Phytotaxa 455 (1): 001–008
https://www.mapress.com/j/pt/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.455.1.1

On the taxonomic status of the varieties of *Chorizanthe angustifolia* (Polygonaceae)

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Abstract

Chorizanthe angustifolia var. *eastwoodiae* was named by Goodman in 1934, but has since generally been ignored as a taxon. A limited number of *C. angustifolia* var. *angustifolia* collections available for comparison and lack of clearly defined characters differentiating the two varieties likely account for the taxonomic concept for *C. angustifolia* that rejects infraspecific taxa. Nevertheless, several characters previously unnoted in floristic literature distinguish var. *angustifolia* from var. *eastwoodiae*. Variety *angustifolia* is a yellow-green plant with straw-colored tepals that are narrow and long-pointed, and has 3 stamens per flower. Variety *eastwoodiae* is a pinkish plant with pink, rounded and often erose tepals, with 8–9 stamens per flower. Morphological differences and comparative DNA sequencing indicate the two varieties are better treated as separate species. A new combination (*C. eastwoodiae comb. et stat. nov.*) is proposed and typification of the name *C. angustifolia* is clarified. A comparison table of closely related *Chorizanthe* is provided.

Keywords: California endemic flora, *Chorizanthe minutiflora*, nomenclatural change

Introduction

The taxonomy of the genus *Chorizanthe* R.Brown ex Bentham (1836: 416) has undergone relatively few changes since Reveal & Hardham (1989) revised the annual members of the genus and, immediately after, added an additional new combination (Reveal & Morgan 1989). Currently, there are 43 annual species with all but one found in North America, and nine perennial species restricted to southwestern South America. The primary change since 1989 has been the addition of two new species, *Chorizanthe minutiflora* Morgan, Styer & Reveal (2014: 1) and *Chorizanthe aphanantha* K.M.Nelson & D.J.Keil (in Nelson *et al*. 2018: 184).

The authors' interest in *Chorizanthe angustifolia* Nuttall (1848a: 17) was stimulated by an encounter with plants in the Burton Mesa area near Lompoc, California. These plants seemed like a close match to the recently described *C. minutiflora*, but were found 125 miles from the only known locations of *C. minutiflora* (Monterey County). We soon realized that the two previously named varieties of *C. angustifolia* are distinct, despite not being recognized in recent floristic treatments. We propose elevating *C. angustifolia* var. *eastwoodiae* Goodman (1934: 42) to species status. Although our initial objective was merely to clarify the taxonomic concept for *C. angustifolia* by illuminating the differences between its two varieties and making a case for recognizing both, our studies support a revised taxonomy for these entities.

Materials and methods

We conducted field studies, examined herbarium collections from BRY, CAS, GH, JEPS, PH, and UC (acronymns following Thiers 2020 [continuously updated]), and grew plants of *C. minutiflora* and both varieties of *C. angustifolia* in a garden in Oakland, California for two seasons.

Accepted by Duilio Iamonico: 26 Jul. 2020; published: 5 Aug. 2020

We evaluated nuclear ribosomal ITS DNA sequence variation (nrITS; ITS 1. 5.8s, and ITS2 regions) among these taxa in a phylogenetic context. Using pressed material from our own collections, we isolated DNA from three accessions for both varieties of *Chorizanthe angustifolia* and two accessions of *C. minutiflora*, followed by PCR and sequencing following the methodology of Johnson *et al.* (2008; GenBank accession numbers MT703944–MT703951). These sequences were initially analyzed with the 56 ITS sequences of *Chorizanthe* subsect. *Pungentes* Goodman (1934: 35) obtained by Brinegar & Baron (2009). We subsequently reduced the dataset to the same 25 accessions used by Brinegar & Baron (2009) in their published phylogenetic analysis (without loss of phylogenetic information), with the addition of our eight sequences, three additional accessions of "*C. angustifolia*" obtained by Brinegar and Baron, and one accession of "*C. angustifolia*" from Kempton (2012). ITS sequences of *Eriogonum nudum* Douglas ex Bentham (1836: 413; from Brinegar and Baron 2009) and *Lastarriaea coriacea* (Goodman) Hoover (1966: 342; from Kempton 2012) were included as outgroups. We aligned sequences with Aliview (Larsson 2014) and used PAUP 4.0a build 167 (Swofford 2002) to conduct parsimony analyses via 10,000 random addition heuristic searches with TBR branch swapping and zero-length branches collapsed, followed by 100,000 replications of fast bootstrapping to assess branch support. We also conducted heuristic searches with various topological constraints to explore the strength of relationships as measured by departure from parsimony.

Results and discussion

Historical background and morphological notes

One of the earliest named species in the genus, *Chorizanthe angustifolia* was described based on a collection by William Gambel (Nuttall 1848a, 1848b). Nuttall's article, "Descriptions of Plants collected by Mr. William Gambel in the Rocky Mountains and Upper California" was published twice (see Reveal & Spevak 1967), with additional morphological details for this species added in the second publication. As noted by Reveal & Spevak (l.c.), Nuttall (1848a) was published between 21 March and 4 April, whereas Nuttall (1848b) was published between 1–8 August. Because Nuttall (1848b) did not cite the first publication in his second publication, taxonomic novelties in the second publication are isonyms (Art. 6.3 Note 2 of ICN; Turland *et al.* 2018).

The majority of the plants described in these publications were collected by W. Gambel, but several were Nuttall's own collections. The protologue states that *C. angustifolia* was collected at "Pueblo los Angeles", but both Goodman (1934) and Reveal & Hardham (1989) concurred that it was most likely collected at Santa Barbara. A more recent collection by Pollard in 1956 (UC1176941! SBBG99170) confirms the presence of the species in Santa Barbara and, as yet, there have been no collections made further south. Given the sparse development of California when Gambel was collecting, it is possible he gave general locations for plants based on his last point of departure or his destination. Some of the other species cited in this article by Nuttall have locality information that is likely inaccurate (e.g., Porter & Patterson 2015).

Chorizanthe angustifolia was recognized as a distinct species only briefly before Torrey & Gray (1870) placed it in synonomy under *C. pungens* Bentham (1836: 419) as "one of the depauparate forms of *C. pungens*". It remained in synonymy until Goodman (1934), in his revision of the genus, recognized it again. In addition, Goodman proposed the new *C. angustifolia* var. *eastwoodiae* [as "*eastwoodae"*]. Subsequent treatments by Munz (1959), Reveal & Hardham (1989), Reveal (2005), as well as both editions of The Jepson Manual (Hickman 1993, Reveal & Rosatti 2012) all recognize *C. angustifolia* without varietal subdivision, while expanding the species description to encompass the floral variation of both varieties.

Goodman (1934) described *Chorizanthe angustifolia* var. *eastwoodiae* as having slightly larger flowers with 8–9 stamens (only 3 stamens occur in var. *angustifolia*). He noted that "most of the '*angustifolia*' material is referable to this less reduced variety". Eleven collections examined by Goodman were identified as var. *eastwoodiae*, whereas only three (including the type) were identified as var. *angustifolia*.

Goodman's problem of only a small number of var. *angustifolia* collections available for examination has not changed substantially over the last 85 years. The paucity of reference material has led to an incomplete understanding of this species. When Reveal & Hardham (1989) carried out field surveys in preparation for their review of *Chorizanthe*, they were barely able to find var. *angustifolia*. Hardham (1989: 90) wrote: "The entire population of *C. angustifolia* with three stamens, thought at the time to be var. *angustifolia* (Goodman 1934) and virtually extinct, barely made a sample large enough for cytological purposes with a few individuals left for seed".

Herbarium collections of *Chorizanthe angustifolia* can be problematic to determine to variety because the fresh plant coloration is usually lost and most collections appear dark-red, brown, or gray. This appears to be what prompted Goodman (1934), who most likely never saw these plants alive, to describe the plants as grayish in color. However, the overall color of the varieties during the active flowering period is entirely distinct (Fig. 1). The appearance of var. *angustifolia* is yellow-green, much like the color of *Lastarriaea* Rémy (1851: 289). They often grow with *Lastarriaea* and when growing together, var. *angustifolia* can be easily mistaken for that plant. The yellow-green plant color was so noted by Hoover (1970) that he erroneously determined plants of var. *angustifolia* (*Hoover 9179* at CAS, OBI, UC) to be *C. procumbens* Nuttall (1848a: 17), a plant that does not occur within 125 miles of coastal San Luis Obispo County. The general color of var. *eastwoodiae* when fresh is pinkish. This is because the flowers are pink, the involucres are often reddish, and the involucral teeth have slightly pinkish margins.

If flowers are visible, the varieties are usually easy to separate. The flowers of the two varieties have differing stamen number, with var. *angustifolia* having only 3, while var. *eastwoodiae* usually has 9. It appears that *Chorizanthe* flowers, like *Eriogonum* flowers, don't always unfurl all stamens at the same time. Sometimes flowers of var. *eastwoodiae* can appear to only have three stamens because the others are still coiled within the corolla. The anthers also seem to disappear readily, most likely the result of pollinators. This might be why Hoover noted on his collection of var. *eastwoodiae* (*Hoover 9180*, CAS, OBI) that the "stamen number seems to vary".

The size and shape of flowers is also distinct between the two varieties. Tepals are straw colored and slightly smaller, with narrow lobes that long taper to a point in var. *angustifolia*. Tepals of var. *eastwoodiae* are pink (sometimes bleached whitish), and are more rounded and blunt, "truncate and erose at apex" (Goodman 1934).

Initially, it was tempting to surmise a nice geographic separation between the two varieties, with var. *angustifolia* primarily in Santa Barbara County, and var. *eastwoodiae* in San Luis Obispo County. Goodman (1934) suggested this probability. But the two occur together in the Nipomo area (San Luis Obispo County), as well as the Vandenberg AFB/ Burton Mesa area (Santa Barbara County). We have noticed that var. *eastwoodiae* may favor looser, softer sand, while var. *angustifolia* may favor the harder packed sand near the periphery of chaparral.

Chorizanthe minutiflora was only recently described, based on plants occurring on the Fort Ord National Monument, the former Fort Ord Military Reservation in Monterey County. Although initially identified as *Chorizanthe angustifolia*, it later became clear that it was distinct from *C. angustifolia* as understood at that time. The primary differences between *C. minutiflora* and *C. angustifolia* were stated to be plant color (yellow-green vs. gray), tepal shape (cuspidate or pointed vs. erose and rounded), and stamen number (3 vs. 6–9). Although these differences hold true for *C. angustifolia* var. *eastwoodiae*, the defining features of *C. minutiflora* exactly match those of *C. angustifolia* var. *angustifolia* except for a slight difference in size. If observed side by side, these two plants are separable, but without a size comparison, it can be difficult to tell them apart. They are separated geographically by about 125 miles.

Molecular data

Brinegar and Baron's (2009) phylogeny of the *Chorizanthe* subsect. *Pungentes* demonstrated that "*C. angustifolia*" (i.e., var. *eastwoodiae;* their accessions only represented this variety) was clearly distinguishable from the other members of *Pungentes* by both nrITS and cpDNA. Our analysis of nrITS (Fig. 2) extends this finding in several taxonomically meaningful ways. The three accessions of *C. angustifolia* var. *angustifolia* form a moderately-supported clade (bootstrap = 63) that together with the two accessions of *C. minutiflora* form a well-supported clade ("*angustifolia-minutiflora*", bootstrap = 91). The nine accessions of *C. angustifolia* var. *eastwoodiae* form a separate clade (bootpstrap = 88) sister to the previous one ("*angustifolia-minutiflora*") in some but not all most parsimonious trees (bootstrap < 50).

Brinegar and Baron's (2009) accessions of *Chorizanthe angustifolia* var. *eastwoodiae* represent two locations in San Luis Obispo County: one from Montana de Oro State Park, the other from Morro Bay. Morro Bay is the type area of var. *eastwoodiae* and ca. 22 miles north of the closest known population of var. *angustifolia*. Kempton's (2012) sequence of *C. angustifolia* var. *eastwoodiae* is from a collection from near Nipomo [*Reveal 8808* per Kempton (2012; but probably *8809*, per Reveal field book)]. Both var. *angustifolia* and var. *eastwoodiae* grow together at this location (Fig. 1). Our accessions include var. *angustifolia* and var. *eastwoodiae* growing together from Nipomo Regional Park, as well as localities where one or the other variety grow exclusive of the other (see Representative specimens examined sections below). Comparative sequencing of nrITS thus parallels our common garden and field experiences. *Chorizanthe angustifolia* var. *angustifolia* is more similar morphologically to *C. minutiflora* than to *C. angustifolia* var. *eastwoodiae*, and there is no evidence of intergradation between the varieties of *C. angustifolia* when found together, or intermediacy/segregation of morphologies observed in individuals we have grown from seed.

FIGURE 1. Specimens of *Chorizanthe angustifolia* (i.e., *C. angustifolia* var. *angustifolia*) and *C. eastwoodiae* (i.e., *C. angustifolia* var. *eastwoodiae*) growing in the same area in Nipomo, California. A–B: *Chorizanthe angustifolia* (*Gowen 1460*, JEPS, BRY); C–D: *Chorizanthe eastwoodiae* (*Gowen 1461*, JEPS, BRY); E: Both taxa growing intertwined.

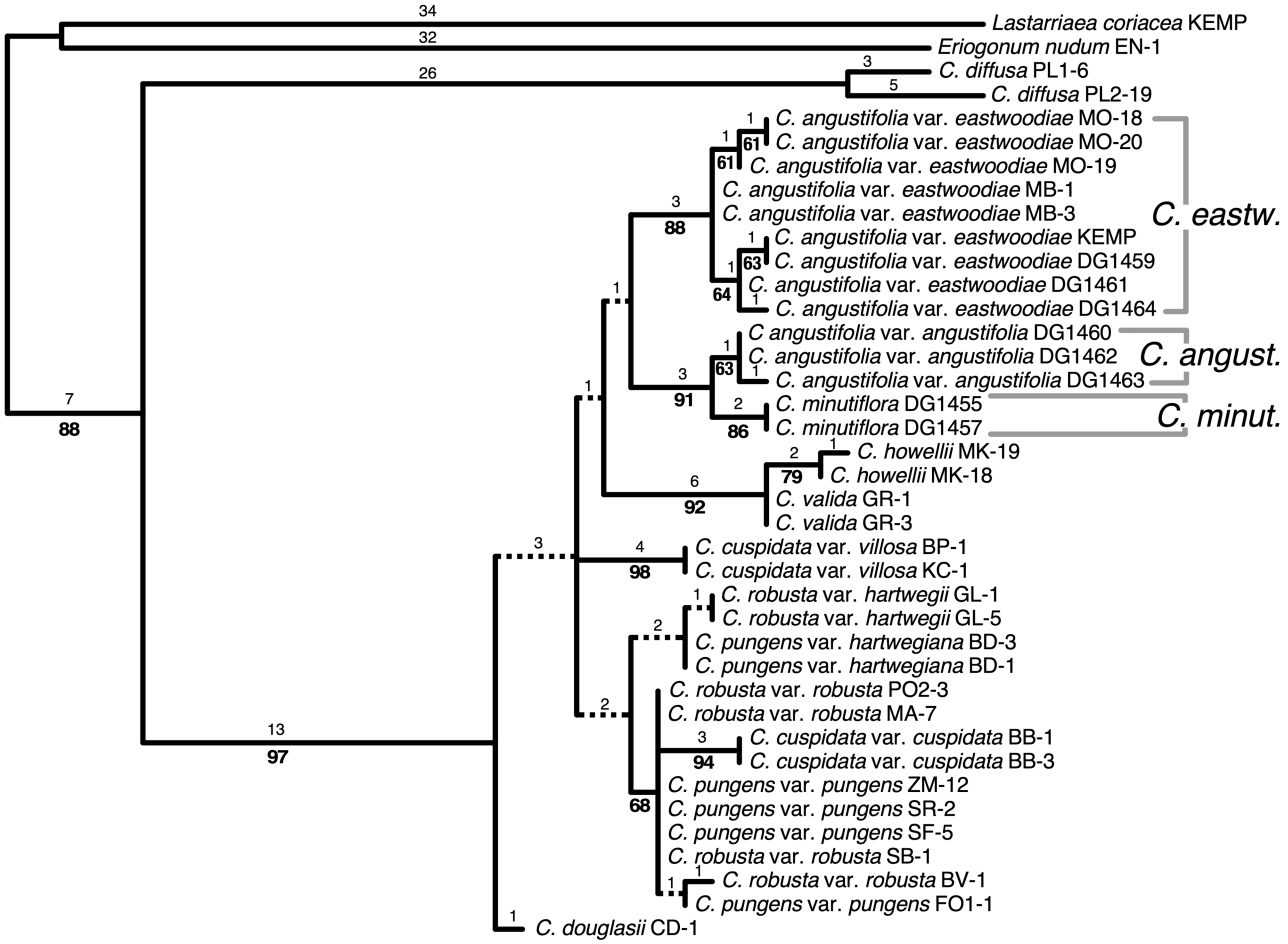

FIGURE 2. One of 256 shortest trees (length = 165 steps) recovered from parsimony analysis of nrDNA ITS sequences (CI = 0.87, RI = 0.90). Branch lengths are indicated above branches, bootstrap support values > 50% are indicated below branches in bold. Branches not resolved on all most parsimonious trees are indicated with dashed lines. Designators following taxon names indicate the published source of the sequence: KEMP = Kempton (2012); DG#### = this study, see representative specimens examined sections for voucher information; all others from Brinegar and Baron (2009). Following the taxonomy proposed here, accessions representing *Chorizanthe angustifolia*, *C. eastwoodiae*, and *C. minutiflora* are indicated along the right side of the figure.

Taxonomic implications and conservation status

Given the ability to distinguish *Chorizanthe angustifolia* var. *eastwoodiae* from *C. angustifolia* var. *angustifolia* both morphologically and molecularly, the maintenance of morphological integrity between taxa when they co-occur, and lack of strong phylogenetic support uniting these taxa, var. *eastwoodiae* should not only be recognized apart from var. *angustifolia*, but is best treated taxonomically at the species level. Because var. *eastwoodiae* is the more common element, this change will necessitate changes to the taxonomic concept currently in use for *C. angustifolia* by working botanists.

It also brings to light the need for a careful conservation assessment for *Chorizanthe angustifolia* (i.e., var. *angustifolia*) given that, as defined by recent floras that do not distinguish varieties, *C. angustifolia* is listed in California as CBR (considered but rejected; California Native Plant Society Rare Plant Program 2020). Our preliminary assessment places this taxon in Red List Category DD (data deficient; IUCN 2019) because so little is known about this taxon. In addition to the representative collections examined, we are aware of only a few additional collections of *C. angustifolia* as defined below. These include: *Keil 18756, 24651, 25270, 25536*; *Baniaga 186* (D. Keil pers. comm. 2019 and images available at http://cch2.org/portal/). Historic locations at Santa Barbara and 7 miles west of Buellton are unlikely to still be extant. More study is needed.

Taxonomic treatment

Chorizanthe angustifolia Nuttall (1848a: 17).

Lectotype (designated by Goodman 1934: 41):—U.S.A. California: Pueblo los Angeles, Upper California, *Gambel* (PH00004283!, image of the lectotype available at https://plants.jstor.org/stable/10.5555/al.ap.specimen.ph00004283; isolectotypes: GH0036060! (https://s3.amazonaws.com/huhwebimages/D8E526D3DB4D47E/type/full/36060.jpg) and K000830333 (https://plants.jstor.org/stable/10.5555/al.ap.specimen.k000830333?searchUri=scope%3Dplants%26so%3Dps_group_by_genus_species%2Basc%26Query%3DSpecies%3Aangustifolia%2520AND%2520Genus%3Achorizanthe%2520AND%2520%28raw_type%3Avisual%2520OR%2520ResourceType%3Aspecimens%29).

– *Chorizanthe angustifolia* Nuttall (1848b: 167), isonym (Art. 6.3 Note 2 of ICN).

Typification of *Chorizanthe angustifolia*:—When describing *Chorizanthe angustifolia*, Nuttall (1848a) cited the collection by William Gambel from Pueblo los Angeles that is represented by three known herbarium sheets distributed at GH, K, and PH. The specimen at PH was indicated as the 'type' by Goodman (1934) or 'holotype' by Reveal & Hardham (1989; these authors annotated the specimen at PH as the 'holotype' and those at GH and K as 'isotypes'). Following Art. 7.11 (Turland *et al.* 2018), "...designation of a type is achieved ... if the type element is clearly indicated by direct citation including the term "type"...". Goodman's statement effected lectotypification even though he cited Nuttall 1848b instead of 1848a, which is simply an error to be corrected; the specimens at GH and K are isolectotypes.

Representative specimens examined:—UNITED STATES OF AMERICA. California: San Luis Obispo County, 3 mi nw of Nipomo, in dry sand, 11 July 1964, *Hoover 9179*, (UC1296193; DS511146; CAS455341); north end of Nipomo Regional Park, 20 May 2018, *Gowen 1460* (JEPS, BRY); north side of Callender Road just east of Hwy 1, 25 April 2019, *Gowen 1495* (JEPS); same place, 13 May 2019, *Gowen 1508* (JEPS). Santa Barbara County, Surf, May 1909, *Brandegee s.n.* (UC131092); Santa Maria, Sand Hills, 13 June 1906, *Eastwood 351* (CAS84872), [1 large plant *C. angustifolia* and 1 small plant *C. eastwoodiae*]; 5 mi s Surf, 14 April 1929, *Ferris 7545* (UC463340; DS206207); 7 mi W of Buellton, 5 May 1929, *Hoffmann s.n*. (JEPS97040); Santa Ynez Valley, 7 miles west of Buellton, 30 May 1929, *Hoffmann s.n*. (JEPS57802); La Mesa above and w of Victoria Street, 10 May 1956, *Pollard s.n*. (UC1176941; CAS412196); Burton Mesa area north of Lompoc, west of Cabrillo High School, 10 May 2008, *Gowen 902* (JEPS117034); same area, 23 May 2017, *Gowen 1416* (JEPS); Vandenberg Village along north side of Hwy 1 at Constellation Road, 20 May 2018, *Gowen 1462* (JEPS, BRY); north of road to residences above La Purisima Mission, 21 May 2018, *Gowen 1463* (JEPS, BRY).

Chorizanthe eastwoodiae (Goodman) D.Gowen & L.A.Johnson, *comb. et stat. nov.* ≡ *Chorizanthe angustifolia* Nutt. var. *eastwoodae* Goodman (1934: 42).

Type:—U.S.A., California: San Luis Obispo County, Morro Bay, sandy soil, San Luis Obispo, 16 May 1928, *Eastwood 15108* (holotype CAS0032860! (image of the holotype available at http://researcharchive.calacademy.org/image_db/botany/cas0032860.jpg); isotype DS32861! (http://researcharchive.calacademy.org/image_db/botany/cas0032861.jpg).

Representative specimens examined:—UNITED STATES OF AMERICA. California: San Luis Obispo County, 1887–1888, *Lemmon 4598* (UC338247); El Pizmo, 23 April 1910, *Condit s.n.* (UC455204); Haynes Ranch, 1 June 1912, *Ingalls s.n.* (CAS84881); Sand Hills near Pismo Beach, 10 June 1917, *Abrams 6516* (DS86089); Morro, 7 April 1927, *Eastwood 14266* (CAS144873); Morro Bay, 16 May 1928, *Eastwood 15102* (CAS158930); Morro Bay, 16 May 1928, *Eastwood 15108* (CAS158932; DS193399); between Guadalupe and Callender, 15 April 1929, *Ferris 7613* (DS206226); Oso Flaco Lake region, 13 May 1950, *Rose 50118* (BRY 135563, UC942871); nw side Oso Flaco Lake, 2 May 1955, *Rossbach 249* (UC1073359); s end Morro Bay (Baywood Park), 17 May 1956, *Munz 22586* (UC1080374); just e Grover City (between Pismo Beach (town) and Arroyo Grande, 8 June 1957, *Bacigalupi & Partridge 5894* (JEPS18487); Los Osos, 6 June 1964, *Hoover 8962* (UC1296111); 3 mi NW of Nipomo, 11 July 1964, *Hoover 9180* (CAS455364); Jack Lake, 15 May 1966, *Hoover 9855* (UC1321235); s end Morro Bay, 9 June 1967, *Hoover 10631* (UC1314946); Nipomo Mesa, along Aden Way, 0.2 mile NW of Pomeroy Road, along both sides of the dirt road. At about 3.5 airline miles NW of Nipomo, 20 June 1987, *Reveal & Broome 6506* (CAS800049); Unical Oil Refinery ca 4 air miles S of Oceano, at bend in Hwy 1, just across railroad tracks from parking area, 23 May 1989,

Ertter 8481 (BRY607434, UC1949263); Nipomo Regional Park, 23 April 2018, *Gowen 1446* (JEPS); both sides of Camino Caballo just west of Pomeroy Road, 23 April 2018, *Gowen 1447* (JEPS); same place, 20 May 2018, *Gowen 1459* (JEPS, BRY); north end Nipomo Regional Park, 20 May 2018, *Gowen 1461* (JEPS, BRY). Santa Barbara County, Surf, May 1909, *Brandegee s.n.* (UC131119); Guadalupe, 20 May 1960, *Butterworth s.n*. (CAS518603); Vandenberg Air Force Base, just W of the junction of the Lompoc-Casmalia Road and Marshallia Ranch Road between the road to Titan Gate and San Antonio Road. About 3.5 airline miles S of Casmalia, 22 June 1987, *Reveal & Broome 6523* (CAS800014); Mission La Purisima, 21 May 2018, *Gowen 1464* (JEPS, BRY).

TABLE 1. Comparison of key morphological features among *Chorizanthe eastwoodiae, C. angustifolia*, and *C. minutiflora,* Uncommon features are in parentheses.

	C. eastwoodiae	***C. angustifolia***	***C. minutiflora***
Plant appearance	Pinkish	Yellow-green	Yellow-green
Involucral tube length	2–2.5 mm	2 mm	1.3–1.7(–2) mm
Flower length	2.5–3 mm	2–2+ mm	1.5–2 mm
Tepal shape	Obovate, apex rounded, sometimes erose	Narrow, apex a long- tapering point	Narrow, apex a long- tapering point
Tepal color	Pink or bleached whitish	Straw-colored	Straw-colored
Stamen number	6–9	3	3

Acknowledgements

We thank the Directors and Curators of the herbaria BRY, CAS/DS, GH, PH, RSA/POM, and UC/JEPS, for access to their collections and D. Keil (Emeritus, OBI) for providing information about collections at OBI. David Styer graciously escorted DG on several occasions to populations of *C. minutiflora* at Fort Ord National Monument. His thorough familiarity of the area can be found in his *Flora of Fort Ord, Monterey County, California*, which was published by the California Native Plant Society in 2019.

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