Nomenclatural Changes for Monardella (Lamiaceae) in California

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Abstract. Nomenclatural changes in Monardella Bentham (Lamiaceae) are introduced to more accurately circumscribe the specific and subspecific entities in the genus in California. Examination of herbarium specimens and digital images and analysis of biogeographical data from additional fieldwork has revealed morphological continuities and discontinuities. Four new species are described: M. boydii A. C. Sanders & Elvin, M. eremicola A. C. Sanders & Elvin, M. mojavensis Elvin & A. C. Sanders, and M. sinuata Elvin & A. C. Sanders. Five new subspecies are described: M. australis Abrams subsp. jokerstii Elvin & A. C. Sanders, M. hypoleuca A. Gray subsp. intermedia A. C. Sanders & Elvin, M. linoides A. Gray subsp. sierrae Elvin & A. C. Sanders, M. sinuata subsp. nigrescens Elvin & A. C. Sanders, and M. undulata Bentham subsp. arguelloensis Elvin & A. C. Sanders. Eight new combinations and/or rank changes are proposed: M. australis subsp. cinerea (Abrams) A. C. Sanders & Elvin, M. breweri A. Gray subsp. glandulifera (I. M. Johnston) Elvin, M. breweri subsp. lanceolata (A. Gray) A. C. Sanders & Elvin, M. breweri subsp. microcephala (A. Gray) Elvin & A. C. Sanders, M. linoides subsp. anemonoides (Greene) Elvin & A. C. Sanders, M. linoides subsp. erecta (Abrams) Elvin & A. C. Sanders, M. undulata subsp. crispa (Elmer) Elvin & A. C. Sanders, and M. venosa (Torrey) A. C. Sanders & Elvin. The description of one taxon is emended: M. undulata subsp. undulata. Lectotypes are designated for M. lanceolata A. Gray and M. sanguinea Greene. We address each of these changes within informal species groupings or allianc-

Key words: California, Lamiaceae, Monardella.

Preparation of a treatment of the genus Monardella Bentham (Lamiaceae) for the second edition of The Jepson Manual: Higher Plants of California (Hickman, 1993) has revealed the need for multiple nomenclatural changes and the description of new taxa. In this paper, we primarily discuss taxa that

occur in southern and central California and their relationships. We did not comprehensively analyze taxa in the *M. villosa* Bentham species complex. Below, we explain changes being made to the existing treatment of the California species of *Monardella* (Jokerst, 1993). Epling, in his 1925 monograph of the genus, grouped species according to their morphological resemblances within four sections. We organized the species into informal groupings that we refer to as species alliances.

The genus Monardella is widespread and rather complex, with over 50 taxa distributed among more than 30 annual and perennial species in western North America. Monardella has a center of distribution in California with approximately 45 taxa in 30 species. Monardella also occurs in Washington, Oregon, Idaho, Nevada, Utah, Colorado, Arizona, and New Mexico, U.S.A., and in Baja California, Mexico. Since 1834, there have been 198 combinations published that have been reshuffled from 93 protologues.

TAXONOMICALLY IMPORTANT CHARACTERISTICS IN MONARDELLA

The more informative morphological characters that have been used to distinguish taxa in *Monardella* include plant habit; leaf, bract, and inflorescence morphology; and pubescence (Gray, 1876, 1886; Abrams, 1912a, b, 1951; Epling, 1925, 1939; Jepson, 1925, 1943; Munz, 1935, 1959, 1974; Jokerst, 1993). The inflorescence in *Monardella* has been commonly called a head (Munz, 1959; Jokerst, 1993). However, it has a branched internal structure and the flowers are not sessile on the apex of the peduncle. It is technically a compact, capitate cyme or glomerule.

The glomerules in *Monardella* are immediately subtended by a series of bracts or modified leaves, and occasionally also by unmodified leaves. Bracts subtending individual flowers or inflorescence branches within the glomerule are occasional and

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much reduced. Leafy structures immediately subtending the glomerule are generally highly modified in Monardella, but are sometimes only slightly modified. This mix of unmodified leaves and the variability of bracts have caused difficulty in the identification of many Monardella specimens. The use of bract sets in separating species groups in Monardella was emphasized by Jokerst (1993), following on the work of Hardham (1966a, b; Hardham & Bartel, 1990), who emphasized this feature in the recognition of species. Unfortunately, the bracts in Monardella do not occur in discrete and static sets readily recognizable by an objective feature, but rather simply grade inward in the glomerule. The distinction between the outermost bracts and the uppermost leaves can be problematic. What some refer to as outer bracts are simply unmodified leaves immediately subtending the glomerule. In some species of Monardella, the bases of the outermost bracts may be broad, thick, and pale, while the distal halves are green and leafy with narrow tips. The number of bracts per plant/species is not fixed. However, there are bract morphological characters that are stable, informative, and important in differentiating between taxa (e.g., length, width, pubescence).

Monardella Bentham, Labiat. Gen. Spec. 331. 1834. TYPE: Monardella odoratissima Bentham, Labiat. Gen. Spec. 332. 1834.

SPECIES ALLIANCES IN MONARDELLA

Epling (1925) grouped taxa according to their morphological resemblances within four "Sections": Section I, Macranthae; Section II, Annuae; Section III, Villosae; and Section IV, Odoratissimae. We present the species discussed in this paper within informal groupings that we refer to as species alliances. We recognize Epling's four sections within our alliances plus two additional ones, Undulatae and Australae. Species of the Undulatae Alliance are subshrubs to shrubs with woody stems and leaves that have wavy to undulate edges. Species in the Villosae Alliance are caespitose to erect suffrutescent perennials to subshrubs with woody stems that are moderately to densely pubescent with some trichomes longer than 0.5 mm. Species in the Australae Alliance are rhizomatous to mat-forming suffrutescent perennials with woody stems with some trichomes longer than 0.5 mm. Species in the Odoratissima Alliance are caespitose to erect, suffrutescent perennials to subshrubs with woody stems that are glabrous to slightly pubescent with trichomes shorter than 0.5 mm. Species in the Annuae Alliance are erect annuals with herbaceous stems.

I. UNDULATAE ALLIANCE

The Undulatae Alliance consists of perennial species that possess leaves with distinct undulate margins and that are associated with coastal dunes and scrub in Santa Barbara and San Luis Obispo counties in central California. This is a group of three closely allied taxa, two of which have been treated both as distinct species and as subtaxa within Monardella undulata Bentham (Bentham, 1834; Jepson, 1901, 1925, 1943; Elmer, 1905; Abrams, 1912a, b, 1951; Epling, 1925; Hoover, 1949, 1970; Munz, 1959; Jokerst, 1992, 1993). This alliance contains one species, M. undulata, with three subspecies, all of which are subshrubs or shrubs.

 Monardella undulata Bentham, Labiat. Gen. Spec. 332. 1834. TYPE: U.S.A. California: 1833, *Douglas s.n.* (holotype, K [digital image]; isotype, GH).

Discussion. The application of the name and circumscription of Monardella undulata needs clarification because the original description (Bentham, 1834) contains characters from more than one taxon. It describes a perennial with leaves that are crisped to undulate, but refers to some characters that correspond with M. crispa Elmer such as the procumbent basal stems ("caule basi procumbente"). The sheets with the type contain collections of more than one taxon. The name M. undulata has long been applied, in part, to an annual plant with undulate leaf margins that grows in sandy soils along the coast of central California. This annual plant is not the species represented by the original description (Bentham, 1834) or by the type specimens. In his description of M. undulata, Bentham (1834) specifically described a plant that has a perennial or suffrutescent base or trunk, but included characters that apply to two different perennial species. Therefore, the description needs to be emended to contain characters representative of only one taxon.

1a. Monardella undulata Bentham subsp. undulata.

Monardella undulata Bentham var. frutescens Hoover, Leafl.
W. Bot. 5: 179. 1949, syn. nov. Monardella frutescens
(Hoover) Jokerst, Phytologia 72: 10. 1992. TYPE:
U.S.A. California: San Luis Obispo Co., N edge of Santa Maria Valley on Arroyo Grande-Guadalupe Rd., 10
July 1947, R. F. Hoover 7289 (holotype, OBI; isotype, CAS).

Subshrub, suffrutescent, strongly scented, 30-70 cm tall, stems woody at base, often pubescent, spreading or appressed puberulent; branches ascending to erect. Leaves clustered at nodes, $10\text{--}30 \times 2\text{--}4$ mm, linear to narrowly (ob)lanceolate, thin, sparsely pubescent, green, margins wavy, petioles subsessile, to 7 mm. Inflorescence generally 1 glomerule per main stem, 10--20 mm wide; bracts $7\text{--}10 \times 3\text{--}5$ mm, lanceolate to narrowly ovate, thin, papery, straw-colored or purple. Calyx 4–6 mm, lobes acute, spreading to ascending pubescent, tube less pubescent, distinctly pedicellate, ca. 1 mm, within the glomerule; corolla blue-purple; stamens exserted, upper lobes gland-tipped; anthers purple.

Discussion. We examined the isotype sheet from GH (Fig. 1) and a high-resolution digital image of the holotype sheet from K. The holotype sheet contains fragments from two collections: Hartweg s.n. (1848, two pieces on the left) and Douglas s.n. (1833, two pieces on the right). The upper right-hand fragment is from a perennial plant and clearly shows more than one season's growth. The other fragment in the Douglas collection could be from an annual plant, but on close examination appears more consistent with new growth as on other specimens of this perennial. The isotype sheet contains fragments from three collections: W. H. Brewer 421 (two pieces on the left), Douglas s.n. (undated, one fragment in the center), and Andrews s.n. (undated, one fragment on the right). The isotype of the Douglas collection matches the upper right-hand holotype fragment, which is from a perennial plant showing more than one season's growth.

The name *Monardella undulata* was first misapplied to an annual plant with undulate leaf margins by Asa Gray in his description of *M. leucocephala* A. Gray (Gray, 1867). He carried this error forward in his 1876 treatment of the genus, which also included a key (Gray, 1876). This erroneous treatment was later adopted by Jepson (1901, 1925, 1943); Abrams (1912a, b); Epling (1925); Hoover (1949, 1970); McMinn, who omits *M. undulata* as a perennial (1939); Howell (1970); Smith (1998); Jokerst (1993); and Matthews (1997). The annual *Monardella* plants with undulate leaves, which have been called *M. undulata* since 1867, have, therefore, never been formally described. These plants are treated below in the Annuae Alliance.

The type specimens of *Monardella undulata* correspond with the plant that has been known as *M. undulata* Bentham var. *frutescens* Hoover and more recently as *M. frutescens* (Hoover) Jokerst, making *M. frutescens* a junior synonym of *M. undulata*. The description and type collection of *M. undulata* are inseparable from *M. frutescens* in plant habit, branching pattern, leaf shape and pubescence, stem pubescence, and bract morphology.

Distribution, ecology, and phenology. Monardella undulata subsp. undulata is endemic to San Luis Obispo County, California. It grows on relictual and/or stabilized sand dunes slightly removed from the immediate coast from Pismo Beach south to the Santa Maria River. It generally flowers from April through November.

Related taxa. Monardella undulata subsp. undulata differs from M. crispa in that its stems are woody and erect to ascending, branching from above with numerous secondary and tertiary branches, and commonly flowering on secondary branches. It has narrower oblanceolate (and less pubescent) leaves. Monardella undulata subsp. undulata intergrades freely with M. crispa in intermediate habitats where the two come into contact (e.g., C. B. Hardham 12891, SBBG; R. F. Hoover 6527, CAS, OBI; D. D. Keck 2211, CAS, DS). There are no apparent intermediate or hybrid specimens between M. undulata subsp. undulata and the Monardella annual (described below) that has undulate leaf margins and occurs in the same general region.

1b. Monardella undulata Bentham subsp. arguelloensis Elvin & A. C. Sanders, subsp. nov. TYPE: U.S.A. California: Santa Barbara Co., Central Coast, Vandenberg Air Force Base, S base on flats/mesa ESE of Point Arguello, NE of Rocky Point, SW of Cypress Ridge, E of Ocean Rd., 34°34′16.1″N, 120°37′57.3″W, 110 m, coastal bluff scrub and grasslands on relictual sand dunes, 29 June 2007, M. A. Elvin & L. Lum 5505 (holotype, UCSB; isotypes, ARIZ, BRY, CAS, CHSC, F, GH, HSU, IRVC, JEPS, K, MO, NY, OBI, RSA, SBBG, SD, UCR, US). Figure 2.

Haec subspecies ab omnibus ceteris subspeciebus habitu frutescente, a *Monardella undulata* Bentham subsp. *undulata* foliis tenuiter pubescentibus, caule crassiusculo magis pubescente et glomerulis magnis, a *M. undulata* subsp. *crispa* (Elmer) Elvin & A. C. Sanders habitu erecto et foliis pubescentibus minoribus angustis differt.

Shrub, 30–100 cm tall, erect; primary axis stout, to 3.5 cm diam., woody at base, multi-branched above, stems sparsely to moderately pilose. Leaves 10–40 \times 3–7 mm, narrowly lanceolate with an obtuse tip to narrowly oblanceolate, \pm fleshy, margins strongly undulate, green. Inflorescence an open compound cyme; glomerules solitary on primary and secondary branches, 18–30 mm wide; bracts 9–13 \times 5–9 mm, lanceolate to narrowly ovate, acuminate, scarious or purple-tinged. Calyx sparsely to moderately hispid, pubescence denser at apex; corolla 10–12 mm, rose to purple.



Figure 1. Monardella undulata subsp. undulata, isotype, center (Douglas s.n. [1 piece]); left, Monardella annual (not M. undulata; Brewer 421 [2 pieces]); and right, Monardella annual (not M. undulata; Andrews s.n. [1 piece] [GH]).

Distribution, ecology, and phenology. Monardella undulata subsp. arguelloensis is closely related to subspecies undulata and M. crispa, sharing similar leaf and bract morphologies. Monardella undulata subsp. arguelloensis is a narrow endemic that only

occurs in the immediate vicinity of Point Arguello in Santa Barbara County, California. Subspecies *arguelloensis* grows on relictual, stabilized sand dunes at 50–150 m and flowers from May through September.



Figure 2. Monardella undulata subsp. arguelloensis Elvin & A. C. Sanders (holotype, M. A. Elvin 5505, UCSB). Image by David Pereksta.

Etymology. The specific epithet refers to the type locality, to which it is endemic, Point Arguello, Santa Barbara County, California.

Related taxa. Monardella undulata subsp. arguelloensis is distinguished from the other subspecies of M. undulata by its habit and larger stature, although it shares similar leaf and bract morphologies. The main stem, or trunk, in subspecies arguelloensis is stout, erect, and up to 3.5 cm in diameter. This taxon, without a doubt, includes the largest plants in

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Monardella. The central stems of subspecies undulata are slender, erect, and less than 1.5 cm in diameter. Primary stems in M. crispa are stout but decumbent, while only its secondary stems are erect and slender. No hybrid or introgressant plants have been observed between subspecies arguelloensis and subspecies crispa.

Paratypes. U.S.A. California: Santa Barbara Co., M. A. Elvin 4955 (IRVC, UCR), 5511 (CAS, IRVC, MO, US), 5514 (IRVC), 5518 (GH, IRVC, NY, UCR), D. E. Hickson 40 (CHSC), 41 (CHSC), 44 (SBBG), 218 (SBBG), 223 (SBBG), 224 (SBBG), 227 (SBBG), A. P. Griffiths s.n. (OBI 58363), s.n. (OBI 58404), s.n. (OBI 58445), s.n. (OBI 58446), s.n. (OBI 58447), s.n. (OBI 58448), 18133 (OBI), D. Keil 19382 (OBI, SBBG), C. F. Smith 12621 (SBBG).

1c. Monardella undulata Bentham subsp. crispa (Elmer) Elvin & A. C. Sanders, stat. nov. Basionym: Monardella crispa Elmer, Bot. Gaz. 39: 46. 1905. Monardella undulata Bentham var. crispa (Elmer) Epling, Ann. Missouri Bot. Gard. 12: 77. 1925. TYPE: U.S.A. California: Santa Barbara Co., Surf, May 1902, A. D. E. Elmer 3965 (holotype, DS not seen; isotypes, DS, MO not seen, US not seen).

Distribution, ecology, and phenology. Monardella crispa is reduced to a subspecies of M. undulata because it overlaps in range with subspecies undulata and freely intergrades with subspecies undulata in intermediate habitats (e.g., partially stabilized dunes) where they overlap in San Luis Obispo County. Subspecies crispa grows on active dunes along the immediate coast from Pismo Beach, San Luis Obispo County, California, south to Honda, Santa Barbara County (ca. five miles south of Surf, the type location). It is similar to other active dune, perennial species in that it has decumbent branches that grow to stay above the shifting sands. Subspecies crispa is moderately to densely lanate on the stems, leaves, bracts, and calyces. The leaves appear pale green or glaucous and are oblong to oblong-linear, with undulate to crisped margins. Mature leaves are usually 7-10 mm wide. The solitary glomerules occur on the primary decumbent stems early in the season. Small, sterile, erect secondary branches occur along the primary stem, which can flower later in the season. It mainly flowers from April through September.

II. VILLOSAE ALLIANCE

The Villosae Alliance consists of perennials and subshrubs that occur in many plant communities from Washington, south through Oregon and California, U.S.A., to Baja California, Mexico. It is a widely divergent group of taxa with incipient speciation occurring throughout its range. Species in this alliance that occur in California include *Monardella hypoleuca* A. Gray (including three subspecies), *M. saxicola* I. M. Johnston, *M. siskiyouensis* Hardham, *M. sheltonii* Torrey (as "sheltoni"), *M. villosa* (including three subspecies), and *M. viridis* Jepson.

 Monardella hypoleuca A. Gray, Syn. Fl. N. Amer. 2: 356. 1878. TYPE: U.S.A. California: southern California, 1876, C. C. Parry & J. G. Lemmon 330 (holotype, GH not seen; isotypes, MO, NY [2]).

Discussion. Monardella hypoleuca is best distinguished by its bicolored leaves, usually with revolute margins. It occurs in chaparral, coastal sage scrub, and pine forest communities in central California (Santa Barbara County), U.S.A., south to northern Baja California, Mexico. It appears to intergrade with M. villosa at the northern edge of its range.

Monardella hypoleuca A. Gray subsp. hypoleuca.

Distribution. Monardella hypoleuca subsp. hypoleuca is found in the western Transverse Ranges, specifically the Santa Monica, Santa Ynez, and Sierra Madre mountains of Los Angeles and Santa Barbara counties, California.

We alter the circumscription of Monardella hypoleuca subsp. hypoleuca only in removing the Santa Ana Mountains populations that have sometimes been included here to a new subspecies described below.

1b. Monardella hypoleuca A. Gray subsp. intermedia A. C. Sanders & Elvin, subsp. nov. TYPE: U.S.A. California: Orange Co., Santa Ana Mtns., upper Holy Jim Canyon, along trail in switchbacks, 33°41′50″N, 117°31′17″W, 976 m, thick chaparral, 2 Sep. 2005, A. C. Sanders & M. A. Elvin 31615 (holotype, RSA; isotypes, GH, IRVC, JEPS, MO, SD, UCR, US). Figure 3.

Haec subspecies inter *Monardellam hypoleucam* A. Gray subsp. *hypoleucam* et subsp. *lanatam* (Abrams) Munz quoad aspectum et foliorum formam intermedia, a hac foliis supra subglabris vel parce pubescentibus et caule parce pubescente, ab illa foliis angustis valde revolutis differt.

Perennial, tufted to matted, rhizomatous, 10–35 cm tall, sparsely short-pubescent. Leaves 20– 50×5 –9 mm, narrowly lanceolate to lanceolate, adaxial surface subglabrous to sparsely pubescent, \pm arched between revolute margins, abaxial surface tomentose. Inflorescence generally solitary; glomerules 20–

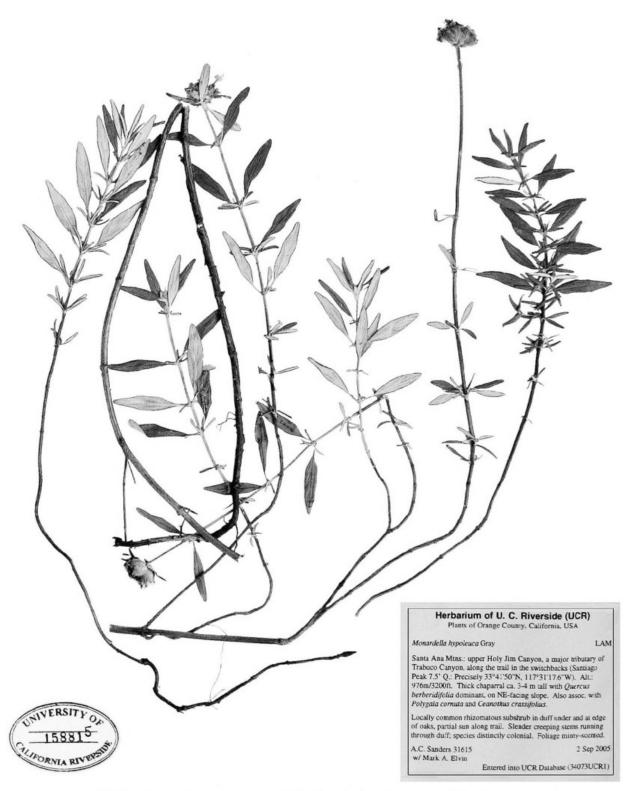


Figure 3. Monardella hypoleuca subsp. intermedia A. C. Sanders & Elvin (isotype, A. C. Sanders 31615, UCR).

35 mm wide; bracts 9–13 \times 4–7 mm, ovate to lanceolate. Calyx 7.5–8.5 mm; corolla 14–17 mm, white to lavender, lobes obtuse; stamens exserted.

Distribution, ecology, and phenology. Monardella hypoleuca subsp. intermedia occurs in mountains and foothills at elevations of 400–1250 m, from the Santa

Ana Mountains in Orange County on the north to the San Luis Rey River Valley on the south, an area that spans portions of Orange, Riverside, and San Diego counties. It generally occurs as an understory species in chaparral, oak woodland, and occasionally coniferous forest. It is a rather localized taxon and is uncommon throughout its range in the Santa Ana and

Palomar mountains, but it can appear to be locally common due to its rhizomatous habit. Subspecies intermedia shares with subspecies hypoleuca relatively glabrous adaxial leaf surfaces and sparse stem pubescence, but it has the narrow and strongly revolute leaf shape of subspecies lanata. It flowers from April through September.

Etymology. The specific epithet refers to the intermediate leaf morphology, appearance, and geographic distribution of this taxon relative to Monardella hypoleuca subsp. hypoleuca and M. hypoleuca subsp. lanata.

Related taxa. We considered the treatment of the three subspecies of Monardella hypoleuca each as distinct species based on discrete characters and geographical separation of each entity. However, given the apparent and limited introgression between subspecies lanata and subspecies intermedia, we think it better at this time to retain them as subspecies of one closely related, currently recognized, wideranging species. Subspecies hypoleuca may be best treated as a discrete species from subspecies lanata and subspecies intermedia based on its distinct geographic range and lack of introgression, but we are being conservative at this point.

Paratypes. U.S.A. California: Orange Co., S. Boyd 8352 (RSA, SD), P. C. Everett 7266 (RSA), J. T. Howell 1094 (RSA), s.n. (IRVC 18585), s.n. (IRVC 18577), s.n. (IRVC 20008), K. G. Marsh s.n. (IRVC 18602), s.n. (IRVC 18642), s.n. (IRVC 25321), P. A. Munz 7742 (GH, LA in UC, POM, UC), J. C. Nevin s.n. (DS 130615), F. W. Peirson 4036 (RSA), F. M. Roberts 1128 (IRVC), 2939 (IRVC), 3115 (IRVC), 4117 (RSA), A. C. Sanders 407 (UCR), 31607 (IRVC, UCR), 31609 (IRVC, UCR), 31613 (CAS, IRVC, K, RSA, SD, UCR), C. B. Wolf 8003 (DS, LA in UC, MO, NY, RSA, UC), J. M. Wood 15 (UCR); Riverside Co., W. P. Armstrong 1277 (RSA, SD), E. LaRue s.n. (UCR 57138), J. C. Roos s.n. (UCR 23575); San Diego Co., D. L. Banks 1256 (RSA), 1648A (RSA), 1805 (RSA), 2229 (RSA), S. Boyd 8333 (RSA), C. Lamareaux 43983 (SD), E. E. Schellenger s.n. (UCC 56935).

1c. Monardella hypoleuca A. Gray subsp. lanata (Abrams) Munz, Aliso 4: 97. 1958. Basionym: Monardella lanata Abrams, Muhlenbergia 8: 39. 1912. TYPE: U.S.A. California: San Diego Co., Descanso Grade near the top, 19 July 1906, K. Brandegee s.n. (holotype, UC 104626).

Distribution. Monardella hypoleuca subsp. lanata is found in the Peninsular Ranges of southern San Diego County, California, U.S.A., and Baja California, Mexico.

 Monardella saxicola I. M. Johnston, Bull. S. Calif. Acad. Sci. 18: 19. 1919. Monardella hypoleuca A. Gray var. saxicola (I. M. Johnston) Jepson, Man. Fl. Pl. Calif. 882. 1925. Monardella viridis Jepson subsp. saxicola (I. M. Johnston) Ewan, Bull. Torrey Bot. Club 64: 521. 1937. TYPE: U.S.A. California: San Bernardino Co., San Antonio Mtns., at start of old trail, near Brown's Flats, 5000 ft., I. M. Johnston 2133 (holotype, DS, MO [photo of holotype]).

Discussion. Monardella saxicola is recognized at the species level. It was treated as a subspecies of M. viridis by Jokerst (1993), but for no stated reason. Monardella saxicola and M. viridis are morphologically distinct and not easily confused, even if specimens without location data are examined. The structure of the trichomes on the leaves is strikingly different. Monardella saxicola is very similar to M. hypoleuca in leaf morphology and pubescence. Johnston (1919) reached this conclusion when he described the species and placed it closest to M. hypoleuca based on its habit and leaf morphology. Jepson (1925) agreed with the close relationship when he placed it as a variety of M. hypoleuca. Both taxa occur in the Transverse Ranges, but M. saxicola occurs in the eastern San Gabriel Mountains while M. hypoleuca occurs in the Santa Monica and Santa Ynez mountains, 135 km to the west. Monardella viridis occurs in the Inner North Coast Ranges, ca. 600 km to the north. This large geographic separation between M. viridis and M. saxicola makes it virtually impossible for genetic material to move between them naturally.

3. Monardella villosa Bentham, Bot. Voy. Sulph. 42. 1844. TYPE: U.S.A. California: Bodegas, *Bentham s.n.* (holotype, K [digital image]).

Discussion. Monardella villosa is a complex species that may have numerous narrow endemics throughout its range.

3a. Monardella villosa Bentham subsp. villosa.

Monardella antonina Hardham, Leafl. W. Bot. 10: 241. 1966, syn. nov. TYPE: U.S.A. California: Monterey Co., 3.7 mi. NE of San Antonio School on rd. from Lockwood to San Ardo, 27 June 1964, C. B. Hardham 12064 (holotype, CAS not seen).

Monardella benitensis Hardham, Leafl. W. Bot. 10: 239.
1966, syn. nov. Monardella antonina Hardham subsp. benitensis (Hardham) Jokerst, Phytologia 72: 9. 1992.
TYPE: U.S.A. California: San Benito Co., Clear Creek in the Diablo Range, 11 July 1965, C. B. Hardham 12672 (holotype, CAS not seen).

Monardella globosa Greene, Pittonia 5: 82. 1902, syn. nov.
 Madronella globosa (Greene) Greene, Leafl. Bot.
 Observ. Crit. 1: 169. 1906. Monardella villosa Bentham subsp. globosa (Greene) Jokerst, Phytologia 72: 14.
 1992. TYPE: U.S.A. California: Alameda Co., Leona,

Aug. 1892, Michener & Bioletti s.n. (holotype, NDG 44399 [digital image]).

Distribution. Monardella villosa Bentham subsp. villosa is found in the coastal mountain ranges of central and northern California.

3b. Monardella villosa Bentham subsp. franciscana (Elmer) Jokerst, Phytologia 72: 14. 1992. Basionym: Monardella franciscana Elmer, Bot. Gaz. 41: 320. 1906. Madronella franciscana (Elmer) Elmer ex A. Heller, Muhlenbergia 2: 244. 1906. Monardella villosa Bentham var. franciscana (Elmer) Jepson, Man. Fl. Pl. Calif. 831. 1925. TYPE: U.S.A. California: San Mateo Co., San Pedro, July 1903, A. D. E. Elmer 4766 (holotype, DS not seen; isotype, CAS).

Distribution. Monardella villosa subsp. franciscana is found in the coastal mountain ranges of central California.

3c. Monardella villosa Bentham subsp. obispoensis (Hoover) Jokerst, Phytologia 72: 14. 1992. Basionym: Monardella villosa Bentham var. obispoensis Hoover, Fl. Calif. 3: 435. 1943. TYPE: U.S.A. California: San Luis Obispo Co., near Cuesta Pass, 20 June 1908, I. J. Condit s.n. (holotype, JEPS [digital image]).

Discussion. Monardella villosa subsp. obispoensis is a difficult taxon to place. It is very distinct in the center of its range and can be separated from all other Monardella taxa by the abundance of long, branched trichomes on its stems and leaves, especially the abaxial leaf surface. However, subspecies obispoensis has a zone of introgression with M. hypoleuca subsp. hypoleuca in the southern portion of its range where a few M. hypoleuca subsp. hypoleuca specimens have some branched trichomes (e.g., D. E. Diehl s.n., POM 70484; H. Baer s.n., POM 18167). It has a larger zone of introgression in the northern portion of its range, where a number of subspecies obispoensis specimens have bicolored and widely triangular-ovate leaves similar to M. villosa subsp. franciscana (e.g., A. P. Griffiths s.n., OBI 58449; C. B. Hardham 10911, SBBG). We placed these specimens in subspecies obispoensis based on the abundance of branched trichomes on their foliage.

III. AUSTRALAE ALLIANCE

The Australae Alliance consists of several geographically isolated taxa that may be relictual remnants on isolated mountaintops. They have morphological characters that are more similar to parapatric taxa in this alliance than to other sympatric species. The taxa in this alliance are mat-forming to rhizomatous perennials that have long trichomes (generally longer than 0.5 mm). Species in this alliance in California include *Monardella australis* Abrams, *M. beneolens* Shevock, Ertter & Jokerst, *M. cinerea* Abrams, *M. stebbinsii* Hardham & Bartel, and a new entity described below. Epling (1925) tentatively included *M. cinerea* in his Section III, Villosae, and *M. australis* in his Section IV, Odoratissimae, as a subspecies of *M. odoratissima*.

 Monardella australis Abrams, Muhlenbergia 8: 34. 1912. TYPE: U.S.A. California: Riverside Co., open forests of Tamarack Valley, July 1901, H. M. Hall 2486 (holotype, DS; isotypes, MO, UC not seen).

1a. Monardella australis Abrams subsp. australis.

Distribution. Monardella australis subsp. australis is found in the San Bernardino, San Gabriel, and San Jacinto mountains, in Riverside and San Bernardino counties, California.

1b. Monardella australis Abrams subsp. cinerea (Abrams) A. C. Sanders & Elvin, comb. et stat. nov. Basionym: Monardella cinerea Abrams, Muhlenbergia 8: 33. 1912. TYPE: U.S.A. California: Los Angeles Co., Mt. San Antonio (Mt. Baldy), 9000 ft. or more, 24 July 1901, L. R. Abrams 1928 (holotype, DS, MO [photo of holotype]).

Discussion. Monardella australis subsp. cinerea is reduced to a subspecies of M. australis based on introgressed and/or hybrid specimens in the San Gabriel, San Bernardino, and San Jacinto mountains (which is outside the traditional range of M. cinerea). Plants in the San Gabriel Mountains range from classic M. cinerea to classic M. australis with a continuous gradient of specimens in between. Additionally, plants approaching (if not indistinguishable from) M. cinerea outside of the traditional range of this species have been collected in the San Bernardino (Elvin 3591, IRVC, UCR; E. C. Van Dyke s.n., CAS 157273) and San Jacinto mountains (R. Hoffmann s.n., SBBG 72009; C. M. Wilder 1, UC).

1c. Monardella australis Abrams subsp. jokerstii Elvin & A. C. Sanders, subsp. nov. TYPE: U.S.A. California: San Bernardino Co., S face of Cucamonga Peak, just W of Day Creek, 25

Aug. 2006, M. A. Elvin & K. VinZant 5085 (holotype, UCSB; isotypes, ARIZ, BRY, CAS, CHSC, F, GH, IRVC, JEPS, K, MO, NY, OBI, RSA, SBBG, SD, UCR, US). Figure 4.

Haec subspecies a *Monardella australi* Abrams subsp. australi foliis serratis et caule ramoso, a *M. australi* subsp. cinerea (Abrams) A. C. Sanders & Elvin foliis longioribus et habitu altiore erectoque differt.

Perennial, tufted to matted, rhizomatous, 15–35 cm tall, sparsely long-spreading and short-glandular pubescent. Leaves 14–30 × 4–8 mm on fertile stems, lanceolate, denticulate to serrate, sparsely long pubescent. Inflorescence an open compound cyme; glomerules one to several per main stem, 8–23 mm wide, often subtended by unmodified leaves; bracts 7–9 × 2–4 mm, narrowly lanceolate to lanceolate, membranaceous, generally inconspicuous in color and size. Calyx 6–8 mm, short-glandular pubescent, lobes long and acute to acuminate; corolla 10–11 mm, white to cream with purple markings appearing pale lavender, stamens exserted.

Distribution, ecology, and phenology. Monardella australis subsp. jokerstii is a rare and localized species. It occurs in the southeastern San Gabriel Mountains, in the vicinity of Cucamonga Peak (Mount San Antonio) and the western portion of Lytle Creek. It was collected once in a wash along the Santa Ana River, in the area currently occupied by the Prado Flood Control Basin, presumably washed down from the mountains above. It can appear to be locally common due to its matted, rhizomatous nature. It grows on talus slopes between breccia, ranging in size from 10-40 cm wide, and on secondary alluvial benches along drainages and washes. It occurs at elevations between 1350 and 1750 m with the Santa Ana River collection an exception at 160 m. It flowers from July through September.

Etymology. The specific epithet refers to James Jokerst, who identified the uniqueness of specimens of this entity by annotation of one of them in 1993 (I. M. Johnston 5118, GH), in honor of his work on this genus prior to his untimely death in 1995.

Related taxa. This plant is closely related to both Monardella australis subsp. australis and M. australis subsp. cinerea. It differs from subspecies australis in having prominent serrations on the leaves, up to 2 mm, and in having branched stems with multiple glomerules in a compound cyme. It differs from M. australis subsp. cinerea in having longer leaves (to 30 mm vs. to 10 mm) and a taller, erect habit (to 35 cm vs. to 15 cm).

Paratypes. U.S.A. California: San Bernardino Co., L. Benson 15036 (POM), I. M. Johnston 5118 (DS, GH, NY, US), D. Swinney 1932 (RSA, UCR), 12 July 1968, L. C. Wheeler s.n. (CAS 972052, NY, RSA 638951, UCR 113687).

IV. ODORATISSIMAE ALLIANCE

The Odoratissimae Alliance consists of plants that range from suffrutescent perennials to shrubs with erect, woody stems. The plants in this alliance are generally glabrous to pubescent (with trichomes up to 0.5 mm) and have similar pubescence on both sides of the leaves. The taxa in this alliance occur in many plant communities throughout the western United States from Colorado to Washington, south through Oregon and California, U.S.A., to Baja California, Mexico. Species in this alliance that occur in California include Monardella follettii (Jepson) Jokerst, M. linoides A. Gray (including five subspecies), M. odoratissima (only two subspecies occur in California), M. palmeri A. Gray, M. purpurea Howell, M. robisonii Epling, M. stoneana Elvin & A. C. Sanders, M. viminea Greene, and three new taxa from the Mojave Desert that warrant recognition, but for which appropriate relationships and ranks are unresolved. Therefore, we tentatively describe each of these three below as species, with the understanding that they may eventually only warrant recognition as subspecies. Epling (1925) grouped M. odoratissima and M. linoides together in Section IV, Odoratissimae, in his monograph. We are also including M. robisonii in the Odoratissimae Alliance based on similarities of its habit and herbage to both M. odoratissima and M. linoides. Monardella robisonii was not described until after Epling wrote his monograph, so its placement was not discussed. We are also including M. palmeri in this alliance based on its glabrous pubescence and apparent close relationship to M. purpurea, which Epling included as a synonym of M. odoratissima in his monograph.

Monardella boydii A. C. Sanders & Elvin, sp. nov. TYPE: U.S.A. California: San Bernardino Co., Ord Mtns., Ord Mtn., Willow Spring Canyon, 5000 ft., 6 Oct. 2007, M. A. Elvin with A. C. Sanders 5811 (holotype, RSA; isotypes, BRY, IRVC, JEPS, MO, UCR, UCSB). Figure 5.

Haec species *Monardellae linoidi* A. Gray similis, sed ab ea inflorescentia ramosa, glomerulis minoribus, bracteis brevioribus (< 10 mm) angustioribus (< 4 mm) et calyce breviore differt.

Subshrub to shrub, 12–40 cm tall, erect; stems visibly woody at base, multi-branched from middle to apex, pubescence fine and dense (mostly 0.03–0.05 mm long), but not completely obscuring epidermis, lacking conoideus glands on stems, aromatic. Leaves $7-15 \times 1-3(-5)$ mm, narrowly

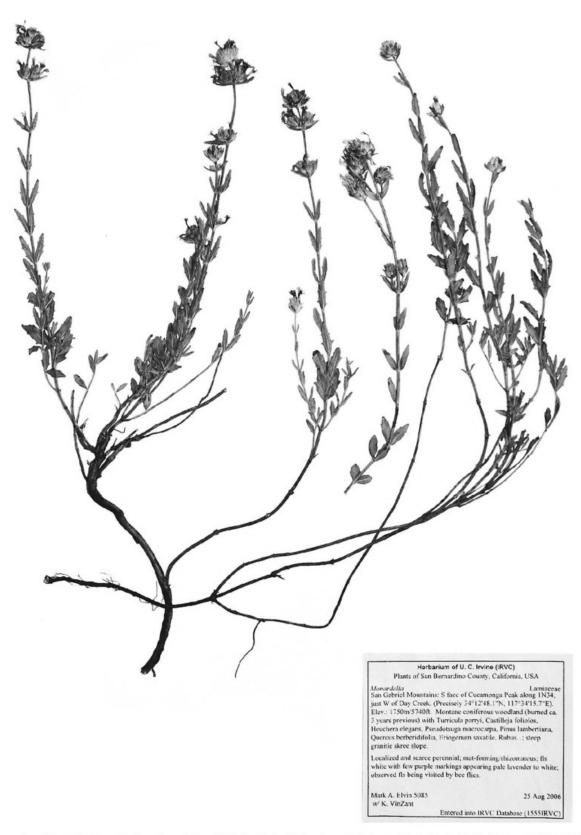


Figure 4. Monardella australis subsp. jokerstii Elvin & A. C. Sanders (holotype, M. A. Elvin & K. VinZant 5085, UCSB). Image by David Pereksta.

elliptic, acute, gray-green or silvery green. Inflorescence an open cyme, (1)3 to 5 glomerules per main stem, 10–20 mm wide; bracts 8– $9 <math>\times$ 2–3 mm, less than or equal to calyces, narrowly elliptic, incon-

spicuous, deciduous, green to purple tinged, acuminate. Calyx 6-8 mm, lobes acute, pubescent, with abundant, spreading, nonglandular trichomes 0.2-0.3 mm long, sparsely and minutely puberulent with



Figure 5. Monardella boydii A. C. Sanders & Elvin (holotype, M. A. Elvin with A. C. Sanders 5811, RSA). Image by David Pereksta.

gland-tipped trichomes 0.01–0.02 mm long. Corolla 10–11 mm, white with purple markings, appearing lavender, pubescent, tube slightly exserted beyond calyx.

Distribution, ecology, and phenology. Monardella boydii is a rare plant known only from the Ord and Rodman mountains in the southern Mojave Desert. It grows in mixed desert scrub, desert riparian scrub, and juniper woodland habitats. It has been documented at elevations between 1400 and 1650 m, primarily in alluvial soils and cracks of bedrock in washes on canyon bottoms and rocky slopes. It flowers from August to October.

Etymology. The specific epithet refers to Steve Boyd of Rancho Santa Ana Botanic Garden Herbarium, who in 1988 led the expedition that first collected this plant in the Ord Mountains of the southern Mojave Desert, far from any other known Monardella populations. This species also commemorates Steve's contributions, dedication, and driving curiosity to understand and explain the unique flora of southern California.

Related taxa. Monardella boydii is a difficult taxon to place. It is similar to, and apparently closely related to, several taxa that occur in the desert, specifically, M. robisonii, M. arizonica Epling, M. linoides s.l., and two other new taxa that occur in the Mojave Desert. It has a series of differences (sometimes small, but still discrete) from these other taxa. Cladograms analyzing morphological characters indicate that its relationship to these other taxa is unresolved. We are provisionally describing M. boydii here as a species because of this lack of resolution in relation to other taxa, and this placement is likely to minimize the necessary taxonomic revisions once more information is obtained (i.e., genetic data). Because of this apparent close relationship with M. robisonii, M. arizonica, M. linoides s.l., and two other new taxa, M. boydii may be best recognized as a subtaxon of one of them.

Monardella boydii is similar to M. linoides s.l. in its habit and the presence of a short, dense, uniform pubescence. Its pubescence is similar to that of M. linoides, even more so than that of M. viminea, which has been placed as a subspecies of M. linoides in various publications (Epling, 1925; Munz, 1974; Jokerst, 1993). Individual trichomes are distinguishable at 10× and, while the pubescence is dense, it does not completely cover the epidermis (as in M. linoides), resulting in the stems appearing greenish with the naked eye. Even with magnification of just 10×, the epidermis can easily be observed. It is distinguished from M. linoides by its branching inflorescence, smaller glomerules (10-20 mm vs. 10-30 mm wide), smaller, narrower bracts (2-3 mm vs. 5-14 mm wide), shorter calyx (6-8 mm vs. 8-9 mm), and its distinct and separate geographic distribution.

Monardella boydii is similar to M. robisonii in its habit, leaf morphology, narrow bracts, and the presence of small glomerules and branching inflorescences. It is distinguished from M. robisonii in

that the calyces contain minute, glandular trichomes (0.01–0.02 mm) and the stem contains minute trichomes (0.03–0.05 mm) and lacks the longer, spreading trichomes (0.1–0.2 mm and 0.3–0.5 mm) and short glandular trichomes (0.01–0.03 mm) of *M. robisonii*.

Monardella boydii is also very similar to two other taxa that occur in mountains of the Mojave Desert (described below) in general habit, bract morphology, and floral morphology (e.g., inflorescence branching pattern, glomerule size). Monardella boydii differs from these taxa in leaf, bract, and pubescence characters and they each have distinct, non-overlapping geographic ranges. These similarities and differences are discussed below.

Paratypes. U.S.A. California: San Bernardino Co., S. Boyd 1704 (RSA), M. A. Elvin 5776 (GH, IRVC, K), 5779 (IRVC, OBI, SBBG, UCSB), 5801 (IRVC, SD), 5802 (IRVC, MO), 5803 (BRY, IRVC), 5804 (IRVC, JEPS), 5805 (CHSC, IRVC), 5806 (IRVC, UCR), 5807 (IRVC, UCR), 5808a, b, c (IRVC), 5809 (IRVC, RSA), 5810 (IRVC, US), 5822 (ARIZ, CAS, IRVC, NY), 6181 (UCSB), 6183 (UCSB), 6184 (UCSB), 6185 (UCSB), 6186 (GH, LA, UCSB), 6187 (UCSB), 6188 (RSA, UCSB), 6189 (BRY, GMDRC, UCSB), 6190 (UCR, UCSB), 6193 (CAS, SD, UCSB), A. C. Sanders 34399 (UCR), 34403 (UCR), 34404 (UCR), 34405 (UCR).

 Monardella eremicola A. C. Sanders & Elvin, sp. nov. TYPE: U.S.A. California: San Bernardino Co., Clark Mtn., Fir Canyon, 5600 ft., 13 Aug. 2001, A. C. Sanders & M. A. Elvin 24570 (holotype, UCR; isotypes, IRVC, RSA). Figure 6.

Haec species quoad habitum, inflorescentiam ramosum, glomerulos parvos et bracteas angustas *Monardellae robisonii* Epling et *M. arizonicae* Epling similis, sed ab eis caulibus glandibus conoideis praeditis, trichomatibus glandularibus patentibus carentibus et calyce breviore differt.

Subshrub to shrub, 15–55 cm tall, erect, camphor-like aroma; stems visibly woody at base, pubescence fine and dense (with some trichomes 0.03–0.08 mm long, and some longer, spreading trichomes approximately 0.2–0.3 mm), but not completely obscuring the epidermis, numerous stout, conoideus glands. Leaves 12–27 × 3–10 mm, narrowly elliptic, acute to obtuse, subsessile, pale or grayish green. Inflorescence an open compound cyme; glomerules solitary on secondary stems, 7–20 mm wide; bracts 4.5–9 × 2–4.5 mm (ca. equal to the calyces), narrowly elliptic to narrowly lanceolate, acute. Calyx 5–7 mm, pubescence nonglandular; corolla 8–11 mm, white with purple markings, appearing lavender.

Distribution, ecology, and phenology. Monardella eremicola is a rare plant of the desert mountains in the northeastern Mojave Desert. It apparently has a limited distribution, having only been documented

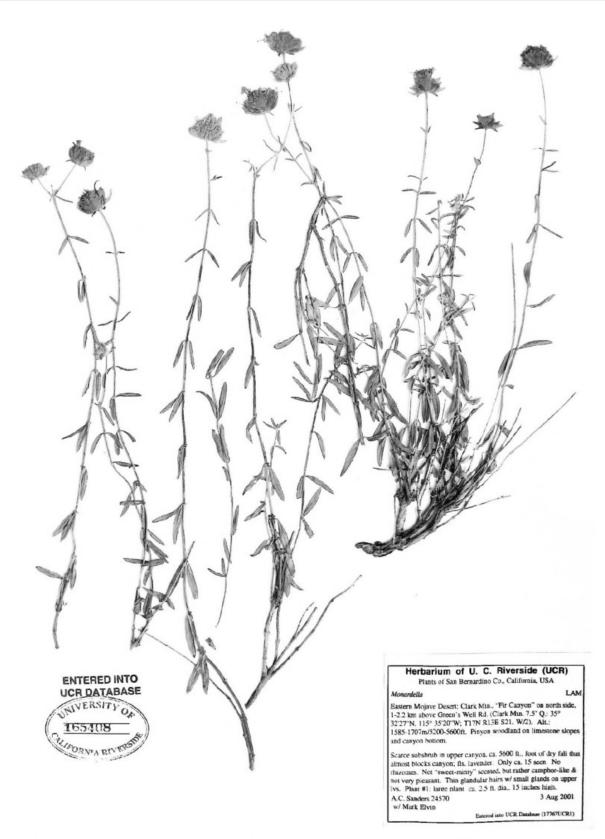


Figure 6. Monardella eremicola A. C. Sanders & Elvin (holotype, A. C. Sanders & M. A. Elvin 24570, UCR).

from the Clark and Kingston mountains of California. Monardella eremicola occurs well above the desert floor at elevations between 1500 and 2100 m. It grows in rock outcrops, among boulders, in boulder cracks, on rocky canyon slopes, and on the margins of desert washes. It is associated with granite or limestone soils in desert riparian scrub and pinyon-juniper woodland and is particularly common in bedrock cracks and on benches along canyon washes. It flowers from June to August. Etymology. The specific epithet refers to the fact that all known collections of this plant have been made in the desert.

Related taxa. Monardella eremicola is a difficult taxon to place. It is similar to, and apparently closely related to, several taxa that occur in the desert, specifically, M. robisonii, M. arizonica, M. linoides s.l., M. boydii, and one other new taxon that occurs in the Mojave Desert. It has a series of differences (sometimes small, but still discrete) from these other taxa. Cladograms analyzing morphological characters indicate that its relationship to these other taxa is unresolved, perhaps due to reticulation. We are provisionally describing M. eremicola here as a species because of this lack of resolution in relation to other taxa, and this placement is likely to minimize the necessary taxonomic revisions once more information is obtained (i.e., genetic data). Because M. eremicola appears to be closely related to M. robisonii, M. arizonica, M. linoides s.l., M. boydii, and one other new taxon, it may best be treated as a subtaxon of one of them. Numerous introgressant specimens occur between M. eremicola, a new subspecies of M. linoides (described below), and M. odoratissima subsp. glauca (Greene) Epling in the mountain ranges of the northern Mojave Desert, particularly in the Panamint and Amargosa mountain ranges of Inyo County. One specimen from the Kingston Mountains (R. F. Thorne 54796, RSA) contains few conoideus glands, but matches the rest of the plants from this area in all other characters, and we are tentatively including it here as M. eremicola. A specimen from northwest Arizona (G. L. Clifton 39183) is intermediate between M. arizonica and M. eremicola in that it contains some characters from both M. eremicola and M. arizonica that the other does not possess (e.g., nonglandular trichomes on the calyx; minute, glandular trichomes on the stem; long, spreading trichomes [0.25-0.5 mm] on the stem).

Monardella eremicola is similar to M. linoides s.l. in its habit, lack of glandular pubescence on the stems and calyces, and leaf length and morphology. It is distinguished from M. linoides by its branching inflorescence; smaller glomerules (7–20 mm vs. 10–30 mm wide); smaller, narrower bracts (2–4.5 mm vs. 5–14 mm wide); shorter calyx (5–7 mm vs. 8–9 mm); sparser, longer pubescence; abundance of conoideus glands on the stem; and its distinct and separate geographic distribution. The stem epidermis of M. eremicola is more visible than in M. linoides because of this sparser pubescence. Individual trichomes are distinguishable at 10× and, while the pubescence is dense, it does not completely cover the epidermis (as in M. linoides), resulting in the stems appearing

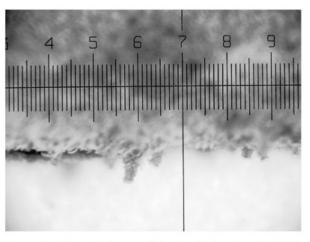


Figure 7. Monardella eremicola A. C. Sanders & Elvin. Conoideus gland. Each unit on the scale equals 0.5 mm. Image by David Pereksta.

greenish with the naked eye. Even with magnification of just 10×, the epidermis can easily be observed. The conoideus glands are miniature, stout protuberances that are subcylindrical to conical in shape and resemble miniature volcanoes (Fig. 7). They are an extension of the epidermis and occasionally have a pubescence similar to that on the adjacent stem. These structures were noticed by Johnston (1919), who called them stalked glands, and by Hardham (in unpublished notes and specimen annotations), who called them hydathodes. Some taxa always have them (e.g., M. lanceolata A. Gray var. glandulifera I. M. Johnston, M. eremicola), but most taxa do not have them.

Monardella eremicola is similar to M. robisonii and M. arizonica in its habit, narrow bracts, small glomerules, branching inflorescences, and presence of longer, spreading trichomes (ca. 0.25 mm) on the stem. It shares with M. robisonii the presence of longer spreading trichomes (0.2–0.3 mm) and lack of glandular pubescence on the calyx. It is similar to M. arizonica in leaf length and width. It is distinguished from M. robisonii and M. arizonica by the presence of conoideus glands on the stems, the absence of spreading, glandular trichomes on the stems, shorter calyces (5–7 mm vs. 6–9 mm and 5–9 mm, respectively), and its distinct and separate geographic distribution.

Monardella eremicola is similar to both M. boydii and another taxon from the mountains of the central Mojave Desert (described below) in general habit, pubescence, bract morphology, leaf morphology, and floral morphology (e.g., inflorescence branching pattern, glomerule size). Monardella eremicola differs from M. boydii in that it contains conoideus glands on the stem; it lacks minute, glandular trichomes on the calyx; it contains longer, spreading trichomes >

0.1 mm on the stem; it has leaves that are > 15 mm long and > 5 mm wide; and its geographic distribution is distinct and separate. It differs from the new Mojave Desert taxon in that it contains conoideus glands on the stem; it lacks minute, glandular trichomes on the calyx; it contains long (0.2–0.3 mm), spreading, nonglandular trichomes on the calyx; the bracts are shorter (4.5–9 mm vs. 10–11 mm); and its geographic distribution is distinct and separate.

Paratypes. U.S.A. California: San Bernardino Co., G. de Nevers 445 (CAS), 268 (CAS, RSA), J. Hendrickson 14057 (NY, SD), E. C. Jaeger s.n. (POM 187366), s.n. (POM 179282), B. A. Prigge 1327 (RSA), 2186 (CAS, RSA), 2198 (RSA, UCR), 1975 (UCR), J. C. Roos 4642 (RSA, UCR), A. C. Sanders 24565 (IRVC, UCR), 24566 (UCR), 24567 (UCR), 24568 (UCR), 24569 (UCR), 24571 (UCR), C. B. Wolf 7577 (DS, RSA, UCR), 7650 (RSA).

3. Monardella linoides A. Gray, Proc. Amer. Acad. Arts 11: 101. 1876. TYPE: U.S.A. California: San Diego Co., mtns. E of San Diego, Oriflame Mine, southern part of San Diego Co., 28 July 1875, D. E. Palmer 296 (holotype, GH; isotypes, MO [annotation by C. Epling: "Gray Herbarium sheet is unnumbered. U. of Calif. sheet is numbered and dated as this is. Two sheets at U.S. Herb. are numbered '261' with no month or day noted. This does compare to Palmer notes."], NY [2], UC, US [2]).

Discussion. Monardella linoides s.l. (including all subtaxa) only seems to hybridize with other Monardella species in three portions of its extensive range: the eastern San Bernardino Mountains, the mountains of the northern Mojave Desert (e.g., the Panamint, White, and Inyo mountains), and the southern Sierra Nevada Mountains region. Notably, M. linoides seems not to form hybrids anywhere in the Peninsular Ranges, not even in the San Jacinto Mountains, where M. linoides subsp. linoides is sympatric with M. australis (a species that it putatively hybridizes with in the San Bernardino Mountains).

3a. Monardella linoides A. Gray subsp. linoides.

Distribution. The range of Monardella linoides subsp. linoides encompasses the Peninsular Ranges in Riverside and San Diego counties, California, U.S.A., and Baja California, Mexico. We tentatively include plants from the Little San Bernardino Mountains (of the Transverse Ranges) that are, for the most part, consistent with M. linoides subsp. linoides. Specimens from the Morongo Valley and Pioneertown areas of the Little San Bernardino Mountains (at the eastern edge of the San Bernardino

Mountains) correspond best with subspecies *linoides*; however, there are slight but consistent differences between the plants in the Little San Bernardino Mountains and those in the Peninsular Ranges. Beyond the plants in the Little San Bernardino Mountains, subspecies *linoides* does not occur north of the Transverse Ranges (i.e., Mojave Desert, Sierra Nevada Mountains), despite numerous, previous reports and determinations (Epling, 1925; Jepson, 1943; Munz, 1974; Jokerst, 1993).

3b. Monardella linoides A. Gray subsp. anemonoides (Greene) Elvin & A. C. Sanders, stat. nov. Basionym: Monardella anemonoides Greene, Pittonia 5: 86. 1902. Madronella anemonoides (Greene) Greene, Leafl. Bot. Observ. Crit. 1: 169. 1906. Monardella linoides A. Gray var. anemonoides (Greene) Jepson, Man. Fl. Pl. Calif. 882. 1925. TYPE: U.S.A. California: Kern Co., Greenhorn Mtns., 6000–7000 ft., 7–15 June 1888, E. Palmer 69 (holotype, US; isotypes, MO, NY).

Distribution and ecology. Monardella linoides subsp. anemonoides is recognized as a subspecies of M. linoides. It is a rather local endemic of the southwestern Sierra Nevada Mountains in Kern and Tulare counties. It is closely allied to both M. linoides subsp. oblonga (Greene) Abrams and an unnamed M. linoides subspecies from the eastern Sierra Nevada Mountains that is described below. The tall, thick stems (to 60 cm, 1-1.5 mm thick just below glomerule) and very large bracts (15–25 \times 10– 14 mm) of subspecies anemonoides are quite distinct and make it rather easy to recognize. A few specimens at the southern edge of its range in the Tehachapi Mountains (Kern Co., Dudley 429 [DS], Dudley 476 [DS, NY, US]) appear to be intermediate between subspecies anemonoides and subspecies oblonga.

3c. Monardella linoides A. Gray subsp. erecta (Abrams) Elvin & A. C. Sanders, comb. et stat. nov. Basionym: Monardella epilobioides Greene var. erecta Abrams, Muhlenbergia 8: 36. 1912. TYPE: U.S.A. California: San Bernardino Co., on dry ridges, Bear Valley, 3 Aug. 1902, L. Abrams 2861 (holotype, DS; isotypes, GH, MO, UC [2], US).

Distribution and ecology. Monardella linoides subsp. erecta is endemic to the eastern San Bernardino Mountains of San Bernardino County, California. The Monardella populations in the San Bernardino Mountains are confusing, with many of the plants containing characters from both M. australis s.l. and M. linoides s.l. It appears likely that these two generally distinct species hybridize here and have formed a large zone of introgression, perhaps because of the distinctive topography of this area. There is no similar geographical feature in other mountain ranges where these two species come into contact. Monardella linoides subsp. erecta represents one end of the spectrum of these plants with regard to habit, pubescence, and leaf and bract morphology, while M. australis subsp. australis represents the opposite extreme. Monardella linoides subsp. erecta is an erect, caespitose plant, 15-30 cm tall, with a short, dense, and uniform pubescence that obscures the epidermis. It has broadly linear to narrowly lanceolate leaves with entire margins, and the narrowly lanceolate bracts are roughly equal to the calyces. Monardella australis subsp. australis is a mat-forming, rhizomatous plant, 10-20 cm tall, with rather long and variable pubescence, lanceolate to narrowly ovate leaves that are entire to weakly serrate, and lanceolate to long acuminate bracts that exceed the calyces.

The type specimens for Monardella linoides var. stricta Parish (San Bernardino Co., S. B. Parish 2077 [holotype, UC; isotype, DS]) and M. epilobioides (San Bernardino Co., S. B. Parish 3008 [holotype, US; isotypes, MO, UC]) represent introgressant individuals that are intermediate in characters between M. linoides subsp. erecta and M. australis subsp. australis. It is also possible that there may be several recognizable entities in the San Bernardino Mountains that are closely related to both M. linoides subsp. erecta and M. australis subsp. australis. It has been observed by one of the authors that there appear to be correlations or groupings of character suites to specific microhabitats and general geographic ranges in this area that may represent local differentiation and incipient speciation associated with localized substrates. We cannot separate these entities at this time and more study is needed.

3d. Monardella linoides A. Gray subsp. oblonga (Greene) Abrams, Ill. Fl. Pacific States 3: 655. 1951. Basionym: Monardella oblonga Greene, Pittonia 5: 83. 1902. Monardella linoides A. Gray var. oblonga (Greene) Munz, Man. S. Calif. Bot. 450. 1935. TYPE: U.S.A. California: Kern Co., in the mtns. S of Tehachapi, 24 June 1889, E. L. Greene s.n. (holotype, NDG 44420 [digital image]; isotype, UC 292735, MO 905498 [photo of UC sheet]).

Distribution. Monardella linoides subsp. oblonga is found in the Tehachapi Mountains of Kern County and the Mount Pinos region of Ventura and Kern counties, California.

3e. Monardella linoides A. Gray subsp. sierrae Elvin & A. C. Sanders, subsp. nov. TYPE: U.S.A. California: Inyo Co., desert slopes near Big Pine Creek at foot of trail to Big Pine Lakes, 8500 ft., 24 July 1934, R. S. Ferris 8983 (holotype, UC; isotypes, DS, NY). Figure 8.

Haec subspecies quoad habitum, pubescentiam, foliorum formam et glomerulos solitarios *Monardellae linoidi* subsp. anemonoidi (Greene) Elvin & A. C. Sanders et subsp. oblongae (Greene) Abrams similis, sed a hac caulibus altioribus et bracteis latioribus, ab illa bracteis minoribus, pedunculo breviore et glomerulis minoribus differt.

Subshrub to shrub, 20–50 cm tall, erect, visibly woody at base, densely pubescent. Leaves 20– 30×4 –10 mm, length to width ratio 3–5:1, lanceolate to broadly (ob)lanceolate, pale green, petioles 2–4 mm, base acute, subglabrous to sparsely puberulent adaxially and sparsely puberulent abaxially (especially on the veins). Inflorescence solitary, peduncles slender (< 1 mm thick just below glomerule), generally 1–7 cm long (from highest definite leaf to glomerule); glomerule 15–25 mm wide; bracts 11– 16×5 –9 mm, broadly lanceolate to narrowly ovate, attenuate, greater than or equal to the calyces. Corolla pale to rose.

Distribution, ecology, and phenology. Monardella linoides subsp. sierrae is the predominant form of M. linoides northwest of the Mojave Desert. It is commonly collected in the Sierra Nevada Mountains at elevations of 1000-3500 m along the ridge and eastern slope, from Kern, through Tulare, Inyo, Fresno, Madera, and Mono counties in California and Washoe and Esmeralda counties in Nevada. It occurs mostly on open, gravelly to rocky slopes with granitic soils in montane coniferous forest, pinyonjuniper woodland, and chaparral. Subspecies sierrae is similar to subspecies anemonoides and subspecies oblonga in habit, pubescence, its solitary glomerules, and leaf morphology. It is distinguished from subspecies anemonoides by its smaller bracts (11-16 \times 5–9 mm vs. 15–25 \times 10–14 mm), shorter peduncles (1-7 cm vs. 5-15 cm), and smaller glomerules (15-25 mm vs. 20-30 mm wide). It is distinguished from subspecies oblonga by its taller stems (20-50 cm vs. 15-25 cm) and wider bracts (5-9 mm vs. 4-7 mm). It flowers June through September. Leroy Abrams noted the distinctiveness of this entity in an annotation on an H. M. Hall 8380 collection (UC).

Etymology. The specific epithet refers to the Sierra Nevada Mountains, where this plant occurs.



Figure 8. Monardella linoides subsp. sierrae Elvin & A. C. Sanders (holotype, R. S. Ferris 8983, UC).

Related taxa. Monardella linoides subsp. sierrae appears to have one zone of limited hybridization and two extensive zones of introgression. It hybridizes with M. odoratissima on the Kern Plateau in the southern Sierra Nevada Mountains, where scattered intermedi-

ate specimens have been found. It intergrades with multiple *Monardella* taxa in two areas, one in the southern Sierra Nevada Mountains extending down into the Tehachapi Mountains of Kern and Ventura counties and one in the desert mountains at the

southern end of Death Valley. Introgressant specimens between M. linoides subsp. sierrae and both subspecies anemonoides and subspecies oblonga occur from the southern Sierra Nevada Mountains south and west into the Tehachapi Mountains. Some of the specimens from this area clearly represent typical material of subspecies oblonga and some represent typical material of subspecies sierrae. Numerous introgressant specimens between M. linoides subsp. sierrae, M. odoratissima, and M. eremicola occur in the mountain ranges of the northern Mojave Desert, particularly in the Panamint and Amargosa mountain ranges of Inyo County. Many of the specimens from this area display a blend of characters intermediate between these three taxa, but do not fit well into any one of them.

Paratypes. U.S.A. California: Fresno Co., F. J. Smiley 646 (GH); Inyo Co., R. Bacigalupi 6067 (UC), E. K. Balls 18030 (RSA), K. Brandegee s.n. (UC 185726), D. Charlton 1990 (RSA, SD), S. F. Cook s.n. (UC 1282601), A. Davidson 2751 (RSA), M. DeDecker 45 (RSA), 2153 (RSA [2]), 2334 (RSA), 2755 (CAS, RSA, UCR), 3872 (RSA), 6231 (RSA [2]), R. S. Ferris 1381 (CAS), M. F. Gilman 1847 (US), G. K. Helmkamp 2445 (UCR), 4282 (UCR), R. Hoffmann s.n. (SBBG 71940), s.n. (SBBG 71945), J. W. Hopkins s.n. (SBBG 71939), D. F. Howe 3053 (SD), J. T. Howell 24150 (CAS, RSA, UCR), 25390 (CAS), 26692 (CAS), 40221 (CAS, NY), E. C. Jaeger s.n. (RSA 50668), s.n. (POM 246676), D. D. Keck 534 (POM, UC), M. Kerr s.n. (SBBG 72005), F. Klyver s.n. (DS 171012), W. Knight 4314 (CAS), R. M. Lloyd 2670 (UC), 2741 (UC), K. Morris 468 (NY), P. A. Munz 16537 (GH, POM, UC, US), F. W. Peirson 1068 (RSA), 7543 (RSA, SD), C. A. Purpus 5089 (GH, UC), P. H. Raven 183 (CAS, UC), 9675 (CAS), J. C. Roos 2836 (DS), L. Rowntree s.n. (CAS 299289), D. W. Taylor 7251 (JEPS), 8220 (CAS), R. F. Thorne 38816 (RSA), C. B. Wolf 3252 (CAS, GH, RSA); Kern Co., D. E. Breedlove 3843 (CAS, DS, MO), C. A. Purpus 5096 (GH, MO, UC, US), E. C. Twisselmann 3061 (CAS [2]), 13726 (CAS), R. Twitchell s.n. (RSA 518326); Madera Co., O. H. Kappler 1911 (LA in UC); Mono Co., M. S. Baker 9088 (CAS), R. C. Barneby 5843 (NY), J. D. Cassel 247 (DS), P. C. Everett 21967 (NY, SD), G. K. Helmkamp 5940 (UCR), J. T. Howell 14264 (LA in UC), M. E. Jones s.n. (CAS 154856, DS 171312, POM 145491, SBBG 71941), D. D. Keck 3882 (DS [2], UC), A. Mardyke s.n. (JEPS 63348), J. D. Morefield 3768 (MO, NY, RSA, UC), A. Noldeke s.n. (CAS 299264), F. W. Peirson 1065 (RSA), 6033 (RSA), 10727 (RSA, UC), 28 July 1933, F. W. Peirson s.n. (RSA), P. H. Raven 9934 (CAS), J. C. Roos s.n. (RSA 658653), L. S. Rose 35349 (CAS, LA in UC), L. Rowntree s.n. (CAS 299290), D. W. Taylor 16877 (JEPS); Tulare Co., C. Bornstein 00-077 (SBBG), S. Boyd 1918 (RSA, UCR), S. Boyd 10561 (RSA), B. Ertter 6330 (NY), H. M. Hall 5268 (DS), 5415 (DS), 8380 (UC), C. B. Hardham 12235 (CAS, GH), K. Harper s.n. (UCR 46141), J. T. Howell 42808 (CAS), 43094 (CAS, NY), 48585 (CAS), J. Keefe 13164 (CAS), N. Meng 433 (SBBG), P. A. Munz 15241 (RSA), D. Myrick 1197 (CAS, SBBG), J. R. Shevock 781 (CAS), E. C. Twisselmann 7837 (CAS), 12651 (SBBG), 14401 (CAS), 18450 (CAS, RSA); Ventura Co., R. Burgess 7644 (IRVC, SBBG). Nevada: Washoe Co., P. B. Kennedy 1925 (CAS); Esmeralda Co., R. S. Ferris 6745 (DS).

4. Monardella mojavensis Elvin & A. C. Sanders, sp. nov. TYPE: U.S.A. California: San Bernardino Co., Mojave Desert, Granite Mtns., above Snake Spring, 4400 ft., 10 Sep. 2008, M. A. Elvin & T. La Doux 6161 (holotype, UCSB; isotypes, JEPS, MO, RSA, UCR). Figure 9.

Haec species Monardellae linoidi A. Gray similis, sed ab ea caulis trichomatibus sparsioribus, inflorescentia ramosa, calyce breviore trichomatibus glandularibus vestito et bracteis angustioribus calycem superantibus differt.

Subshrub to shrub, 30–60 cm tall, erect; stems visibly woody at base, multi-branched from middle to apex, pubescence fine, dense, and short (ca. 0.03 mm), partially obscuring epidermis, aromatic. Leaves 8–20 × 2–4 mm, narrowly elliptic, acute, gray-green or silvery. Inflorescence an open compound cyme with 3 to 7 glomerules per stem; glomerules 10–20 mm wide; bracts 10–11 × 2–5 mm, longer than calyces. Calyx 5–7 mm, lobes acute, puberulent and with spreading gland-tipped hairs; bracts becoming pale and scarious inward, the outermost often green and leaf-like, narrowly ovate with acuminate tips. Corolla 10–11 mm, white with purple markings, appearing lavender, pubescent, tube exserted from calyx.

Distribution, ecology, and phenology. Monardella mojavensis is presently known from five mountain islands in the arid ranges of the eastern Mojave Desert in California (Old Woman, Granite, Old Dad, and Providence mountains) and southwestern Nevada (Newberry Mountains). It may be more widely distributed in California and southern Nevada and could also occur in northwestern Arizona. It grows in mixed desert scrub, pinyon-juniper woodland, and desert riparian scrub habitats. It has been documented at elevations between 800 and 1500 m. It grows among granite boulders and on decomposed granite soils but has also been collected on limestone soils. Microhabitats include flats, boulder fields, washes, crevices among boulders, and cliffs. Leroy Abrams noted the distinctiveness of this entity in an annotation on a K. Brandegee s.n. collection (UC 104649). It flowers from May to August.

Etymology. The specific epithet refers to the Mojave Desert in the western United States, where all known collections have been made.

Related taxa. Monardella mojavensis is a difficult taxon to place. It is similar to, and apparently closely related to, several taxa that occur in the desert, specifically, M. robisonii, M. arizonica, M. linoides s.l., M. boydii, and M. eremicola. It has a series of differences (sometimes small, but still discrete) from these other taxa. Cladograms analyzing morphological

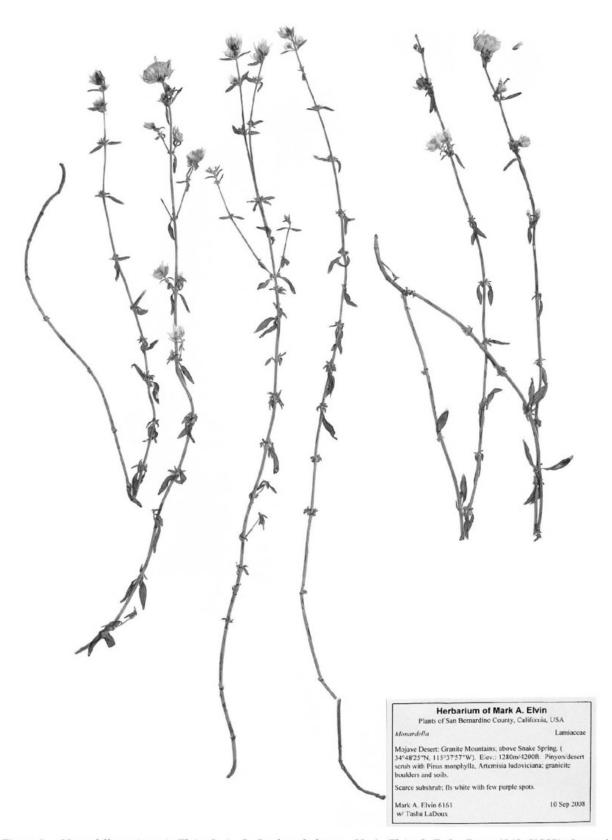


Figure 9. Monardella mojavensis Elvin & A. C. Sanders (holotype, M. A. Elvin & T. La Doux 6161, UCSB). Image by David Pereksta.

characters indicate that its relationship to these taxa is unresolved. We are provisionally describing *M. mojavensis* here as a species because of this lack of resolution in relation to other taxa, and this placement is likely to minimize the necessary taxonomic

revisions once more information is obtained (i.e., genetic data). Because *M. mojavensis* appears to be closely related to *M. robisonii*, *M. arizonica*, *M. linoides* s.l., *M. boydii*, and *M. eremicola*, it may best be treated as a subtaxon of one of them.

Monardella mojavensis is similar to M. linoides s.l. in its habit, leaf width, and the presence of a short, dense, uniform pubescence. Individual trichomes are distinguishable at 10× and, while the pubescence is dense, it is less dense than that of M. linoides and does not completely cover the epidermis (as in M. linoides), resulting in the stems appearing greenish with the naked eye. Even with magnification of just 10×, the epidermis can easily be observed. It is distinguished from M. linoides by its branching inflorescence; smaller glomerules (10-20 mm vs. 10-30 mm wide); smaller, narrower bracts (2-5 mm vs. 5-14 mm wide); shorter calyces (5-7 mm vs. 8-9 mm); the presence of glandular trichomes on the calyces; and its distinct and separate geographic distribution.

Monardella mojavensis is similar to M. robisonii in habit, leaf morphology, bract length and width, and the presence of small glomerules and branching inflorescences. It is distinguished from M. robisonii in that the calyx contains minute, glandular trichomes (0.01–0.02 mm) and spreading, glandular trichomes (0.06–0.1 mm); the stem contains minute trichomes (0.03–0.05 mm) and lacks the longer, spreading trichomes (0.1–0.2 mm and 0.3–0.5 mm) and short glandular trichomes (0.01–0.03 mm) of M. robisonii; its shorter calyces (5–7 mm vs. 6–9 mm); and its distinct and separate geographic distribution.

Monardella mojavensis is also very similar to M. boydii and M. eremicola in general habit, bract morphology, and floral morphology (e.g., inflorescence branching pattern, glomerule size). Monardella mojavensis differs from M. boydii in bract length (10-11 mm vs. 8-9 mm); it lacks spreading, glandular trichomes and contains spreading nonglandular trichomes (0.2-0.3 mm) on the calyces; and it has a distinct and separate geographic range. Monardella mojavensis differs from M. eremicola in that it lacks conoideus glands on the stem; lacks longer spreading trichomes (> 0.1 mm) on the stem; the leaves are shorter and narrower; the bracts are longer (10-11 mm vs. 4.5–9 mm); it contains glandular trichomes on the calyces; and its geographic distribution is distinct and separate.

Paratypes. U.S.A. California: San Bernardino Co., B. Baldwin 273 (RSA), Mrs. K. Barnes s.n. (LA 62688 in UC), D. Bradbury 277 (RSA [2]), K. Brandegee s.n. (UC 104649), J. Donahue 76214 (RSA), M. A. Elvin 6151 (JEPS, UCSB), 6152 (UCR, UCSB), 6153 (UCSB), 6154 (UCSB), 6155 (UCSB), 6156 (GMDRC, JEPS, RSA, UCSB), 6157 (BRY, UCSB), 6158 (SD, UCSB), 6159 (GH, OBI, UCSB), 6160 (CAS, LA, UCSB, US), 6162 (NY, SBBG, UCSB), E. C. Jaeger s.n. (POM 254461), M. E. Jones 25505 (POM), J. R. Haller 1329 (UCSB), s.n. (UCSB 10511), J. Hendrickson 12734 (RSA), 12747a (NY), 18834 (RSA), P. A. Munz 4234 (POM), B. Pitzer 4013 (UCR), D. Silverman 7 (SD, UCR), B.

A. Stein 43 (RSA [2]), R. F. Thorne 50689 (RSA). Nevada: Clark Co., J. S. Holland 1440 (UCR, UNLV not seen), G. E. Marrs-Smith BLM 30 (UCR, UNLV not seen).

- Monardella odoratissima Bentham, Labiat. Gen. Spec. 332. 1834. TYPE: U.S.A. Washington: Columbia River and White Mtns., *Douglas s.n.* (holotype, K [digital image]).
- 5a. Monardella odoratissima Bentham subsp. odoratissima.

Distribution. Monardella odoratissima subsp. odoratissima occurs in southern Washington and northern Oregon. This subspecies does not occur in California. No material that has been collected in California conforms to material from the type locality.

5b. Monardella odoratissima Bentham subsp. glauca (Greene) Epling, Ann. Missouri Bot. Gard. 12: 62. 1925. Basionym: Monardella glauca Greene, Pittonia 4: 321. 1901. Madronella glauca (Greene) Greene, Leafl. Bot. Observ. Crit. 1: 169. 1906. Monardella odoratissima Bentham var. glauca (Greene) H. St. John, Res. Stud. State Coll. Wash. 1: 64. 1929. TYPE: U.S.A. Oregon: eastern Oregon, 21 June 1898, Cusick 1956 (holotype, US not seen; isotypes, GH not seen, MO not seen).

Discussion. Monardella odoratissima subsp. glauca is recognized as a subspecies of M. odoratissima. It was treated as a full species by Jokerst (1993), but for no stated reason. Subspecies glauca plants are highly variable, and there is a large zone of introgression between subspecies glauca and M. pallida A. Heller along the crest of the Sierra Nevada Mountains. Plants in California attributed to M. odoratissima subsp. parvifolia (Greene) Epling are misapplied to that name and are part of the abovementioned hybrid swarm.

5c. Monardella odoratissima Bentham subsp. pallida (A. Heller) Epling, Ann. Missouri Bot. Gard. 12: 66. 1925. Basionym: Monardella pallida A. Heller, Muhlenbergia 1: 36. 1904. Madronella pallida (A. Heller) A. Heller, Muhlenbergia 1: 138. 1906. TYPE: U.S.A. California: Nevada Co., ridge near lower end of Donner Lake (S side), 17 July 1903, A. A. Heller 6959 (holotype, MO not seen; isotypes, DS not seen, GH not seen, UC not seen, US not seen).

Discussion. Monardella odoratissima subsp. pallida is recognized as a subspecies of M. odoratissima. It was treated as a full species by Jokerst (1993), but

for no stated reason. There is a vast zone of introgression with subspecies glauca along the crest of the Sierra Nevada Mountains. Subspecies pallida generally has leaves that closely subtend the glomerules, but are not modified. Some call these leaves bracts. They are generally green, but some plants have slightly modified leaves in this position and when these are purplish some suspect hybridization with subspecies glauca.

6. Monardella robisonii Epling, Man. S. Calif. Bot. 451, 600. 1935. TYPE: U.S.A. California: Riverside Co., Keys Ranch, Little San Bernardino Mtns., among boulders and crevices, 20 Apr. 1934, C. Epling s.n. (holotype, LA 62494 in UC).

Discussion. Monardella robisonii has been thought to be closely related to M. linoides based on similarity in habit and leaf morphology (Epling, 1939), and one of the authors has expressed doubts about their separation. These species have been separated largely on the basis of differences in their pubescence (Epling, 1935, 1939; Abrams, 1951; Munz, 1974; Jokerst, 1993), which is long, spreading, and variable in length and direction on M. robisonii in contrast to the short, appressed, and uniform pubescence of all subspecies of M. linoides. Monardella robisonii is best distinguished by its long, spreading trichomes (0.3–0.5 mm long), branching inflorescence, narrow bracts, and glandular trichomes on the stem. It occurs in the San Bernardino Mountains at the southern edge of the Mojave Desert. Monardella robisonii differs from M. linoides in that it has (1) minute, glandular trichomes (0.01-0.03 mm) under the rather long, spreading pubescence on the stems; (2) small bracts (9-12 imes 3-5 mm) that are generally equal to the calvees; (3) leaves that are generally wider than the linear to narrowly lanceolate leaves of M. linoides; (4) smaller glomerules (7–20[–25] mm wide); and (5) multi-branching inflorescences; but it lacks the short, dense, uniform pubescence that obscures the epidermis of M. linoides.

V. ANNUAE ALLIANCE

The Annuae Alliance consists of erect, annual plants that occur throughout California including coastal, montane, and desert habitats. Plants in this alliance occur throughout California and into southwestern Nevada, U.S.A., and northern Baja California, Mexico. The plants of this alliance can be distinguished by their stature (herbaceous stems), annual growth form, lanceolate foliage, and pubescence. Much of the variation in these plants occurs in characters associated with the flowers (i.e., bracts, calyces). Several species in this alliance are narrow endemics (two of

which are considered extinct, neither having been seen since 1941), but a few are quite wide-ranging with one species occurring from northern California, U.S.A., to Baja California, Mexico. Species in this alliance in California include *Monardella breweri* A. Gray, *M. candicans* Bentham, *M. douglasii* Bentham (including two subspecies), *M. exilis* (A. Gray) Greene, *M. lanceolata* (including three varieties), *M. leucocephala*, *M. pringlei* A. Gray, and a new taxon described below (including two subspecies).

 Monardella breweri A. Gray, Proc. Amer. Acad. Arts 7: 386. 1867. TYPE: U.S.A. California: Contra Costa Co., Corral Hollow, E side of north Coast Range, E of Mt. Diablo, 3 June 1862, Brewer 1213 (holotype, GH; isotypes, UC not seen, US not seen).

Discussion. Monardella breweri occurs throughout California's Coast, Transverse, Sierra Nevada, and Peninsular ranges. We recognize this species as comprising four subspecies, including M. lanceolata and its sometimes recognized varieties M. lanceolata var. glandulifera and M. lanceolata var. microcephala A. Gray.

1a. Monardella breweri A. Gray subsp. breweri.

Distribution and ecology. Monardella breweri subsp. breweri occurs primarily in the South Coast Range from Ventura County northward to Alameda County, but extends southeast into the Tehachapi, San Gabriel, and western San Bernardino mountains. The type was collected from the northernmost station for this species.

1b. Monardella breweri A. Gray subsp. glandulifera (I. M. Johnston) Elvin, comb. et stat. nov. Basionym: Monardella lanceolata A. Gray var. glandulifera I. M. Johnston, Bull. S. Calif. Acad. Sci. 18: 20. 1919. TYPE: U.S.A. California: Los Angeles Co., Brown's Flat, San Gabriel Mtns., 4300 ft., 1 Sep. 1918, I. M. Johnston 2139 (holotype, POM not seen; isotypes, DS, UC).

Discussion. Monardella breweri subsp. glandu-lifera is recognized as a subspecies of M. breweri. It was described as a variety of M. lanceolata (Johnston, 1919), separated based on the abundance of conoideus glands on the stem and other characters (e.g., pubescent calyx sinuses). It was recognized as a variant of M. lanceolata by Munz (1974) and then synonomized with M. lanceolata by Jokerst (1993) as "generally indistinct."

Distribution and ecology. Monardella breweri subsp. glandulifera is a local endemic of the southern San Gabriel Mountains in Los Angeles County, California. While it does occur within the range of M. lanceolata, it differs from it in its smaller stature, smaller glomerules, and the abundance and density of conoideus glands on the stem. Conoideus glands occur on some M. lanceolata specimens, but are found only in very low densities. Monardella lanceolata specimens that have conoideus glands are sparsely distributed across the southern slopes of the Transverse Ranges. This may indicate that reproductive isolating mechanisms have not fully developed between M. breweri subsp. glandulifera and M. lanceolata. Monardella breweri subsp. glandulifera is similar to M. lanceolata var. microcephala in its stature, small glomerules, and the size of its bracts. It differs from it in that its stems are covered with an abundance of conical glands, the sinuses of the calvx are pubescent, and it has a distinct geographic range in the San Gabriel Mountains, ca. 195 km northwest of the Jacumba Mountains, where M. lanceolata var. microcephala reaches its northern limit.

1c. Monardella breweri A. Gray subsp. lanceolata (A. Gray) A. C. Sanders & Elvin, comb. et stat. nov. Basionym: Monardella lanceolata A. Gray, Proc. Amer. Acad. Arts 11: 102. 1876. Madronella lanceolata (A. Gray) Greene, Leafl. Bot. Observ. Crit. 1: 169. 1906. TYPE: U.S.A. California: Mariposa Co., Yosemite Valley, July 1866, H. N. Bolander 6320 (lectotype, designated here, GH; duplicate, US not seen).

Monardella sanguinea Greene, Pittonia 5: 86. 1902.
Madronella sanguinea (Greene) Greene, Leafl. Bot.
Observ. Crit. 1: 169. 1906. Monardella lanceolata A.
Gray var. sanguinea (Greene) Jepson, Man. Fl. Pl.
Calif. 883. 1925. TYPE: [U.S.A.] California: San Diego
Co., 1881, G. W. Dunn s.n. (lectotype, designated here,
NDG 44439 [digital image]).

Distribution and ecology. Monardella breweri subsp. lanceolata occurs in the Sierra Nevada Mountains (in California and Nevada), the Cascade Ranges (and adjacent Klamath Range), the Transverse Ranges (San Bernardino, San Gabriel, and Tehachapi mountains), and the Peninsular Ranges, as well as in coastal valleys and plains of southern California.

Related taxa. Monardella breweri subsp. lanceolata is very similar to subspecies breweri. They share habit, leaf morphology and size, stem and leaf pubescence, and floral morphology including glands on the tips of the uppermost two petals. They are often difficult to separate because they overlap and intergrade for some 240 km between the San Bernardino and Santa Ynez mountains in the Transverse Ranges. The distinction between these species blurs and disappears in this vast region where the reproductive isolating mechanisms between these two species appear to be weak at best. Many collections in this zone of introgression possess characters of both taxa. The two subspecies differ mainly in bract shape and venation. The bracts of subspecies lanceolata are lanceolate-ovate or narrower, have acute (but not acuminate) tips, are weakly to strongly cross veined, and may or may not be tinted purple.

No type specimen has been published for Monardella lanceolata, and Gray (1876) did not cite any specimens in his description of the species. He simply listed the range for the plant as "California, from Plumas to San Diego Co.," which suggests he had seen a number of specimens from scattered localities. A specimen at NY, Palmer 294 (NY, MO not seen), is listed on the NY website as "Type," but with no supporting reference. Abrams (1912b) listed Palmer 294 as a paratype under his circumscription of M. lanceolata var. microcephala. We reviewed specimens that were likely to have been seen by Gray or that were in the Gray Herbarium at the time he described M. lanceolata (including Palmer 294). Based on the information available in the literature (including the description for M. lanceolata), we selected H. N. Bolander 6320 as the most representative specimen and hereby designate it as the lectotype.

Greene wrote "Type!" on two of the three specimens that he mentioned in the *Monardella sanguinea* protologue, but he did not explicitly designate one specimen as type. We reviewed digital images of these specimens; the first specimen that Greene mentions in his description (*G. W. Dunn s.n.*, NDG 44439) is the most representative and we therefore designate it as lectotype here.

1d. Monardella breweri A. Gray subsp. microcephala (A. Gray) Elvin & A. C. Sanders, comb. et stat. nov. Basionym: Monardella lanceolata A. Gray var. microcephala A. Gray, Syn. Fl. N. Amer. (ed. 2) 2(1): 459. 1886. TYPE: U.S.A. California: San Diego Co., Potrero, 24 July 1883, Orcutt 928 (holotype, MO not seen; isotypes, GH [2]).

Monardella peninsularis Greene, Pittonia 5: 87. 1902.
Madronella peninsularis (Greene) Greene, Leafl. Bot.
Observ. Crit. 1: 169. 1906. TYPE: Mexico. Baja
California: "from some uncertain station in the northern part of the peninsula of Lower California," 6 June
1885, C. R. Orcutt s.n. (holotype, NDG 44430 [digital image]).

Distribution and ecology. Monardella breweri subsp. microcephala is similar to subspecies lanceolata, to which it has generally been allied. Munz (1959) mentions it as a minor variant under M. lanceolata; Jokerst (1993) thought that named "forms" [subtaxa] of M. lanceolata were indistinct, but did not formally address M. breweri subsp. microcephala; Wiggins (1980) treated it as a variety of M. lanceolata and considered it to be the only taxon of M. lanceolata present in Baja California, Mexico. It is predominantly a plant of northern Baja California, Mexico, but extends into southern San Diego County, California, U.S.A., where the type was collected. This plant is apparently rare north of Mexico.

Related taxa. Monardella breweri subsp. microcephala is characterized by very small glomerules (7-15 mm broad, rarely to 20 mm), a highly branched habit with short internodes, and glomerules in a ± cymose arrangement. Both subspecies breweri and subspecies lanceolata have larger glomerules that tend to be solitary at the ends of the relatively few and long inflorescence branches. Subspecies microcephala plants are generally short (9-30 cm), as compared to 15-65 cm for subspecies breweri and lanceolata, even when they are well developed. It has a conspicuously short and bushy habit compared to subspecies breweri and lanceolata. The bracts of subspecies microcephala seem to nearly always lack purple pigments, as do many subspecies lanceolata specimens, unlike bracts of subspecies breweri, which are almost always purple tinted. Perhaps the most notable characters of subspecies microcephala are that its bracts are extremely short (5-7 mm), no longer than the calyces that they subtend, and generally lanceolate-ovate. Conversely, the bracts of subspecies lanceolata are longer (10-15 mm), extend beyond the calyces that they subtend, and broader. Even diminutive plants of subspecies lanceolata have bracts that are at least 10 mm long and exceed the calyces. Monardella breweri subsp. microcephala rarely has leaves that subtend the glomerules, and if it does they tend to be short. Conversely, subspecies breweri and subspecies lanceolata often have long leaves immediately subtending the glomerule that extend beyond it. Subspecies microcephala has five to six bracts per glomerule, whereas subspecies breweri and subspecies lanceolata generally have eight to 10 bracts per glomerule. Subspecies microcephala calyces are short (ca. 6-7 mm), but are only slightly shorter than subspecies breweri and lanceolata, whose calyces are ca. 6.5-7.5 mm. The low number of flowers per glomerule (three to 25) appears to be the major factor governing glomerule size and the main defining character for this taxon. As is expected with

subspecies, there is a large zone of introgression with numerous intermediate specimens between subspecies microcephala and lanceolata. Abrams (1912b) noted an abundance of specimens in southern California (specifically in central San Diego County) that demonstrate a clear gradient between subspecies microcephala and subspecies lanceolata.

Monardella douglasii Bentham, Labiat. Gen. Spec. 332. 1834. Madronella douglasii (Bentham) Greene, Leafl. Bot. Observ. Crit. 1: 168. 1906. TYPE: U.S.A. California: northern California, s.d., Douglas s.n. (holotype, K [digital image]; isotype, K [digital image]).

Distribution. Monardella douglasii occurs in the foothills of the coastal mountain ranges adjacent to and south of San Francisco Bay.

3. Monardella sinuata Elvin & A. C. Sanders, sp. nov. TYPE: U.S.A. California: Santa Barbara Co., Burton Mesa, W of Santa Lucia Canyon, N of Lakes Canyon, 15 May 2006, M. A. Elvin, L. Lum & L. Ballard 4904 (holotype, UCSB; isotypes, IRVC, JEPS, MO, RSA, UCR, US). Figure 10.

Haec species a *Monardella breweri* A. Gray foliis margine undulato et bracteis anguste ovatis scariosis vel viridibus differt.

Annual, erect, gracile, 8–65 cm tall, simple or sparsely to moderately branched, sparsely pubescent, stems straw to tan. Leaves 10–55 × 3–8 mm, in axillary clusters, linear to oblanceolate, ± fleshy, subglabrous to sparsely pubescent, margins weakly to strongly wavy. Inflorescence open compound cyme; glomerules 10–25 mm wide; bracts 7–12 × 3–9 mm, elliptic to narrowly ovate, tips obtuse to acute, but not attenuate, scarious to green, purple-tinged or not. Calyx lobes acute, densely pubescent, tube less pubescent than lobes; corolla 14–20 mm, upper 2 lobes gland-tipped, lavender to purple.

Etymology. The specific epithet refers to the sinuous leaf edges.

Related taxa. Monardella sinuata is an annual plant with undulate leaf margins that occurs along the central coast of California. It has long been mistakenly called M. undulata, but as noted above, the type specimen and description of M. undulata are of a perennial plant. The annual with undulate leaf margins has not been described to date, even though it is well known to California botanists.

The exact relationship of *Monardella sinuata* to other similar *Monardella* species is not obvious. Epling (1925) placed *M. undulata* in the annual

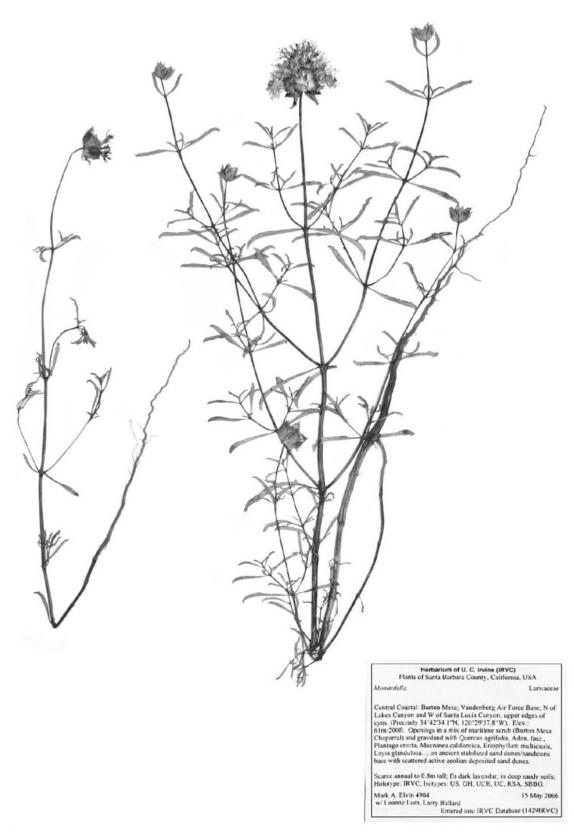


Figure 10. Monardella sinuata Elvin & A. C. Sanders subsp. sinuata (holotype, M. A. Elvin et al. 4904, UCSB). Image by David Pereksta.

section, Section II, Annuae, even though under his concept *M. undulata* included perennials and subshrubs as well. *Monardella sinuata* has clear affinities with the other undulate-leaved *Monardella*

taxa with which it has typically been associated. However, overall, it is more similar and appears to be more closely allied with *M. breweri*, *M. douglasii*, and other annual *Monardella* species, based on its leaf and

bract morphology, pubescence, stature (herbaceous stems), the presence of glands on the tips of the upper petals, and especially its annual habit. *Monardella sinuata* primarily differs from the other annual *Monardella* species in its possession of undulate leaf margins. Based on these characteristics, we are including it in the annual species alliance.

Paratypes. U.S.A. California: San Luis Obispo Co., B. Anderson 173 (OBI), A. Eastwood 14954 (CAS), C. Epling s.n. (IRVC 4605), A. P. Griffiths s.n. (OBI 58373), s.n. (OBI 58377), s.n. (OBI 58392, UCR 115289), s.n. (OBI 58393), s.n. (OBI 58394), s.n. (OBI 58395), C. B. Hardham 7047 (SBBG), 12070 (SBBG), G. K. Helmkamp 5676 (UCR), s.n. (UCR 13783), R. F. Hoover 7304 (CAS [2], DS, OBI [2]), 9033 (CAS, OBI), D. F. Howe 3568 (SD), M. P. Ingalls s.n. (CAS 25461), J. D. Jokerst 2902 (CHSC), D. Keil 16322 (OBI, SBBG), B. Miossi 141 (OBI), R. J. Rodin 6080 (OBI), F. Rush s.n. (OBI 13617), M. E. Schneider s.n. (OBI 26262), R. W. Summers 656 (CAS [2]), E. C. Twisselmann 2428 (CAS [2]); Santa Barbara Co., L. E. Allen s.n. (SBBG 45184), s.n. (SBBG 45719), E. R. Blakley 3487 (SBBG), D. E. Breedlove 4140 (CAS, DS), J. Broughton 1191 (SBBG), P. Burns 100 (UCSB), E. R. Chandler 3746 (OBI, SBBG), E. Collins 31 (UCSB), K. C. Danielsen 7 (UCSB), 55 (UCSB), L. W. Edge 189 (SBBG), s.n. (SBBG 53007), W. R. Ferren LP-107 (UCSB), LP-426a (UCSB), H. C. Forbes LP-122 (IRVC, UCSB), A. P. Griffiths s.n. (OBI 58369), J. R. Haller 1714 (UCSB), D. Hickson 16 (UCSB), R. Hoffmann s.n. (SBBG 6420), s.n. (SBBG 72003), D. F. Howe 3562 (SD), D. Keil 24596 (OBI), 25350 (OBI), H. L. Mason 408 (DS), H. E. McMinn 1041 (DS), M. Olson 225 (UCSB), B. Orr LP-92 (UCSB), H. M. Pollard s.n. (SBBG 41747), P. H. Raven 15513 (DS), L. Roundtree s.n. (CAS 299291), C. F. Smith 6286 (SBBG), 8018 (SBBG), 9957 (SBBG), A. Whistler 1A (UCR, UCSB); Ventura Co., N. French 311 (UC), D. Howe 4924 (SD); county not listed, St. Simeón, s.d., Gambel s.n. (GH), s.d., E. Palmer 362 (GH).

Monardella sinuata Elvin & A. C. Sanders subsp. sinuata.

Distribution and ecology. Monardella sinuata subsp. sinuata occurs in coastal areas from Morro Bay in San Luis Obispo County south to Surf in Santa Barbara County with historical collections in Ventura County, California; however, it has not been collected or reported from Ventura County since 1976, and there is little suitable habitat remaining where it formerly occurred (M. A. Elvin & R. Burgess, pers. obs.). Monardella sinuata is restricted to sandy soils in coastal strand, dune scrub, openings in sagebrush scrub, coastal chaparral, and coastal oak woodlands from sea level to approximately 300 m. It flowers from April through September. It is rather uncommon overall, but can be locally common.

There is an undated collection by Gambel (Gambel s.n., GH), with the label as "St. Simeón" (presumably San Simeon, San Luis Obispo County), that may be from north of the otherwise known range of subspecies

sinuata. This collection is intermediate between subspecies sinuata and another, more northerly, subspecies (described below) in bract characters. Some other subspecies sinuata plants from the Morro Bay area also tend toward some aspects of the northern subspecies in that they exhibit some darkening of the tips of the calyces, slightly darkened bract veins, and a more compact habit relative to the plants from Santa Barbara County. However, they still fit better within subspecies sinuata and we include them there.

3b. Monardella sinuata Elvin & A. C. Sanders subsp. nigrescens Elvin & A. C. Sanders, subsp. nov. TYPE: U.S.A. California: Marin Co., Point Reyes Peninsula, 12.5 mi. from Inverness, sandy knoll on crest of ridge, 18 May 1938, A. Carter 1417 (holotype, GH; isotypes, DS, RSA not seen, UCR). Figure 11.

Haec subspecies a *Monardella sinuata* Elvin & A. C. Sanders subsp. *sinuata* caule robusto fuscato et bracteis latioribus brevioribus apice nigrescentibus venis furvis differt.

Annual, erect, stout, 8–45 cm tall, branched throughout to simple, sparsely pubescent, stems dark. Leaves $10{\text -}30 \times 4{\text -}10$ mm, in axillary clusters, lanceolate to narrowly oblanceolate, \pm fleshy, margins weakly wavy. Inflorescence cyme or compact cyme; glomerules $10{\text -}35$ mm wide; bracts $9{\text -}16 \times 6{\text -}12$ mm, elliptic to ovate, obtuse to acute, but not attenuate, scarious to green, purple-tinged or not, tips dark (black), veins dark (black) and spreading hairy. Calyx pubescent, lobes dark-tipped and acute; corolla $14{\text -}20$ mm, upper 2 petals gland-tipped, lavender to purple.

Distribution, ecology, and phenology. Monardella sinuata subsp. nigrescens ranges from just south of Monterey Bay in Monterey County, north to Point Reyes in Marin County, California. It is restricted to sandy soils in dunes, dune scrub, and openings in coastal scrub with occurrences documented in Marin, San Francisco, Santa Cruz, Contra Costa, Santa Clara, San Mateo, and Monterey counties, California. It grows from sea level to approximately 300 m elevation and flowers from May through July. It is apparently very uncommon.

Etymology. The subspecific epithet refers to the black (dark) tips on the calyces and bracts and the dark bract veins.

Discussion. Monardella sinuata plants in the northern part of the species range differ from those in the southern portion, and are here recognized as a distinct subspecies. The bract tips and veins are noticeably dark brown to black. The glomerules are larger (10–35 mm vs. 10–25 mm wide for subsp.



Figure 11. Monardella sinuata subsp. nigrescens Elvin & A. C. Sanders (holotype, A. Carter 1417, GH).

sinuata) and the bracts are wider, shorter, and darker. The stems are stout, robust, and dark.

Paratypes. U.S.A. California: Marin Co., A. Eastwood 4773 (CAS, GH), 18858 (CAS), 5 May 1901, A. Eastwood s.n.

(GH), A. D. E. Elmer s.n. (CAS 25467, DS 64344), C. B. Hardham 10447 (CAS), A. A. Heller 15732 (DS), D. F. Howe 4251 (SD), s.n. (SD 88517), J. T. Howell 53725 (CAS), G. T. Robbins 3895 (CAS, OBI), G. B. Rosshach 778 (DS), C. B. Wolf 5776 (GH); Monterey Co., E. Cannon s.n. (CAS 25462), P. F. Covel 1478 (CAS, SBBG), L. E. Cox s.n. (DS 23588), W.

R. Dudley s.n. (DS 23587), A. Eastwood 6041 (CAS), A. D. E. Elmer 4379 (CAS), L. A. Greata 615 (DS), A. A. Heller 8426 (DS, GH), R. F. Hoover 9113 (CAS, OBI), J. Jokerst s.n. (CHSC 67992), V. Keresztury s.n. (CHSC 67993), E. A. Purer 3838 (SD), 3861 (SD), F. G. Woodcock s.n. (CAS 299262); San Francisco Co., A. Eastwood s.n. (CAS 25463), J. T. Howell 11431 (CAS, GH), W. N. Suksdorf 786 (GH); Santa Cruz Co., W. R. Dudley s.n. (DS 572519, DS 63417), R. S. Ferris 11138 (DS, GH), V. F. Hesse 981 (CAS), J. H. Thomas 6016 (DS, SD); s. loc., H. N. Bolander 69 (GH), Hartweg 1912 (GH).

4. Monardella venosa (Torrey) A. C. Sanders & Elvin, comb. et stat. nov. Basionym: Monardella candicans Bentham var. venosa Torrey, Pacific Railr. Rep. 4(5): 123. 1857. Monardella douglasii Bentham var. venosa (Torrey) Jepson, Fl. Calif. 3: 443. 1943. Monardella douglasii Bentham subsp. venosa (Torrey) Jokerst, Phytologia 72: 12. 1992. TYPE: U.S.A. California: Yuba Co., plains of the Feather River near Marysville, 25 May 1854, Bigelow s.n. (holotype, NY not seen; isotypes, GH not seen, US not seen).

Monardella douglasii Bentham var. parryi Jepson, Man. Fl. Pl. Calif. 884. 1925. TYPE: U.S.A. California: Butte Co., Chico, May 1882, C. C. Parry s.n. (holotype, UC 104634; isotype, UC 104635).

Discussion. Monardella venosa is recognized at the species level. Jepson (1943) first recognized the close relationship between M. douglasii and M. venosa by making M. venosa a variety within M. douglasii. Jokerst (1992) also recognized this close relationship and elevated M. venosa to the subspecific level. We now recognize M. venosa as a full species, but maintain that there is a close relationship between the two species.

Distribution and ecology. Monardella venosa occurs in the foothills of the western Sierra Nevada and southwestern Cascade mountain ranges in Butte, Mono, Tuolumne, and Yuba counties, California. It is morphologically distinct from M. douglasii in bract shape, size, and architecture; glomerule size; and stem stoutness and is therefore treated as a separate species. There are no collections that we have seen that express intermediate characters between M. venosa and either M. douglasii or M. candicans. It is biologically isolated from M. douglasii because the two species are separated by the floor of the San Joaquin—Sacramento Valley, a distance of more than 90 km with no suitable habitat.

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