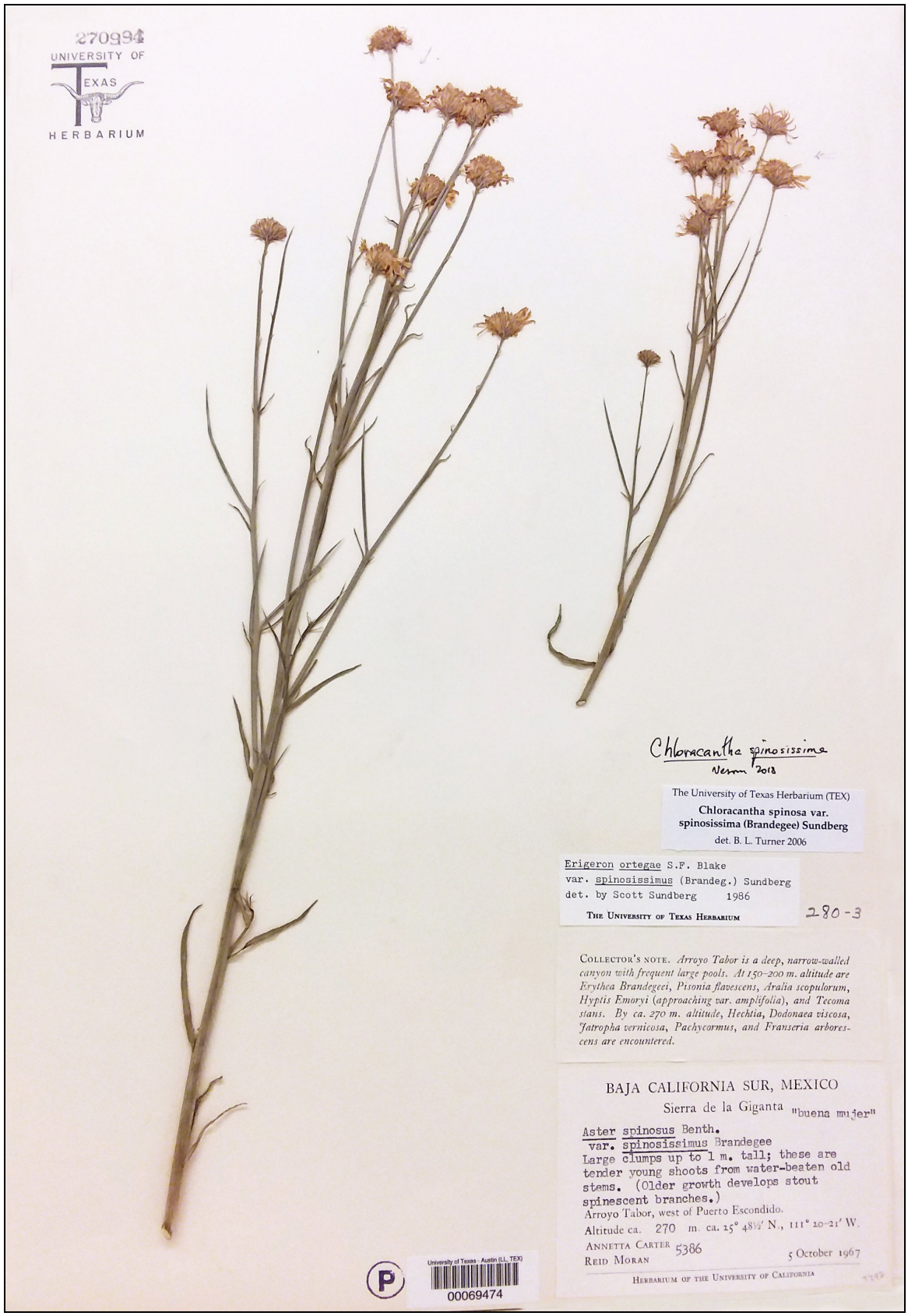


Figure 5. *Chloracantha spinosissima*, Baja California Sur.

Figure 6. *Chloracantha spinosissima*, Baja California Sur.

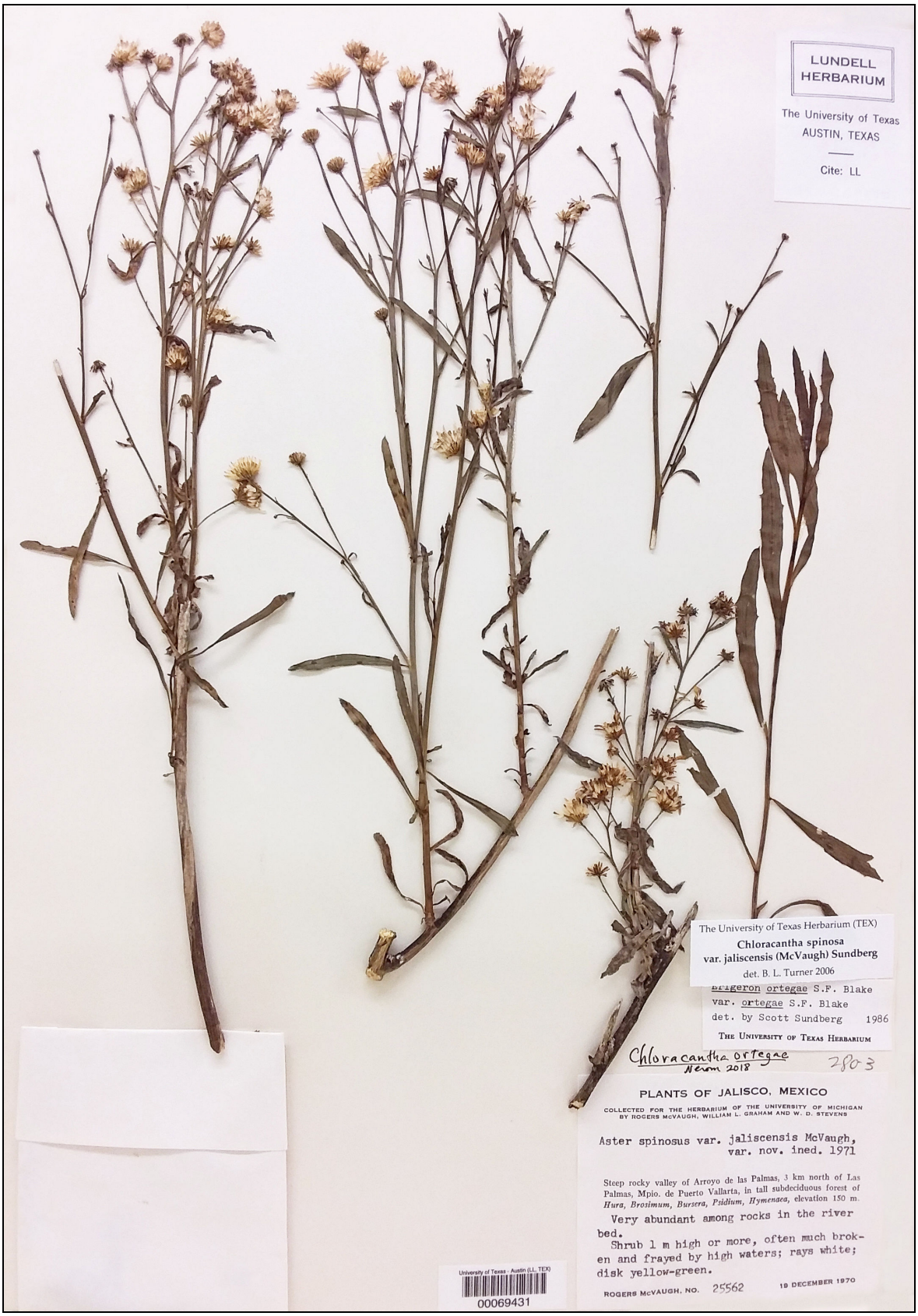


Figure 7. *Chloracantha ortegae*, Jalisco.

Figure 8. *Chloracantha ortegae*, Sinaloa.

Figure 9. *Chloracantha australis*, Nicaragua.

Figure 10. *Chloracantha australis*, Guatemala.

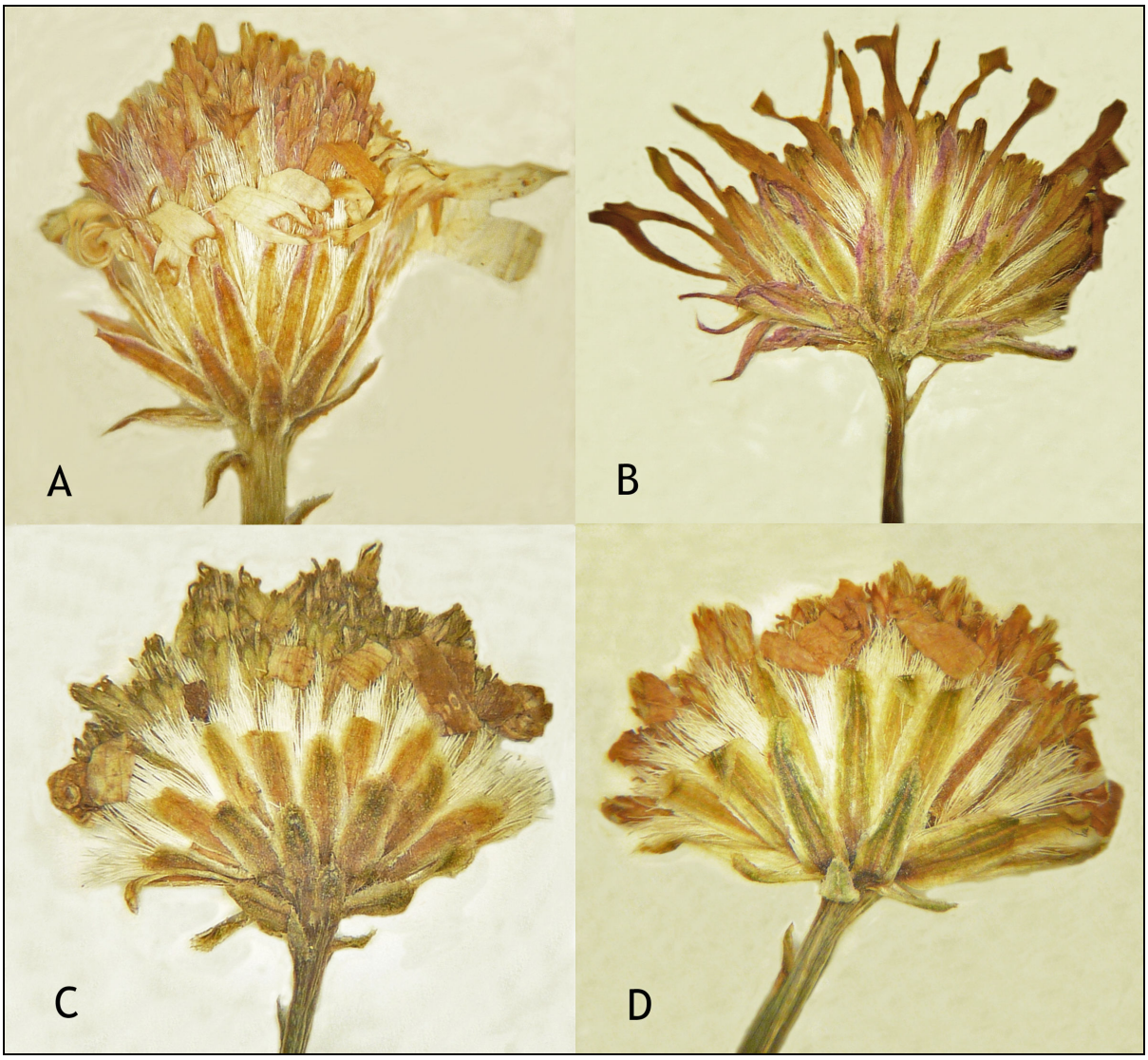


Figure 1. Characteristic involucral morphology of *Chloracantha* species. A. *Chloracantha spinosa*. B. *Chloracantha spinosissima*. C. *Chloracantha ortegae*. D. *Chloracantha australis*.

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