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A NOTE ON NORTH AMERICAN *TORREYOCHLOA* (POACEAE),
INCLUDING A NEW COMBINATION

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ABSTRACT

Torreyochloa is morphologically distinct from *Glyceria* and *Puccinellia*, two genera with which it often has been associated closely; a recent phylogenetic analysis of representative species of Poaceae subfamily Pooideae, based on chloroplast DNA restriction site variation, supports the conclusion that these three genera are not closely related to one another within the subfamily. *Torreyochloa* has been interpreted most often as comprising four or more species in North America, plus two others in eastern Asia. However, several authors, focusing on various combinations of these taxa, have brought the distinctness of all of these taxa into question. Herbarium studies suggest that just two species warrant recognition in North America, *T. pallida* (Torrey) Church and *T. erecta* (A. Hitchc.) Church. The former species is highly polymorphic; elements assignable to this species, and best recognized as varieties, include the type variety plus taxa that have been recognized as *T. fernaldii* (A. Hitchc.) Church and *T. pauciflora* (J.S. Presl) Church. A new combination for the latter taxon, as a variety of *T. pallida*, is proposed.

KEY WORDS: *Glyceria*, *Puccinellia*, *Torreyochloa*, Poaceae

While preparing a taxonomic treatment of *Torreyochloa* for the revised *Manual of North American Grasses*, I have examined the collections of CAS, RSA, UC, and US, a total of more than one thousand specimens. My conclusions will be summarized in the *Manual* treatment, but in association with the necessary publication of a nomenclatural adjustment it seemed useful to offer a brief review of the taxonomic history of *Torreyochloa*, along with observations in support of the taxonomic changes I favor, and some comment on areas that warrant additional study.

In 1949, Church presented a comparative study of variation in morphological and cytological characters of *Glyceria* and *Puccinellia*. His analysis

revealed, first, that many characters differentiate these genera, and second, that a small group of species customarily included in *Glyceria*, on the basis of gross morphology, resemble *Puccinellia* more closely in several characters (e.g., leaf sheath open, lodicules hyaline and elongate, stigmas sessile on pistil, and base chromosome number $x = 7$, as in *Puccinellia*, vs. sheath closed, lodicules fleshy and usually truncate, styles present, and $x = 10$, in the remaining species of *Glyceria*). On the basis of these and other characters, Church segregated this group of species from *Glyceria* and treated them as the new genus *Torreyochloa*.

Shortly thereafter, Clausen (1952) suggested that the species of *Torreyochloa*, in line with the many characters they share with *Puccinellia*, should be assigned to the latter genus rather than maintained as a separate genus. Church (1952), in reply, reemphasized the differences between *Torreyochloa* and *Puccinellia*. Among the characters that differentiate these two genera are the prominence of lemma nerves in the former, vs. obscure nerves in the latter, and a series of characters of the pistil and caryopsis (Church 1952). Church has been followed in his recommendation that the species in question be removed from *Glyceria*, but authors have differed on the question of how they should be treated. In subsequent floristic works, these species have been recognized either as *Torreyochloa* (Welsh 1974; Dore & McNeill 1980), or as species of *Puccinellia* (e.g., Hitchcock 1969; Munz 1973; Holmgren & Holmgren 1977).

A recent phylogenetic analysis of chloroplast DNA restriction site variation in Poaceae subfamily Pooideae (Soreng, *et al.* 1990) included representatives of *Glyceria*, *Puccinellia*, and *Torreyochloa*. The results of that study are consistent with Church's contention that all three of these genera represent distinct lineages within the subfamily: *Glyceria* is grouped with the tribe Meliceae and *Puccinellia* with Poeae (both as expected), while *Torreyochloa* is grouped with Aveneae.

Six principal taxa are widely recognized in *Torreyochloa*, each at times as a species. Of these six, two occur in each of the following three regions: 1) eastern North America (*T. pallida* [Torrey] Church [the type species of the genus] and *T. fernaldii* [A. Hitchc.] Church); 2) western North America (*T. pauciflora* [J.S. Presl] Church and *T. erecta* [A. Hitchc.] Church); and eastern Asia (*T. natans* [V. Komarov] Church and *T. viridis* [Honda] Church). Additional taxa have been recognized by various authors, usually at the varietal level (cf. Hitchcock 1969; Munz 1973; Taylor & MacBryde 1978; Boivin 1981).

Despite the widespread recognition of six or more species of *Torreyochloa*, their distinctness, and hence their species status, has been called into question by various authors. Fassett (1946) presented evidence that *T. pallida* and *T. fernaldii* are only varietally distinct. Clausen (1952, p. 44) went further, in suggesting that all of the taxa in North America "comprise a series and essentially replace each other geographically and altitudinally," and that they "may all belong to a single polytypic species." Koyama & Kawano (1964)

interpreted the two eastern North American taxa and the two Asian taxa as constituting two vicariant pairs (*T. fernaldii* with *T. natans*; *T. pallida* with *T. viridis*), presented evidence that none of these four is distinct, and treated them as varieties of *T. pallida* (nested as pairs within two subspecies).

My observations, which have been limited to North American *Torreyochloa*, largely confirm those of Fassett (1946), Clausen (1952), and Koyama & Kawano (1964) concerning the absence of species distinctions among these taxa. In particular, I concur with Fassett (1946) in finding that, of the four principal North American taxa, the distinction that is most difficult to maintain is between the two eastern taxa, *T. fernaldii* and *T. pallida*. The reader is referred to Fassett's paper for a summary of characters that apportion many specimens, but not nearly all, to one of the two groups. Although a strong bimodality in form is evident, intermediate individuals are not rare. The geographic range of *T. fernaldii* extends from Newfoundland westward to the eastern prairie (plus a few disjunct sites farther to the north and west), and southward to West Virginia and Tennessee (Koyama & Kawano 1964; pers. obs.). The range of *T. pallida* sens. strict. extends from Nova Scotia westward to the eastern prairie, and southward, principally in the Appalachian Mountains, to Georgia. Thus, the ranges of these two elements are widely overlapping, with that of *T. fernaldii* extending farther to the north, and that of *T. pallida* farther to the south. Morphologically intermediate individuals appear to be limited to a range extending from southeastern Canada to Connecticut, and westward to Minnesota. Detailed population studies might clarify the nature of variation at sites at which intermediate individuals occur, but observations to date suggest that the taxon known as *T. fernaldii* is best recognized as a geographic variety of *T. pallida*.

My observations also detect no consistent difference between *T. pallida* and the principal western North American form, usually recognized as *T. pauciflora*. Western plants tend to be more robust in vegetative characters than eastern plants (20-142 cm vs. 18-110 cm tall; reproductive stems 1.3-4.8 mm vs. 0.6-3.0 mm in diameter at base; widest cauline leaf blades of reproductive stems 3.6-17.5 mm vs. 1.5-11.4 mm wide), while the lengths of anthers of western plants fall towards the lower end of the range observed in eastern specimens (0.5-0.7 mm vs. 0.3-1.5 mm long). However, as is evident from these ranges, the means and extremes may differ, but no diagnostic character consistently differentiates the groups.

The largest plants in western North America occur near sea level, and those from higher elevations are progressively smaller. Above ca. 2000 m, two groups of plants occur. One group bears compact, ovate to obovate panicles, ca. 6-10 cm long and ca. 2-3 times as long as wide; these plants have been recognized as *T. californica* (Beetle) Church, but a continuous series of intermediates between these and the robust coastal forms suggests that species status is not warranted. Plants of the second high elevation group, identifiable as *T. erecta*,

bear leaves ≤ 7.2 mm wide, and a linear panicle ≤ 1.0 cm wide and ≥ 5.5 times as long as wide. This character combination is unique in North America.

These observations together suggest that North American *Torreyochloa* is best recognized as comprising two species, the widespread and polymorphic *T. pallida* (sea level to 3500 m elevation, Newfoundland to Georgia and westward to the eastern prairie, plus Alaska to California and eastward to the Rocky Mountains) and *T. erecta* (2000-3500 m elevation in the Sierra Nevada and Cascade Ranges, in California, Nevada, and Oregon). If the eastern Asian taxa also are regarded as conspecific with *T. pallida*, as maintained by Koyama & Kawano (1964), the geographic range of this species is correspondingly greater. As discussed above, three principal geographic varieties of *T. pallida* can be distinguished in North America. The correct names for these taxa, at the varietal rank, are *T. pallida* var. *pallida*, *T. pallida* var. *fernaldii* (A. Hitchc.) Dore, and for the taxon previously recognized as *T. pauciflora*, the following new combination.

Torreyochloa pallida (Torrey) Church var. *pauciflora* (J.S. Presl) J.I. Davis, *comb. nov.* BASIONYM: *Glyceria pauciflora* J.S. Presl, in C. Presl, *Reliq. Haenk.* 1:257. 1830.

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**MANFREDA CHAMELENSIS (AGAVACEAE: POLIANTHEAE), A NEW
SPECIES FROM WESTERN MÉXICO**

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ABSTRACT

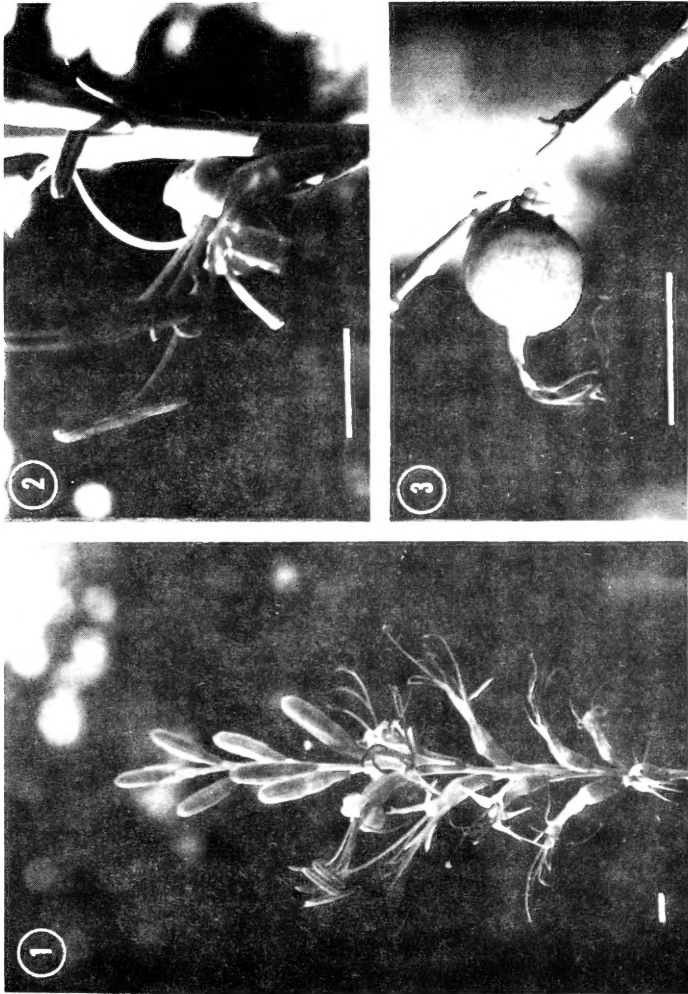
Manfreda chamelensis *spec. nov.* is described from coastal Jalisco, México. Its relationships with *M. brachystachya* (Cav.) Rose and *M. jaliscana* Rose are discussed.

KEY WORDS: *Manfreda*, Agavaceae, Poliantheae, México

Continued studies of the flora of the Estación de Biología Chamela U.N.A.M. and surrounding area of coastal Jalisco, México have resulted in the discovery of various novelties, among them the following.

Manfreda chamelensis E. Lott & S. Verhoek, *spec. nov.* TYPE: MÉXICO. Jalisco: Mpio. La Huerta: Arroyo Las Maderas, antiguo camino a Nacastillo, 8 Dic 1982, E. Lott & T. Wendt 1663 (HOLOTYPE: MICH; Isotypes: BH, CAS, MEXU). Figs. 1-3.

Ex caterva *Manfredae brachystachyae* (Cav.) Rose; differt a *M. jaliscana* Rose staminibus 1.5-2.5 cm exsertis et tubo supra ovarium non constricto; differt a *M. brachystachya* (Cav.) Rose tubo florali brevioris et capsula globosa sine rostro; differt ab ambabus habitatione terris inferis in sylva tropica decidua vel subdecidua.



Figures 1-3. *Manfreda chamelensis*. 1. Portion of inflorescence. 2. Flower. 3. Fruit. Photos by S.H. Bullock from *Solis Magallanes* s.n. White lines represent 1 cm.

Geophytes, reproducing vegetatively by buds from the rhizome; roots fleshy, rhizome 3-15 cm long, 2-3 cm diam, upright, cylindrical, with small white pointed buds; remnants of leaf base membranous, not separating into fibers. Leaves to 9 in a rosette, herbaceous to somewhat fleshy, brittle, spreading, narrowly channeled, nearly conduplicate near the base; laminae 40-75 cm long, 2-5 cm wide, linear to linear lanceolate, dark green, purple speckled near the base; apex acute; base narrow; margins with a narrow yellowish cartilaginous band, minutely denticulate, the teeth regular; veins papillate above and below. Inflorescence 75-120(-205) cm tall; rachis slender, glaucous, the flowering portion 10-20 cm long, bearing 10-25(-35) flowers, the second internode 0.5 cm long; bracts of scape to ca. 8 cm long, few, abruptly smaller than the leaves, linear lanceolate, acute, thin; floral bracts 3-5 mm long, triangular; bracteoles 1-2 mm long, triangular. Flowers sessile; buds clavate, the apex obtuse; mature flowers nearly erect, green; ovary 0.5-1 cm long, ca. 0.2 cm wide, oblong to ovate, not protruding into the tube; tube 0.6-1.3 cm long, longer than the ovary, funnellform, tepals 0.8-1.1 cm long, reflexed to tightly revolute at anthesis, oblong, shorter than the tube, the apex slightly swollen, obtuse; apical tuft small, narrowly triangular; filaments slender, bent near tip in bud, inserted at top 1/2 of the tube, exceeding the tube by 1.5-2.5 cm, straight, slender, green, densely purple speckled; anthers (1.0-)1.3-1.5 cm long, minutely papillate; style at first short, strongly bent toward lower lobes, at maturity straight, exerted by 2.5-3.5 cm; stigma clavate, trigonous, the furrows not extending past the apex. Capsule 1.2-1.6 cm long, 1.0-1.5 cm wide, glaucous, globose, the withered flower persistent; seeds 5-6 mm and 4-5 mm on the radial margins, \pm cuneiform.

The specific epithet refers to the town of Chamela, Jalisco.

Additional collections examined: MEXICO. Jalisco: Mpio. La Huerta: Arroyo Colorado, Estación de Biología Chamela, s.d., *Solis Magallanes s.n.* (Plants in cultivation at Est. Biol. Chamela); Pueblo Careyes, 24 Jul 1986, *Lott & Atkinson 2817* (MEXU); Rancho Cuixmala, Cumbres 1, Upper Arroyo Cajones, 14 Jan 1991, *Lott, et al. 3271* (UCR).

Manfreda chamelensis E. Lott & S. Verhoek belongs to a group of species related to *M. brachystachya* (Cav.) Rose. Of these, it appears to be most closely related to *M. brachystachya* and *M. jaliscana* Rose. It is similar to both species in the presence of papillate cells over the veins and in the openness of the inflorescence. It differs from both species by its shorter floral bracts (Table 1), filaments bent near the tip at bud opening, and the absence of coarse fibrous remnants of old leaves. Further, *M. chamelensis* differs from *M. brachystachya* by its shorter floral tube and globose, beakless capsule, and from *M. jaliscana* by its wider leaves and shorter styles and filaments (Verhoek-Williams 1975).

The new species is known only from the vicinity of Chamela, Jalisco, where it is uncommon along arroyos in tropical deciduous and semideciduous forest, at elevations of about 50-75 m. Flowering occurs in December.

Table 1. Some characters distinguishing *Manfreda chamelensis* from *M. brachystachya* and *M. jaliscana*.

Characters	<i>M. chamelensis</i>	<i>M. brachystachya</i> ¹	<i>M. jaliscana</i>
Remnant leaf bases	not separating into fibers	separating into stiff fibers at top, 5-12 cm long	separating into stiff fibers at top, 4-7 cm long
Leaves	40-75 x 2-5 cm	mostly 37-77 x 1-6-4.8 cm	mostly 49-78 x 0.6-1.4(-2.8 cm)
Floral bract length	0.3-0.5 cm	1.0-3.2 cm	0.6-1.0 cm
Tube length	0.6-1.3 cm	(0.9-)1.3-2.8 cm	0.4-1.0 cm
Filaments	bent near tip at bud break	bent at upper third in bud	bent near midpoint in bud
Stamens exceeding tube	1.5-2.5 cm	(1.6-)2.0-3.5 (-4.7) cm	(4.8-)5.2-7.6 cm
Style exceeding tube	2.5-3.5 cm	2.4-3.7(-7.4) cm cm	(5.6-)6.2-8.4(-9.8)
Capsule	globose; 1.2-1.6 x 1.0-1.5 cm, beak absent	oblong; 1.8-2.9 x 1.1-1.6 cm, with beak 0.2-0.3 cm	globose to oblong; 1.1-2.7 x 1.2-1.7 cm, with beak 0.2-0.3 cm
Habitat	tropical deciduous and semideciduous forest, 50-75 m	oak-pine forest, 180-2450 m	oak forest, pine forest, 760-1050 m

¹Data for *Manfreda brachystachya* and *M. jaliscana* from Verhoek-Williams (1975).

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We are grateful to F. Chiang C. and G. Nesom for the Latin diagnosis and to T.F. Daniel and J.L. Villaseñor for reviewing the manuscript. S.H. Bullock kindly supplied the photographs. We thank T.H. Atkinson for technical assistance.

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**CHLORACANTHA, A NEW GENUS OF NORTH AMERICAN ASTEREAEE
(ASTERACEAE)**

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ABSTRACT

Aster spinosus Bentham (= *Erigeron ortegae* S.F. Blake), a species widely distributed from Central America into the southwestern United States, is treated as a new genus, **Chloracantha**, with a single species, **C. spinosa** (Benth.) Nesom, *comb. nov.* Although *C. spinosa* produces no terminal resting buds and displays a herbaceous aspect in its permanently green stems without periderm, it behaves more 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. Such a distinctive growth form is not known in any of the more than 500 species of *Aster* or *Erigeron*, the two genera with which the species has been allied, or in any other potentially closely related taxa. Studies of restriction site variation in chloroplast DNA suggest that the closest relative of *C. spinosa* is the genus *Boltonia* and that these two taxa apparently are more closely related to the lineage that includes *Heterotheca* than that of *Aster*; *Erigeron* is yet more distantly related.

KEY WORDS: *Chloracantha*, *Erigeron*, *Aster*, *Heterotheca*, *Boltonia*, Astereae, Asteraceae

Bentham (1839) described a distinctive plant from México as *Aster spinosus* Benth., now known to represent a species widely distributed from Central

America through México and into the southwestern United States. Its taxonomic residence until the present has primarily been the genus *Aster* L. The first reservation regarding its placement was registered by Greene (1897), who placed it in *Leucosyris* E. Greene, enlarging that genus from monotypic to ditypic. His rather forced view of the similarity between *A. spinosus* and the type species of *Leucosyris* (*Leucosyris carnosus* [A. Gray] E. Greene = *Linosyris carnosus* A. Gray = *Aster carnosus* [A. Gray] A. Gray ex Hemsl. = *Aster intricatus* [A. Gray] S.F. Blake = *Machaeranthera carnosus* [A. Gray] Nesom) was noted only in the description of "pale green reedy almost leafless stems and permanently white corollas, the rays either very short or wanting" (p. 244). Jones (1980) placed the same two species in sect. *Spinosi* (Alexander) A.G. Jones of *Aster* subg. *Oxytripolium* (DC.) Torr. & Gray, but Jones & Young (1983) soon questioned the close relationship between them. *Linosyris carnosus* was removed from *Aster* and replaced into the monotypic *Leucosyris* by Sundberg (1986); alternatively, Nesom (1990) transferred the species to the genus *Machaeranthera* Nees, but in any case, it clearly is not closely related to *A. spinosus* (see additional comments below). *Aster spinosus* was maintained in *Aster* in a cladistic analysis of the genus (Jones & Young 1983), where *A. spinosus* was positioned as a member of the *Tripolium* group (including the *Oxytripolium* group).

The taxonomic overview of *Aster* provided by Semple & Brouillet (1980) placed *A. spinosus* with *A. pauciflorus* Nutt. in an informal group of two species they referred to as "subg. *Leucosyris*." On the basis of morphology, hybridization experiments, and chromosome number of $n = 9$, Sundberg (1986) concluded that *A. pauciflorus* was an isolated element within *Aster*, perhaps with a portion of its phylogenetic roots near *Machaeranthera* sect. *Psilactis* (A. Gray) Turner & Horne (= *Psilactis* A. Gray). The recent molecular studies by Morgan (1990) have indicated that *A. pauciflorus* is indeed closely related to both the *Oxytripolium* group of *Aster* and *Psilactis*, which also has proved to be closely related to *Aster*. *Aster spinosus* is not part of the phylad that includes *Aster* and *Psilactis*, according to the molecular data.

A morphological similarity between *Aster spinosus* and the genus *Erigeron* was early recognized by Blake (1924), who described one of the geographical variants of the species as *E. ortegae* S.F. Blake, not realizing that it was conspecific with a previously described and well known species. In a study of *Aster* subg. *Oxytripolium* and taxa historically included with it, Sundberg (1986) also perceived a more comfortable fit for *A. spinosus* within *Erigeron* and placed it there, using Blake's epithet ("ortegae") and an accompanying set of varietal nomenclature. He annotated specimens with these names, but his proposed taxonomic changes and new varietal taxa have not been formalized.

Nesom (1989a) hypothesized that the closest relative of *Aster spinosus* was the North American *Erigeron oxyphyllus* E. Greene, and in collaboration with S. Sundberg, created a new section for the two as *Erigeron* sect. *Spinosi*

(Alexander) Nesom & Sundberg. *Erigeron byei* Sundberg & Nesom, a species recently described from northwestern México, was tentatively added as a third species to this group. *Erigeron oxyphyllus*, however, has proved to be a true *Erigeron*, one of the thirteen species of *E. sect. Pycnophyllum* Cronq., closely centered around *E. foliosus* Nutt. (Nesom 1991b). The position of *E. byei* remains equivocal (see comments below).

Most recently, on the basis of restriction site analysis of chloroplast DNA among a wide selection of genera of North American Astereae, Morgan (1990) discovered that *Aster spinosus* is phyletically removed from true *Aster* and even further distant from *Erigeron*; instead, it appears to be a weakly related, basal member of the much more strongly defined phylad that includes *Heterotheca* Cass., *Pityopsis* Nutt., *Chrysopsis* (Nutt.) Ell., *Bradburia* Torr. & Gray, *Osbertia* E. Greene, and *Croptilon* Rafin. Morgan's data included *Aster spinosus* and *Croptilon*; Suh's analysis (1989), which included all of the genera above except *Osbertia* and *Aster spinosus*, was of primary significance in defining the *Heterotheca* phylad. He found that the genus *Boltonia* L'Herit., like *A. spinosus*, is best placed as a weakly associated basal member of this same lineage. A morphologically based hypothesis of the phylogeny of this group will be presented by Nesom (1991a), and a summary of this and the other broad phyletic lines that exist within North American Astereae, based on cpDNA restriction site data and emphasizing primary groupings of genera rather than the more tenuously defined phylogenetic connections between these groups, is presented in Nesom, et al. (1990).

Although the molecular data provide evidence that the phylogenetic origin of *Aster spinosus* is independent of *Aster* and *Erigeron*, the relatively generalized features of capitular, floral, and fruit morphology of this species have not provided an unequivocal basis for an alternative placement or even its rejection from either genus. In the present paper, we add critical observations regarding the morphological differences between *A. spinosus* and *Machaeranthera carnosa* as well as all species of both *Aster* and *Erigeron*. A technical description of the species follows its formal nomenclatural treatment at the end of the paper; a more detailed narrative of the distinctive vegetative features of *A. spinosus* is presented here in order that it can be contrasted with its putative relatives.

Vegetative morphology of *Aster spinosus*

The following observations were made by the first author from a vigorous colony of plants cultivated for five years in the back yard of his residence in Austin, augmented by study of natural populations in Travis Co., Texas, which proved to be essentially identical in growth pattern to the cultivated plants. The latter were begun from rhizomes transplanted from Hays Co., Texas, on the floodplain of the Pedernales River, ca. 1 mile northwest of the Travis Co.

line; a voucher specimen (*Nesom s.n.*) of these plants, showing different stages of growth, is deposited at LL,TEX. Anatomical observations have been made from hand sections of fresh stems.

The first year stems (here referred to as "ramets") arise from stout rhizomes and grow quickly to produce a strictly erect, central axis with numerous, narrowly oblanceolate leaves. On the upper 70-80% of the main stem, each of the axillary buds develops without dormancy directly into a sharply ascending branch, all of which produce a full complement of leaves but no lateral branches. The stems are determinate, and maximum vertical growth appears to be attained first year. Single capitula are produced at many of the stem apices, and, lacking terminal buds, the terminal portions of all stems die at the season's end, leaving long (1-3 dm), thin, dead but persistent branch tips. The lower portions of many of the lateral branches remain alive over the winter, but other of the lower branches die back to near their point of origin at the main stem.

All portions of the stems are distinctively green and glaucous, and these plants have been regarded as "herbaceous," either directly or by implication from the generic description, in almost all published treatments, although they have often been noted to be basally woody. In contrast, Wiggins (1980) and McVaugh (1984) have clearly distinguished it as shrubby or suffrutescent. The first year stems remain flexuous but a vascular cambium is produced very early, and by about 4 weeks the cambium is completely cylindrical. Growth rings are weakly if at all developed, but the stem diameter expands significantly to a maximum of about 9 mm, and the base of the stem becomes particularly woody. A cork cambium apparently never forms, and all stems, including the main axis of each ramet, remain green with a smooth, waxy epidermal surface for their whole life, the cortex and epidermis keeping pace in expansion with that of the secondary xylem. Except for this, the secondary growth is otherwise mostly similar to that of typical woody stems.

On the lower part of the stem, where lateral branches are not produced immediately with the leaves, a small axillary bud (primary bud) is evident at each node. In each of the upper nodes with lateral branches, a second axillary bud (serial bud) is produced. All axillary buds first appear simply as leaf primordia, but by late in the growing season, undeveloped buds (both primary and serial) become enclosed by ca. 8-12, brown sclerified scales 0.5-1.0 mm long with rounded, minutely fimbriate-cililate margins. Early in the growing season of the second year, most of the (serial) buds on the upper half of the main stem produce fascicles of leaves, these apparently on short shoots, a few of which may elongate into relatively short stems. Both the first set of leaves and the later-produced fascicles are quickly deciduous and most if not all have been shed by the time of flowering. A few of the lower (primary) buds usually open in subsequent years, and the main growth of individual ramets past the second year is mostly limited to short branches produced by these

buds and (primary) buds on the original set of lateral branches. Most ramets do not live past 3 or 4 years; they die and are replaced by new ones from the rhizomes in various parts of the clones.

In some of the geographic races of *Aster spinosus*, the primary lateral branches are characteristically modified into short, stout thorns (the epithet "spinosus" is technically a misnomer). The plants from Texas as well as the rest of the southwestern United States belong to the typical race (Sundberg 1991), where thorns are weaker and less commonly produced.

Flowering occurs in the late summer and fall. The capitula are produced at the stem apices as well as very short (3-15 mm long), bracteate stems that arise from the uppermost buds.

Aster spinosus distinguished from *Machaeranthera carnosus*, *Aster*, and *Erigeron*

The chromosome number of *Aster spinosus* ($n = 9$) separates it from *Machaeranthera carnosus* ($n = 5$, see Nesom 1990b), and despite Greene's hypothesis of close relationship between these two species, they are similar in little else than their shrubby, rhizomatous habit, and even then, the latter produces neither thorns nor axillary buds with bud scales. The subulate leaves of *M. carnosus*, its corollas and phyllaries without orange resinous veins, lance-attenuate style tips, sericeous achenes, basally flattened pappus bristles, and chromosome number are features in common with *Machaeranthera*.

All species of *Erigeron* as well as a large segment of *Aster* have a chromosome number of $n = 9$, but no species of *Aster* or *Erigeron* produces thorns or bud scales. *Aster spinosus* has been placed with the *Oxytripolium* group primarily on the basis of its glabrous stems and leaves, and slender, strictly erect stems, although these species of *Aster* have $n = 5$. Except for the peculiar growth habit, the morphological characters that distinguish it from *Aster* are mostly those that are more similar to *Erigeron*: the lack of green herbaceous apical regions of the phyllaries, the presence of prominent, orange resinous veins in the disc corollas, and deltax collecting appendages of the style branches. The latter feature was the only one specifically mentioned by Blake (1924) in his decision to place *E. ortegae* in *Erigeron* rather than *Aster*.

The genus *Erigeron* has seemed variable enough to accommodate even a species as peculiar as *Aster spinosus*, but continuing study of interspecific relationships within the genus has shown that *E. oxyphyllus*, with which it was associated (Nesom 1989a), is a species closely related to *E. foliosus* (Nesom 1991b). Although it is largely lacking in vestiture, the leaves of *E. oxyphyllus* are basally ciliate, the phyllaries are minutely glandular, and sparsely strigose, the achenes are strigose and 2-4 nerved, and it does not produce a system of spreading, underground rhizomes like that of *A. spinosus*.

Besides its growth habit, the phyllary morphology of *Aster spinosus* is the only feature that is not matched by any species of *Erigeron* or close relatives.

The nearly oblong phyllaries produce hyaline margins that extend about the rounded apex, and the dense concentration of stomates give the lateral surfaces a punctate appearance. The nervation of three parallel veins that has been noted as distinctive cannot be emphasized as an indicator of close relationship, because similar nervation occurs in almost all species of *Trimorpha* Cass. (Nesom 1989b) and *Couzya* L. (Nesom 1990a), both genera apparently closely related to *Erigeron*, as well as a number of species of *Erigeron* in different sections (Nesom 1989a). Three nerved phyllaries are almost certainly primitive among these taxa.

The hypothesis that *Erigeron byei* is closely related to *Aster spinosus* (Nesom 1989a; Sundberg & Nesom 1990) was based heavily on their nearly identical phyllaries, rhizomatous habit, and persistently green glabrate stems and leaves. Plants of *E. byei*, however, are diminutive relative to *A. spinosus* and they produce persistent basal leaves and annual stems without axillary resting buds. Further, their achenes are more characteristic of *Erigeron* in the strigose vestiture and (2-3-)4(-5) nerves. The chromosome number of $n = 9$ is of equivocal significance. While we believe that the evolutionary affinities of *E. byei* may yet prove to lie with *A. spinosus*, outside of *Erigeron*, there is insufficient evidence at present to make the nomenclatural transfer formal.

Aster spinosus distinguished from taxa of the *Heterotheca* lineage

The molecular data of Morgan and Suh, as noted above, indicate that *Aster spinosus* and *Boltonia* are apparently more closely related to the *Heterotheca* lineage than any other, although they are associated with it as basal members. Except for these two taxa, however, the other genera closely related to *Heterotheca* produce prominently pubescent vegetative organs, yellow ray flowers, disc style branches with linear-lanceolate appendages, and densely strigose-sericeous achenes. *Boltonia* and *A. spinosus* are strikingly similar between themselves in their glabrate stems and leaves, quickly deciduous leaves, white ray flowers, disc style branches with deltate appendages, and their glabrous or minutely pubescent achenes. Both have a chromosome number of $n = 9$; this number is also hypothesized to be primitive within the *Heterotheca* lineage (Nesom 1991a). *Boltonia* differs from *A. spinosus* in its flattened, weakly to strongly winged achenes with a pappus of two thick awns and series of much shorter, thinner bristles, and while the plants are also rhizomatous and perennial, they produce shorter rhizomes and do not form large colonies like *A. spinosus*. The strictly annual stems of *Boltonia* do not produce axillary buds or thorns. *Boltonia* includes five species, all restricted to the eastern United States (see Anderson 1987 for a review of the genus), where they are mostly allopatric with *A. spinosus*.

Perenniality in *Aster*, *Erigeron*, and other American Astereae

All species of *Aster* (excluding subg. *Conyzopsis* [Torr. & Gray] A. Gray = *Brachyactis* Ledeb.) are perennial except several of sect. *Oxytripolium* and *Psilactis* (= *Machaeranthera* sect. *Psilactis*, see previous comments). The above ground parts are primarily herbaceous, but some species produce stems that are woody at least at the base (e.g., *A. novae-angliae* L.). No resting buds with bud scales are produced, however, and in all taxa the vegetative parts die back to ground level at the end of each season. The perennating meristems are restricted to the shoot apex.

The situation is similar in *Erigeron*, where most species also are perennial, but it is a larger genus including a greater number of species that produce woody stems. Species with woody bases are found in a number of different sections, and even in sect. *Olygotrichium* Nutt., where the species are characteristically annual (Nesom 1989a), *E. modestus* A. Gray and *E. bigelovii* A. Gray are clearly perennial and produce woody stem bases. The species of sect. *Polyactis* (Less.) Nesom are primarily perennial with woody rhizomes and lower stems; in *E. polycephalus* (Larsen) Nesom of that section, the woodiness extends further up the stems so that the plants may be referred to as "subshrubs." Some insular species of *Erigeron* of disparate phylogenetic origin within the genus have developed a subshrubby, "rosette" habit. These plants have long, mostly unbranched stems with leaves clustered near the stem tips (see Nesom 1989a, following "*Darwiniothamnus* Harling," for further comments and examples). In all of these species, however, the perennating buds are restricted to the shoot apices, there are no axillary resting buds, and there are no buds at all enclosed by bud scales.

The perennial species of the *Heterotheca* lineage are similar in growth habit to those in *Aster* and *Erigeron*. Even among other genera of other American Astereae that produce true shrubs, such as *Acamptopappus* A. Gray, *Baccharis* L., *Chrysothamnus* Nutt., *Hazardia* E. Greene, *Isocoma* Nutt., *Machaeranthera* (e.g., *M. restiformis* B. Turner and *M. carnosa*), and *Xylorhiza* Nutt., as well as many others, new growth is mostly or completely initiated from the meristems of the shoot apices. Lateral buds are difficult to discern and bud scales even more so, perhaps partially because most specimens are collected during periods of growth soon after the breaking and expansion of meristems. In any case, we have not seen what could be unequivocally interpreted as bud scales among any of these. Of the American genera with a shrubby habit, some species of *Baccharis* produce determinate stems and are similar in general aspect to *Aster spinosus*, but in all species of the former examined, including a number from both North and South America, we have seen only unprotected primordia in the leaf axils.

A new genus for *Aster spinosus*

We conclude that *Aster spinosus* is morphologically anomalous within the boundaries of both *Aster* and *Erigeron*, and there is no evidence for its putatively close relationship with *Machaeranthera (Leucosyris) carnosa*. It is not impossible that the distinctive features of *A. spinosus* might have arisen from ancestors in one or the other of these genera, but the studies of cpDNA restriction site variation do not support this hypothesis. Although these are the only genera with which it has been formally associated, molecular evidence indicates that it is probably more closely related to the genus *Boltonia* and then to the lineage that includes *Heterotheca* and its relatives. We acknowledge the phyletic isolation of *A. spinosus* and propose to accommodate it within the tribe Astereae by erecting a new genus, the name chosen in reference its evergreen, thorny ("spiny") stems.

Chloracantha Nesom, Suh, Morgan, Sundberg, & Simpson, *gen. nov.* TYPE: *Chloracantha (Aster) spinosa* (Benth.) Nesom.

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

Astro ac Erigeronti similis sed caulibus spinosis perennibus sem-perviventibus viventibus per annos 2-4 et gemmis axillaribus ad maturitatem squamis obtectis differt.

Chloracantha spinosa (Benth.) Nesom, *comb. nov.* BASIONYM: *Aster spinosus* Benth., *Pl. Hartweg.* 20. 1839. TYPE: MÉXICO. Aguascalientes (according to McVaugh 1984): [ca. 1836], *K.T. Hartweg 148* (HOLOTYPE: K, MICH-photo!, TEX-photo!; Isotypes: BM, CGE, GH!). *Leucosyris spinosa* (Benth.) E. Greene, *Pittonia* 3:244. 1897.

Erigeron ortegae S.F. Blake, *Proc. Biol. Soc. Washington* 37:55. 1924. TYPE: MEXICO. Sinaloa: Balboa, Jan 1923, *J.G. Ortega 4974* (HOLOTYPE: US!).

Glabrous or glabrate, glaucous, perennial subshrubs forming large clones, spreading by stout rhizomes that eventually becoming densely woody and irregularly thickened, the main stems strictly erect, 0.5-1.5(-2.5) m tall, with lateral branches sharply ascending, the latter sometimes modified as thorns. Leaves all cauline, alternate, uninerved, 1-5 dm long, oblanceolate, entire or very rarely with 1-2 pairs of small teeth, early deciduous, glabrous except the

margins sometimes sparsely ciliate and the upper surface sometimes with scattered minute hairs. Heads broadly turbinate to hemispheric, produced singly in loose, corymboid panicles; buds erect; receptacles shallowly convex, smooth to shallow foveolate, epaleate; phyllaries strongly graduated in (3-)4-5 series, the inner 4.5-7.5 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 flowers 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 flowers numerous, hermaphroditic, fertile, the corollas yellow with orange resinous veins, narrowly funnelform, (3.2-)3.5-6.0 mm long, the lobes deltate; style with a bulbous base, the branches with deltate to triangular collecting appendages 0.1-0.2 mm long. Achenes glabrous, slightly compressed, 1.5-3.5 mm long, with 5(-6), whitish to golden brown nerves; carpopodium 4-8 cells high; pappus of 30-60 whitish, slender, terete, barbellate bristles in ca. 2 series, about as long as the disc corollas, usually with a few with much shorter outer setae. Chromosome number, $n = 9$ pairs (summary of original and previously published counts in Sundberg 1986).

Panamá to Guatemala, widespread in México, southwestern United States from southern California as far north as southern Utah and east to Oklahoma, Texas, and Louisiana; in a variety of habitats, though most commonly near water, mostly at low elevations but at some sites up to nearly 2000 m; flowering Jun-Oct in the northern part of its range, nearly all year in the south.

Geographic variation within *Chloracantha spinosa* has been studied by Sundberg (1986), who presents its infraspecific taxonomy in this volume (Sundberg 1991).

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ERRATUM—*ISOCOMA PLURIFLORA* (TORR. & A. GRAY) E. GREENE

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In a recent paper (Taxonomy of *Isocoma* (Compositae: Astereae), *Phytologia* 70:69-114. 1991.), I consistently treated the name of a common species from the south central United States and México as *Isocoma plurifolia*. I am grateful to Dr. A. Cronquist, however, for pointing out that the correct epithet is "*pluriflora*" rather than "*plurifolia*," based on *Linosyris pluriflora* Torr. & A. Gray, and the correct name in *Isocoma* is *I. pluriflora* (Torr. & A. Gray) E. Greene.

INFRASPECIFIC CLASSIFICATION OF *CHLORACANTHA SPINOSA*
(BENTH.) NESOM (ASTERACEAE) ASTEREAEE

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ABSTRACT

Four allopatric varieties of *Chloracantha spinosa* (Benth.) Nesom are recognized, based on head size, number of phyllaries and florets, phyllary shape, anther length, abundance of stem spines, spine length, achene length, pappus bristle length, and characteristics of the terminal cells of the pappus bristles.

KEY WORDS: Asteraceae, Astereae, *Chloracantha*, *Aster spinosus*, North America, Central America

Arguments for the placement of *Aster spinosus* Benth. in the monotypic genus *Chloracantha* Nesom, Suh, Morgan, Sundberg, & Simpson are presented in Nesom, *et al.* (1991) in this volume. The transfer of the species is based on its distinctive vegetative morphology and on studies of chloroplast DNA restriction fragment length polymorphisms that demonstrate a closer affinity to *Boltonia* and possibly to *Heterotheca* rather than to *Aster* or *Erigeron*, to which it has been allied in the past (Sundberg 1986). In this paper the infraspecific classification of *Chloracantha spinosa* (Benth.) Nesom is presented.

Chloracantha spinosa is a widespread weed in the southern United States from southern California to southern Louisiana, ranging to the north in Arizona, New Mexico, and Texas with scattered localities in Nevada, Utah, and Oklahoma, and to the south throughout México to northwestern Panamá (Fig. 1). Historically, three varieties have been recognized within the species. Brandegee (1917) segregated *Aster spinosus* var. *spinossissimus* Brandegee of Baja California Sur from the typical variety on the basis of its numerous rigid spines and larger heads. McVaugh (1972) treated variety *jaliscensis* McVaugh as a distinct taxon, citing lack of spines, leafiness at anthesis, differences in phyllary number, phyllary morphology, and differences in pappus and achene length. In this paper, variety *strictospinosa* Sundberg is described. Its stout, ascending

spines are not found elsewhere within the species and it has a combination of other morphological features that is unique within the species.

Two pairs of closely related varieties of *Chloracantha spinosa* are readily apparent. Varieties *jalscensis* and *strictospinosa*, which form one pair, have shorter and more delicate pappus bristles, broader phyllaries with wider hyaline margins and rounded apices, shorter disk florets, fewer ray florets, and are found in more moist, tropical regions than varieties *spinosa* and *spinosissima*.

TAXONOMIC TREATMENT

Chloracantha spinosa (Benth.) Nesom, *Phytologia* 70:378. 1991. Based on *Aster spinosus* Benth., *Pl. Hartw.* 20. 1839. TYPE: MÉXICO. *Hartweg 148* (HOLOTYPE: K, photograph of holotype MICH!, TEX!; Isotypes: BM!, CGE, GH!). McVaugh (1984) lists the type from Aguascalientes. *Leucosyris spinosa* (Benth.) E. Greene, *Pittonia* 3:244. 1897.

Perennial, shrublike herbs, from stout rhizomes. Stems erect, 0.5-2.5 m tall, much branched, striate, often angled on smaller branches, glabrous, 5-25 mm in diameter and woody at the base, usually with stout ascending or curved-divaricate spines below and unarmed branches above, sometimes spiny or unarmed throughout. Leaves basally disposed on main stem, usually absent at anthesis, oblanceolate to spatulate, 1-4 cm long, sessile, venation brochidromous, with one prominent midvein, glabrous except for sparsely ciliate margins and occasional trichomes on the upper surface, trichomes uniseriate, appressed, with attenuate or filiform terminal cell, 0.1-0.2 mm long; margins entire or with 1-5 small teeth, apically acute to rounded; leaves of lateral branches lanceolate, grading into bracts in the capitulescence. Capitula numerous in cymose capitulescence, with wiry, ascending, naked branches and scattered capitula terminating bracteate branchlets 2-8(-11) cm long or disposed towards the upper side of the branch on branchlets 0.1-3 cm long, erect in bud; involucre broadly cylindrical turbinate to subhemispherical, rounded and somewhat fleshy at base or with a shallow circular depression surrounding the peduncle (larger heads), 1.0-7.5 mm tall; phyllaries 20-55, imbricated, in 3-5 series, glabrous, herbaceous, with (1-)3(-5) golden brown nerves, subulate to linear-lanceolate (elliptic-lanceolate), margins hyaline, sometimes expanded above, subentire to conspicuously ciliate, apically acute to rounded. Ray florets 10-33 in 1 series; corollas white, sometimes tinged with purple at tips when young, drying white, ligulate portion 3.5-7.7(-10.2) mm long, (0.5-)0.7-2 mm wide tube moderately puberulent. Disk florets (13-)20-70; corollas yellow, sometimes tinged with green when fresh or drying purplish, (3.2-)3.5-6.0 mm long; limb tubular-funnelform but somewhat asymmetrical, slightly gibbous adaxially, expanded 0.6-1 mm above the insertion of the filaments, 1.8-3.5 mm long; lobes asymmetrical, the abaxial ones longer than the adaxial, acute, erect, 0.5-1 mm long; tube puberulent; style branches 0.9-1.1(-1.5) mm long,

appendage acute to deltoid, 0.1-0.2 mm long; style base bulbiform; anthers 1.1-2.0 mm long, distal 1/3 of filament collar cells usually with nodular thickenings; anther appendage lanceolate-ovate. Achenes glabrous, fusiform, somewhat radially compressed, (1.2-)1.5-3.5 mm long; tan with 5-6, conspicuous, golden brown ribs; carpopodia 4-8 cells high, grading into the body of the achene; pappus of 30-60 white to buff subequal bristles 2.5-6.0(-6.5) mm long, often with a few outer bristles 1-2 mm long.

DISTRIBUTION: Widespread, weedy subshrub in moist areas along irrigation ditches, streams, and freshwater swamps, sometimes phreatophytic in drier habitats; southern California to southern Louisiana; north to Arizona, New Mexico, and Texas, with scattered localities in Nevada, Utah, and Oklahoma; south through México to northwestern Panamá (Fig. 1; a list of specimens examined is available from the author and is deposited at TEX).

KEY TO VARIETIES

Pappus bristles 4.5-6.0(-6.5) mm long, delicate, with cells near tips tightly appressed; disk florets (21-)30-70; ray florets 20-33; middle phyllaries subulate to lanceolate, apex acute to attenuate, occasionally rounded by an extension of the narrow hyaline margins.

Plants usually sparsely spiny, with many spineless wandlike branches above, spines usually shorter; achenes (1.2-)1.5-2.0(-2.3) mm long; involucre 4.0-5.5(-6.0) mm tall, with 25-45(-52) phyllaries; disk florets (21-)25-50(-55); ligules 3.5-5.0(-7.0) mm long; anthers 1.1-1.5 mm long; widespread in southern states of the U.S., lowlands of Sonora and Sinaloa, Baja California Norte, and the central plateau of México.1. var. *spinosa*.

Plants densely spiny; achenes 2.8-3.5 mm long; involucre (5.0-)6.5-7.5 mm tall, with (35-)45-55 phyllaries; disk florets (40-)50-70; ligules 5.2-7.7(-10.2) mm long; anthers 1.5-2.0 mm long; Baja California Sur.2. var. *spinossissima*.

Pappus bristles 2.5-3.5(-3.9) mm long, coarser, with cells near tips divergent at ends and relatively more dense; disk florets (13-)18-30(-34); ray florets 10-23; middle phyllaries lanceolate elliptic to elliptic, apex rounded.

Plants usually without spines; Sierra Madre Occidental in Sonora and Sinaloa to western Durango, Nayarit, and Jalisco.3. var. *jaliscensis*.

Plants densely spiny; Michoacán, México, to Panamá.4. var. *strictospinosa*.

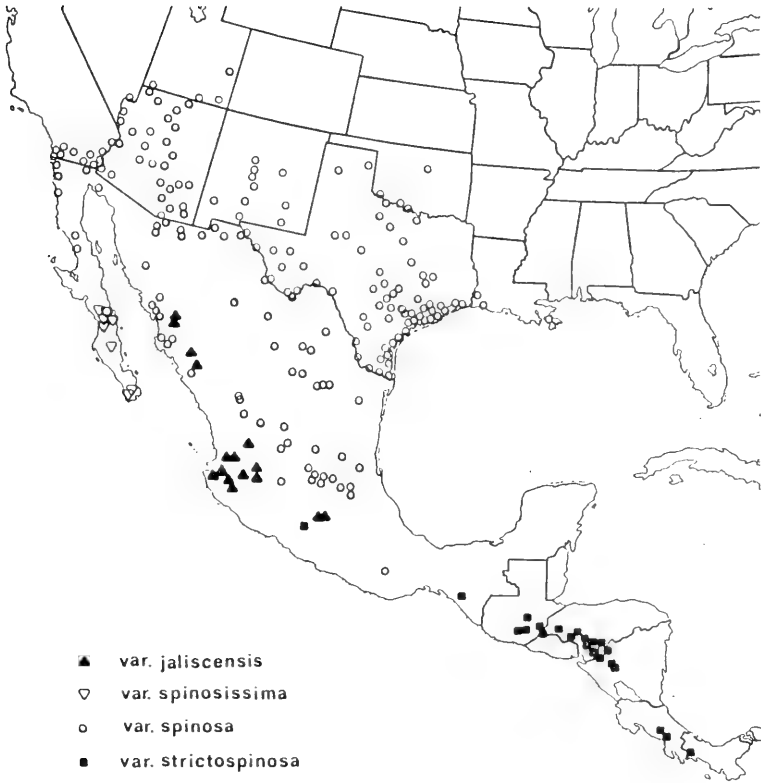


Figure 1. Distribution of *Chloracantha spinosa*.

1. *Chloracantha spinosa* (Benth.) Nesom var. *spinosa*

Plants usually moderately spiny at base, occasionally copiously spiny or unarmed. Involucres 4.0-5.5(-6.0) mm tall; phyllaries 25-45(-52), imbricated in 4-5 series, middle phyllaries subulate to lanceolate, apex acute or occasionally somewhat rounded by a hyaline margin. Ray florets 20-33, ligulate portion 3.5-5.0(-7.0) mm long, (0.5-)0.7-1.3 mm wide. Disk florets (21-)25-50(-55); corollas 4.0-5.2(-6.0) mm long, lobes 0.5-0.7(-1.0) mm long, limb (1.8-)2.4-3.0 mm long; anthers 1.1-1.5 mm long. Achenes (1.2-)1.5-2.0(-2.3) mm long; pappus bristles 4.5-6.0(-6.5) mm long. Chromosome number $n = 9$ (Table 1).

DISTRIBUTION: Widespread on moist loam or sandy soil along streams, irrigation ditches, and freshwater swamps; southern California to Louisiana, north to Nevada, Utah, and Oklahoma, south in México to the state of México; collections from cultivated areas in the Valley of Oaxaca may be introductions from farther north.

This variety is highly variable in spininess and the abundance of leaves at flowering time. There is apparently no correlation between these characters and geographical distribution. 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 of salt buildup (Burk 1977). Their growth form may be partly due to high salinity in these areas. A collection (Keil, et al. 16615) from the coast of Sonora north of Guaymas (in "Maytenus-dominated shrubland and tidal mudflat area") is intermediate between var. *spinosa* and var. *spinosissima*. It has the short achenes of the former, has large heads of the latter, and is intermediate between the two in ligule length, anther length, and spininess. It was collected near sea level, close to the southern limit of a portion of the Sonoran Desert that Shreve & Wiggins (1964) termed the "Central Gulf Coast." This region also encompasses part of the eastern coast of Baja California, including a portion of the range of var. *spinosissima*. It may be a salt form of variety *spinosa* or may be a product of gene exchange between the two varieties.

2. *Chloracantha spinosa* (Benth.) Nesom var. *spinosissima* (Brandegee)

Sundberg, *comb. nov.* BASIONYM: *Aster spinosus* Benth. var. *spinosissimus* Brandegee, Univ. Calif. Publ. Bot. 6:375. 1917. TYPE: MEXICO. Baja California Sur: San Gregorio, 1 Feb 1889, Brandegee s.n. (HOLOTYPE: UC!; Photograph of holotype: TEX!; Isotypes: PH!, US!).

Involucres (5.0-)6.0-7.5 mm tall; phyllaries (35-)45-55, imbricated in 4-5(-6) series; middle phyllaries subulate to lanceolate, with a narrow, hyaline, often purple tinged margin, apex acute to attenuate. Ray florets 20-28; ligulate portion 5.2-7.7(-10.2) mm long, 1.3-2.0 mm wide. Disk florets (40-)50-70; corollas (4.5-)5.0-6.0 mm long, lobes 0.7-1.0 mm long, limb 2.7-3.5 mm long;

TABLE 1. Chromosome numbers of *Chloracantha spinosa*. All counts are $n = 9$. Counts followed by literature citations were reported as *Aster spinosus*; others are unpublished counts by SS. * = mitotic count (others meiotic counts); ! = voucher seen; SS = S. Sundberg.

Chloracantha spinosa var. *spinosa*:

USA: Arizona: Coconino Co.: just below Lee's Ferry, *Raven 13132!* (Raven, *et al.* 1960); Marble Canyon, *Brown & Parfitt 900!* (Brown & Clark 1979); Maricopa Co.: 1.2 mi W of Buckeye, *SS & Hardison 2110!*; 3 mi E of Buckeye, *SS & Hardison 2111!*; E of Buckeye, Hwy. 85 & Watson Rd, *SS & Lee 2687!*. California: Imperial Co.: canal on W outskirts of El Centro, *Raven 16833!* (approx. count: Solbrig, *et al.* 1964); *coll. unknown (Huziwara 1965); N of Brawley, Hwy. 86, *SS 2085!*; just N of Imperial City along Hwy. 86, *SS 2086!*; 5.2 mi W of Westmorland along Hwy. 86, *SS & Hardison 2103!*; E end of Brawley, *SS & Hardison 2104!*; 7.9 mi S of jct. of Hwy. 111 & Hwy. 78 *SS & Hardison 2105!*; E of Calexico along Hwy. 98, *SS & Hardison 2106!*; S of Niland, *SS 2672!*; E of Brawley along Hwy. 78, *SS 2678!*. Texas: Bee Co.: S of Beeville, Hwy. 181, *SS & Hardison 2163!*; Reeves Co.: Balmorhea, *Sikes 90!* (Powell & Sikes 1970); Travis Co.: Austin, *Watson 550!* (Watson 1973); Austin, *SS 1206!*, *SS 1356!*.

MÉXICO: Chihuahua: W of Presidio, *SS & Lavin 2710!*. Coahuila: 5.5 mi E of Nazareno, *Keil & McGill 8010!* (Keil & Stuessy 1975). Durango: Durango, *King 3727!* (Turner, *et al.* 1961); 13 mi N of Durango, *King 3753!* (Turner, *et al.* 1961). Oaxaca: 10 mi NE of Oaxaca, *King 3518!* (Turner, *et al.* 1961).

Chloracantha spinosa var. *jaliscensis*:

MÉXICO: Jalisco: W of Ameca, *SS & Lavin 2952!*; 18 km N of Talpa, *Lott, et al. 1346!*; just N of El Jacal, *Ayers, et al. 266!*.

anthers 1.5-2.0 mm long. Achenes 2.8-3.5 mm long; pappus bristles 40-50, white, delicate, 4.8-5.5 mm long, outer cells of bristles appressed.

DISTRIBUTION: Baja California Sur, from hills W of Bahía Concepción to the south, on alluvial soil in arroyos, elev. 250-700 m.

Variety *spinosissima* is a densely spiny, large headed counterpart of the widespread, weedy variety *spinosa*.

3. *Chloracantha spinosa* (Benth.) Nesom var. *jaliscensis* (McVaugh) Sundberg, *comb. nov.* BASIONYM: *Aster spinosus* Benth. var. *jaliscensis* McVaugh, Contr. Univ. Michigan Herb. 9:363. 1972. TYPE: MÉXICO. Nayarit: among rocks in the stream above La Laguna, 3 km NE of Santa María del Oro, elev. ca. 1000 m, 16 Sep 1960, *McVaugh 19049* (HOLOTYPE: MICH!; Photograph of holotype: TEX!; Isotypes: DUKE!, ENCB!, LL!, US!).

Erigeron ortegae S.F. Blake, Proc. Biol. Soc. Wash. 37:55(-56). 1924.

TYPE: MÉXICO. Sinaloa: Balboa, Jan 1923, *Ortega 4974* (HOLOTYPE: US!).

Plants usually unarmed throughout, occasionally with divergent spines near base. Involucre 4.5-5.1(-5.5) mm tall; phyllaries 20-32(-37), imbricate in 4-5 series, middle phyllaries elliptic-lanceolate, apex rounded. Ray florets 10-20, ligulate portion 4.5-6.7 mm long, 1.2-1.7 mm wide. Disk florets (13-) 18-25(-34); corollas 3.1-4.0(-4.5) mm long, lobes 0.5-0.9 mm long, limb 2.0-2.5(-3.2) mm long; anthers 1.1-1.4 mm long. Achenes 2.1-2.8(-3.4) mm long; pappus bristles 2.5-3.5 mm long. Chromosome number $n = 9$ (Table 1).

DISTRIBUTION: Western slope of the Sierra Madre Occidental in southern Sonora to Sinaloa and western Durango, Nayarit, and Jalisco.

About half of the herbarium specimens of this variety are leafy, flowering shoots. These specimens usually show signs of damage due to grazing. Plants of var. *spinosa*, when repeatedly pruned, often have a few leaves at flowering time, suggesting that the leafiness of many collections of var. *jaliscensis* may be due to grazing. At the margins of distribution of var. *jaliscensis* occur forms that are intermediate between this variety and others. The only spiny collections of the variety are from such areas. Thus, collections from Cofradía (vicinity of Culiacán, Sinaloa, 20 Oct 1904, *Brandege s.n.* at UC), from Tamazula, Durango (*Gentry 5260* at ARIZ, DS, GH, MEXU, MICH, MO, NY, UC) and from La Junta, Estado de México (*Matuda 29808* at NY, US) have the typical short pappus, long achenes, and rounded phyllaries but are spiny. One collection (*Gentry 505* at DS) from the vicinity of Alamos, Sonora, includes stems that appear to be typical of var. *jaliscensis* and a single stem that is intermediate between var. *jaliscensis* and var. *spinosa*. This specimen agrees in all ways with my circumscription of var. *jaliscensis* except in having pappus bristles that are up to 4.5 mm long.

4. *Chloracantha spinosa* (Benth.) Nesom var. *strictospinosa* Sundberg, var. nov. TYPE: HONDURAS. Dept. Morazán: Río Caparosa, near Zamorano, flowers white, shrub to 1 m, on rocks, alt. 800 m, 1 Jan 1963, *Williams 23285* (HOLOTYPE: LL!; Isotypes: ARIZ!, DS!, F!, MEXU!, MICH!, MO!, NY!, PH!, UC!, US!).

Achaenia 2.2-3.0 mm longa, setae pappi 2.9-3.5(-3.9) mm longae; a *Chloracanthae spinosae* (Benth.) Nesom var. *jaliscensi* (McVaugh) Sundberg plantis crebre spinosis spinis validis differt.

Plants densely spiny with stout, ascending spines; stems divaricately branched. Involucres (4.5-)5.0-6.0(-6.5) mm tall; phyllaries 20-30(-35), imbricated in 3-4 series; middle phyllaries lanceolate-elliptic, apex rounded. Ray florets 14-23, ligulate portion (4.4-)5.2-6.0 mm long, 1.2-2.0 mm wide. Disk florets 22-30 (-34); corollas (3.2-)3.5-4.3 mm long, lobes 0.5-0.7 mm long, limb (1.8-)2.4-3.0 mm long; anthers 1.2-1.5 mm long. Achenes 2.2-3.0 mm long; pappus bristles 2.9-3.5(-3.9) mm long.

DISTRIBUTION: Michoacán, México, through Guatemala, El Salvador, Nicaragua, and Costa Rica to northwestern Panamá. Illustration: D'Arcy (1975): fig. 35.

Additional specimens examined: COSTA RICA: Río Virilla, *Allen 578* (F); Río Virella, *Pittier 10* (GH, US); Río Torres, Cartago, *Smith 4870* (F, GH, NY, US); Rancho Flores, *Tonduz 2179* (US); Río Tirriti, San Jose, *Tonduz 7060* (F, GH, MO, NY, US); Río Tiliri at Anones bridge, *Tonduz 7327* (DS, F, GH, MICH, NY, UC, US).

EL SALVADOR. Río Guaza, *Calderon 1933* (GH, US).

GUATEMALA. Casillos, Río San Rafael, *Aguilar 343* (F); Dept. Quiche, *Aguilar 804* (F); Agua Caliente, *Greenman & Greenman 5924* (GH, MO); El Rancho, *Kellerman 5328, 7646* (F); Paso de Jelha, *Pittier 1821* (F); Santa Rosa, *Smith 3424* (F); Santa Rosa, *Smith 4210* (F, GH, NY, US); near Jutiapa, *Standley 60543* (F); northwest of Jutiapa, *Standley 76288* (F); near Zapaca, *Standley 72089* (F); vicinity of Jutiapa, *Standley 75833* (F); near Jalapa, *Standley 77159* (F, NY, US); 4-6 miles north of Chiquimula, Río Chiquimula, *Steyermark 30279* (F); vicinity of Jalapa, *Steyermark 32131* (F).

HONDURAS. Escuela Panamericana de Agricultura, Zamorano, *Carlson 3190* (F); Río Choluteca *Carlson 2597* (F); Siguatepeque, Comayagua, *Clcwell 3731* (MO, US); Yeguaré River, Morazán, *Glassman 2013* (F, NY, TEX, UC); 5 km E of Zamorano, Morazán, *Meyer 9942* (MO); Choluteca River, near Ojo de Agua, El Paraiso, *Morton 7144* (F, US); Río Yeguaré, *Molina 5031* (F); Río Guacerique, NW of Tegucigalpa, Morazán, *Mohna 18572* (F, GH, NY, US); Río Mejojote, 9 km from Gracias, Lempira, *Nelson, et al. 202* (MO); Río Yeguaré, *Rodriguez 970* (F); Santa Inés, *Rodriguez 1525* (F); Las Casitas, *Standley, et al. 584* (F); Río Humuya, *Standley, et al. 5432* (F); Siguatepeque,

Standley, et al. 6433 (F); San Marcos de Colón, *Standley 15807* (F); Marcala River, La Paz, *Standley 24275* (F, NY, US); 2 miles west of Guinope, *Williams & Molina 10321* (F); Río Yeguaré near Casitas, El Paraiso, *Williams & Molina 11058* (F, GH).

MEXICO. Chiapas: Rancho La Aurora, *Sanchez 1078* (ENCB, UC); Michoacán: cliff over Balsas River, *Hinton 5610* (GH, MEXU, MO, NY, US).

NICARAGUA: 6.5 km from Ocotal, Nueva Segovia, *Moreno 14444* (TEX); La Estanzuela, Estelí, *Moreno 24379* (TEX); Santa María de los Pinos, Nueva Segovia, *Moreno, et al. 24764* (TEX); on rocks in Río Estanzuela, SW of Estelí, Estelí, *Williams & Molina 20187* (DS, UC); La Guava, Estelí River, Estelí, *Williams & Molina 42478* (US, MICH).

PANAMÁ: Valley of upper Río Chiriquí Viejo, Chiriquí, *White & White 108* (MO).

This variety is most closely related to variety *jaliscensis*, sharing a short pappus and lanceolate elliptic to elliptic middle phyllaries. It may be distinguished from the latter in its spininess (dense, usually ascending in var. *strictospinosa* vs. usually absent, or divergent when present in var. *jaliscensis*) and its geographical distribution. Variety *strictospinosa* usually has broader hyaline phyllary margins and longer, more numerous disk florets, although there is a great deal of overlap in these characters. The new variety is named "strictospinosa" for its rigid spines.

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BOOKS RECEIVED

Heliconia, An Identification Guide. Fred Berry & W. John Kress. Smithsonian Institution Press, 470 L'Enfant Plaza, Suite 7100, Washington, D.C. 20560 U.S.A. 1991. viii. 334 pp. \$16.95 (paper) ISBN 1-56098-007-9; \$35.00 (cloth) ISBN 1-56098-006-0.

This book is primarily a guide for visual identification of many taxa of *Heliconia*. There are no identification keys as such, although the pages of the book are color coded with combinations of certain characters of the plants. The initial 60 pages of the book are devoted to a general description of *Heliconia* and other members of the Zingiberales, habitats, distribution, breeding, taxonomy, collecting, and conservation of *Heliconia*. The bulk of the text is devoted to photographs and descriptive synopses of the plants. Many of the taxa included are cultivars, but a number of wild members of the genus are also included. The photography is excellent and the photographs, along with the brief descriptions of diagnostic features of the plants will facilitate identification of specimens.

Reproductive Versatility in Grasses. G.P. Chapman (ed.). Cambridge University Press, 40 West 20th Street, New York, NY 10011, U.S.A. 1991. xiii. 296 pp. \$75.00 (hardcover) ISBN 0-521-38060-X.

Fourteen authors have contributed 10 chapters to this volume. Topics range from a taxonomic overview of the Poaceae to *in vitro* propagation of grasses. Some chapters deal with subjects as specific as "the spikelet" and others are as wide ranging as "grass succession, utilization and development."

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