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Authors: Elvin, Mark A., Kelley, Ronald B., and Drew, Bryan T.

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Vegetative and Trichome Morphology Distinguish the *Monardella ovata* Species Complex from the *Monardella odoratissima* Species Complex: Taxonomic Studies in *Monardella* (Lamiaceae) VII

Mark A. Elvin,[1,2,5] Ronald B. Kelley,[3] and Bryan T. Drew[4]

[1]University of California Los Angeles, UCLA Herbarium, Department of Ecology and Evolutionary Biology, Los Angeles, California 90095, USA; markaelvin@ucla.edu
[2]US Fish and Wildlife Service,* Ventura Fish and Wildlife Office, 2493 Portola Rd., Suite B, Ventura, California 93003, USA
[3]Eastern Oregon University, Department of Chemistry and Biochemistry, La Grande, Oregon 97850, USA; rkelley@eou.edu
[4]University of Nebraska Kearney, Department of Biology, Kearney, Nebraska 68849, USA; drewbt@unk.edu
[5]Author for correspondence

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Abstract—*Monardella* (Lamiaceae) is a taxonomically complex western North American genus ranging from the Pacific coast to the western slopes of the Rocky Mountains and from southern British Columbia in Canada to the Cape region of Baja California Sur in Mexico. We applied a combination of gross vegetative morphology, trichome morphology and abundance/distribution, and molecular data to clarify taxonomic discontinuities, specifically regarding the monophyly of plants formerly treated within *Monardella odoratissima*. The data suggest a clear distinction between the non-monophyletic *M. odoratissima* species complex and the *M. ovata* species complex, thus resolving taxonomic ambiguities within and between them. We formally recognize plants from southern Oregon, northern California, and western Nevada previously misapplied to *M. odoratissima* as belonging to the *M. ovata* species complex. We introduce the following taxonomic and nomenclatural revisions: describe *M. ovata* Greene subsp. *lenmaniae* as a novel subspecies; present *M. ovata* subsp. *pallida* at a new position and rank; recognize *M. modocensis, M. ovata*, and *M. rubella* as accepted taxa; designate lectotypes for *M. modocensis* and *M. rubella*; and designate *M. californica* and *M. tortifolia* as new synonyms under *M. ovata*.

Keywords—California, cryptic diversity, monophyly, Nevada, Oregon.

Monardella Benth. (Lamiaceae) is a taxonomically complex western North American genus that ranges from the Pacific coast to the Rocky Mountains and from southern British Colombia in Canada to the Cape Region of Baja California Sur in Mexico. Although *Monardella* occurs over a broad range in western North America, the genus has a clear center of distribution in California (Elvin and Sanders 2009; Sanders et al. 2012; Elvin et al. 2015, 2019; Jepson Flora Project 2021). While a consensus regarding the accepted number of species and taxa within *Monardella* (including the synonymous genus *Madronella* Greene) is lacking, the genus is currently comprised (depending on the reference) of approximately 50 species and 70 to 80 taxa (Epling 1925, 1951; Abrams 1951; Hitchcock et al. 1959; Peck 1961; Hitchcock and Cronquist 1973; Munz 1959, 1974; Jokerst 1992, 1993, 2002; Elvin and Sanders 2009; Sanders et al. 2012; Elvin et al. 2013, 2014, 2015, 2019; COL 2018; GBIF 2018; ITIS 2018; IPNI 2019; TPL 2019; Tropicos 2019; US Department of Agriculture, Natural Resource Conservation Service 2019; WCSPF 2019; Jepson Flora Project 2021).

While researching *Monardella* for the Oregon Flora Project, the Jepson Flora Project, and a comprehensive monograph of the genus, it has become clear that major diversity exists beyond what is currently recognized, and that taxonomic revisions are necessary to more accurately and consistently depict the taxonomic diversity that occurs within *Monardella* in Oregon, California, and elsewhere (Elvin et al. 2019). Most of our current research has been focused within and adjacent to Oregon, but because of the distributions of the taxa involved, this analysis has necessarily had to expand into areas of neighboring states, primarily Washington, Nevada, and California. Specifically, we needed to address the taxonomy of perennial *Monardella* plants primarily from the mountains of southern Oregon, northern and central-eastern California, and western Nevada, that are hereafter referred to as the *M. ovata* species complex (see Figs. 1, 2).

Uncovering phylogenetic diversity is critically important but often not straightforward (Baldwin 2019; Baleeiro et al. 2019). Unrecognized species diversity is often "hidden" within the guise of a species complex (Bickford et al. 2007; Baldwin 2019; Baleeiro et al. 2019). A species complex is generally defined as containing more than one species with close evolutionary relationships harboring limited morphological and/or genetic gaps. One such example exists within the California Floristic Province based *M. ovata* species complex. The *M. ovata* species complex is a morphologically similar but taxonomically problematic assemblage with unrecognized diversity. It was previously composed (in part) of two currently recognized taxa: *M. odoratissima* Benth. subsp. *pallida* (A.Heller) Epling and *M. odoratissima* Benth. subsp. *glauca* (Greene) Epling. However, we argue the species complex is best represented by five taxa: *M. modocensis* Greene, three subspecies of *M. ovata* Greene, and *M. rubella* Greene.

During the previous two centuries, many *Monardella* specimens throughout western North America (both within and outside of California) have been labeled as or called *M. odoratissima* Benth., presumably because they all had a similar general habit and gestalt (Gray 1876, 1878; Coulter 1885; Epling 1925, 1951; Jepson 1925, 1943; Peck 1941, 1961; Abrams 1951; Davis 1952; Harrington 1954; Hitchcock et al. 1959; Munz 1959; St. John 1963; Martin and Hutchins 1981; US Department of Agriculture, Soil Conservation Service 1982; Cronquist et al. 1984; Welsh et al. 1987; Albee et al. 1988; Kartesz 1988; Jokerst 1993; Sanders et al. 2012; Elvin and Sanders 2009; Drew et al. 2018; CPNWH 2019; IMRHN 2019; NANSH 2019; SEINet 2019). However, with a more in-depth analysis and using additional

FIG. 1. Estimated distributions of recognized taxa within the *Monardella ovata* Greene species complex based on georeferenced specimen collections, ecological and geological data, and fieldwork: 1. *Monardella ovata* (dashed boundary): 1A. *Monardella ovata* subsp. *ovata* (blue). 1B. *Monardella ovata* subsp. *lenmaniae* Elvin, R.B.Kelley, & B.T.Drew (orange). 1C. *Monardella ovata* subsp. *pallida* (A.Heller) Elvin, R.B.Kelley, & B.T.Drew (green). 2. *Monardella modocensis* Greene (yellow). 3. *Monardella rubella* Greene (red). Taxon boundaries developed by Mark A. Elvin and Bryan T. Drew and map compiled and produced by Sarah Friedrich.

characters (e.g. gross morphology, trichome morphology and indument, molecular data), it becomes evident that the specimens referred to as *M. odoratissima* outside of Washington should not be treated as *M. odoratissima*, even in a broad sense. *Monardella odoratissima* (in the historical broad sense) is not monophyletic, requiring novel or other available names to be applied to those *Monardella* taxa in the areas where the name *M. odoratissima* has been misapplied.

Historically, the *M. ovata* species complex, as defined here, has been subsumed within the *M. odoratissima* species

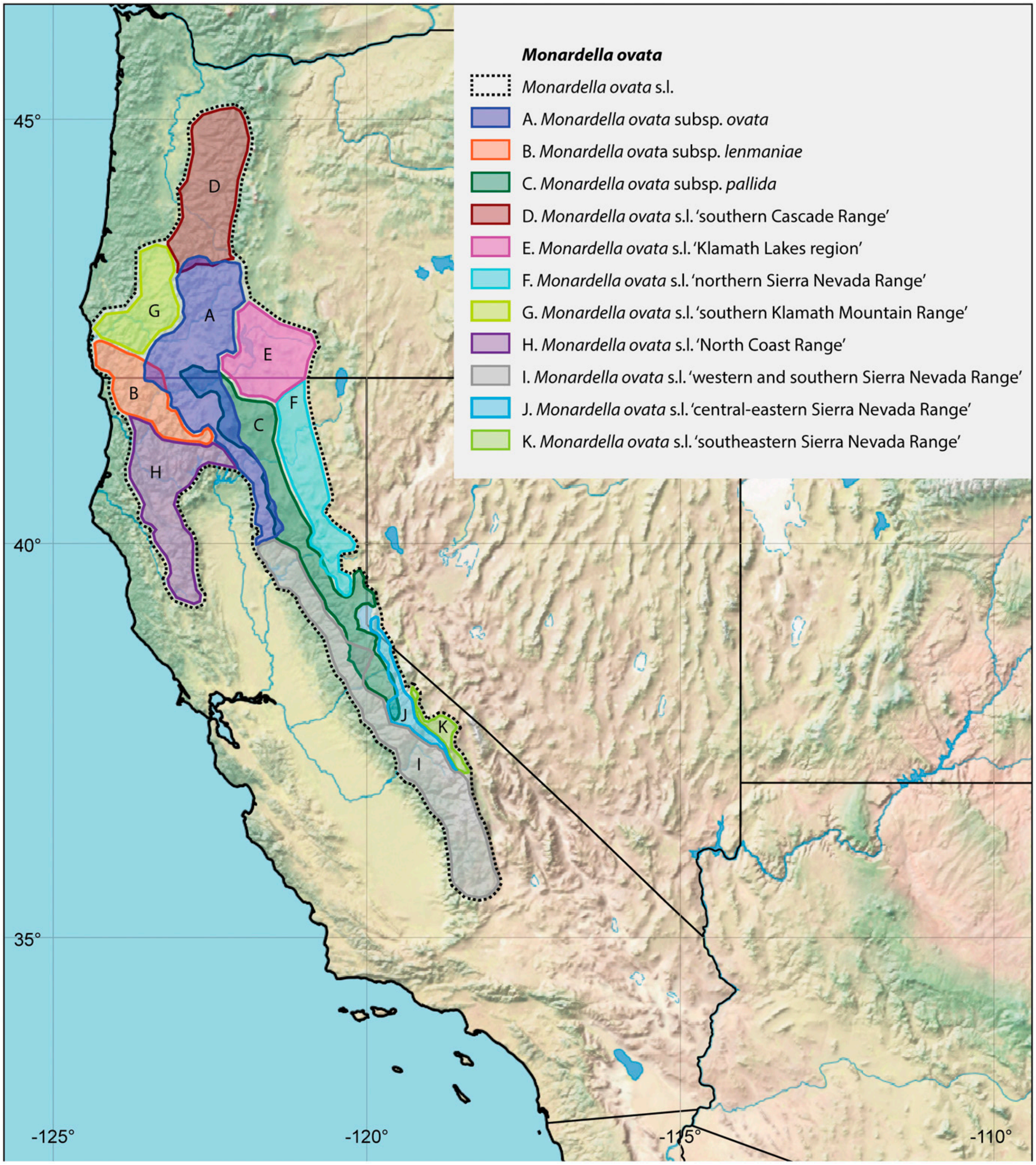

FIG. 2. Estimated distributions of recognized taxa and 'morphotypes' within *Monardella ovata* Greene based on georeferenced specimen collections, ecological and geological data, and fieldwork: *Monardella ovata* (dashed boundary): A. *Monardella ovata* subsp. *ovata* (blue). B. *Monardella ovata* subsp. *lenmaniae* Elvin, R.B.Kelley, & B.T.Drew (orange). C. *Monardella ovata* subsp. *pallida* (A.Heller) Elvin, R.B.Kelley, & B.T.Drew (green). D. *Monardella ovata* 'southern Cascade Range' (maroon). E. *Monardella ovata* 'Klamath Lakes region' (fuchsia). F. *Monardella ovata* 'northern Sierra Nevada Range' (aqua). G. *Monardella ovata* 'southern Klamath Mountain Range' (lime). H. *Monardella ovata* 'North Coast Range' (mauve). I. *Monardella ovata* 'western and southern Sierra Nevada Range' (grey). J. *Monardella ovata* 'central-eastern Sierra Nevada Range' (light blue). K. *Monardella ovata* 'southeastern Sierra Nevada Range' (yellow-green). Taxon boundaries developed by Mark A. Elvin and Bryan T. Drew and map compiled and produced by Sarah Friedrich.

complex (Gray 1876, 1878; Coulter 1885; Epling 1925; Jepson 1925, 1943; Peck 1941, 1961; Abrams 1951; Munz 1959, 1974; Kartesz 1988; Jokerst 1993; Sanders et al. 2012), ostensibly for convenience, but also because of a lack of in-depth analysis due to a insufficient diversity of specimens, and time and/or technological constraints. In this manuscript, we address and describe the taxonomy of the *Monardella ovata* species complex, differentiate it from the *M. odoratissima* species complex, present one novelty, one nomenclatural change in position, recognize several previously published names as accepted, and recognize two specific names as synonyms under *M. ovata* to facilitate a more precise and cohesive treatment of the genus *Monardella*.

Materials and Methods

Taxon Sampling and Phylogenetic Analyses—To establish that taxa within the *Monardella odoratissima* species complex are not monophyletic, we analyzed a dataset containing 14 samples (13 taxa). Within this dataset, 11 samples (10 taxa) were from *Monardella* while three other genera, *Acanthomintha* (A.Gray) A.Gray, *Pogogyne* Benth., and *Pycnanthemum* Michx. were used as an outgroup based on Silveira and Simpson (2013) and Drew et al. (2017). *Pycnanthemum* served to root the tree based on Drew et al. (2017).

We extracted DNA from silica-dried leaves using the DNeasy Plant Mini Kit (Qiagen, Valencia, California, USA). Our alignment contained 123 low copy nuclear loci that were obtained using the Anchored Hybrid Enrichment method of Lemmon et al. (2012). The Florida State University Center for Anchored Phylogenomics (www.anchoredphylogeny.com) performed library preparation, enrichment, assembly, and alignment of all loci (see Kriebel et al. [2019] for a detailed description of procedure). The final alignment contained 294,507 nucleotides. The raw sequence reads are available at the NCBI Sequence Read Archive (BioProject PRJNA809707).

For phylogenetic analyses, we conducted a maximum likelihood (ML) analysis using RAxML v. 8.2.12 (Stamatakis 2014) and Bayesian inference (BI) using MrBayes v. 3.2.7 (Ronquist et al. 2012) as implemented on the CIPRES cluster (Miller et al. 2010). For both ML and BI analyses, we used the GTR + G + I model of evolution and otherwise used default settings (other than "temp" settings, see below). For our ML analysis we conducted 100 bootstrap (BS) replicates. Our BI analyses consisted of five million generations. Chain convergence was assessed by checking that the standard deviation of split frequencies (SDSF) fell below 0.01 and the Potential Scale Reduction Factor (PSRF) approached 1.00. Due to the large size of the data matrix and large number of ambiguous sites, the SDSF did not remain below 0.01 in our MrBayes analyses. However, we ran three separate analyses using temp settings of 0.2, 0.15, and 0.1, and all three analyses recovered topologies identical to the ML analysis. We discarded the first 50% of the trees as burn-in and used the "All Compatible Groups" option to assemble the remaining trees and apply posterior probability (PP) values.

Taxonomic Determinations—We acquired data from thousands of herbarium specimens, digital images of specimens, live specimens (in situ and ex situ), databases, fieldwork, and from presentations and manuscripts. We used standard techniques to acquire gross morphological data by examining herbarium specimens, information in previous publications, and by using light microscopy (LM). We used LM and scanning electron microscopy (SEM) to assess trichome morphology and abundance/distribution. For the LM studies, we used a dissecting microscope at magnifications from 10–64×, measurements were taken with a micrometer at either 10 × or 50×. We searched the works of previous researchers for karyologic data. We then compared the morphological data to molecular data (Fig. 3; Drew et al. 2018; Hays et al. 2019). We also incorporated information from associated disciplines regarding geological, ecological, and biogeographical data to gain a holistic understanding of the edaphic conditions and environmental factors that may be contributing to selective pressures that influence our perceptions of diversity in *Monardella*.

Trichome Nomenclature—Numerous researchers have determined that the morphology of trichomes have taxonomic and systematic value and present a robust method to distinguish between taxa, mostly at the specific and subspecific ranks (Sanders 1987; Cantino 1990; Peirson et al. 2006; Menezes de Sequeira et al. 2008; El Beyrouthy et al. 2009; Moon et al. 2009, 2010; Celep et al. 2011; Osman 2012). Plant trichomes and pubescence have been used and considered to be valuable to delineate taxonomic entities for more than 100 yr. Trichome morphology and abundance/distribution (indument) has phylogenetic value in *Monardella* (Elvin et al. 2013, 2014, 2015, 2019). However, while trichomes are still widely used to delineate taxa, there is not a single or primary system of nomenclature to classify or describe the variety and complexity of trichomes.

We use trichome terminology that follows Carlquist (1961) and Uphof (1962) for basic morphology and Roe (1971) and Prabhakar and Leelavathi (1989) for nomenclatural systems. The 'series' distinguishes between different types of trichomes based on the number of cells that comprise their width, i.e. uniseriate (one cell wide; US) or multiseriate (two or more cells wide; MS). The 'type' distinguishes between different types of trichomes based on a trichome's total number of cells, i.e. unicellular (one cell; UC), bicellular (two cells; BC), multicellular (two or more cells; MC). We join the respective abbreviations together to identify the type of trichome that occurs on a particular structure (e.g. stem, leaf, calyx) within a given taxon, e.g. USMC for a uniseriate multicellular trichome, UC for a unicellular trichome (Fig. 4). All MSMC trichomes found so far in *Monardella* are capitate and have a glandular multicellular head and a multiseriate multicellular base. The MSMC capitate trichomes can be either sunken, sessile, subsessile (somewhat, not completely sessile), or stalked. Sunken MSMC capitate trichomes are imbedded into the structure, in our case the leaf, and have a very short multiseriate multicellular base (Fig. 4A). Sessile MSMC capitate trichomes have a very short multiseriate multicellular base/stalk that is roughly equal to the leaf surface (Fig. 4B). Subsessile MSMC capitate trichomes have a short multiseriate multicellular base/stalk that is 0.02–0.04 mm tall (Fig. 4C). Stalked MSMC capitate trichomes have a multiseriate multicellular stalk/base that is ≥ 0.06 mm tall (Fig. 4D). For trichome abundance/distribution we used a standard scale with the following categories: abundant, common, frequent, occasional, rare, very rare, not present. Given the importance of trichomes in Lamiaceae, and *Monardella* specifically, a more detailed microscopic analysis of trichome morphology for the entire genus is warranted.

Results and Discussion

Phylogenetic Results—*Monardella* was recovered as monophyletic in both ML and BI analyses (Fig. 3; BS = 100; PP = 1.00). The two representatives of the *Monardella odoratissima* species complex, a specimen of "*M. odoratissima*" from Ouray County, Colorado and *M. ovata* Greene subsp. *pallida* (A.Heller) Elvin, R.B.Kelley, and B.T.Drew, [=*M. odoratissima* subsp. *pallida* (in part)], see below) from Nevada County, California were not monophyletic (Fig. 3). The *M. ovata* subsp. *pallida* accession was in a well-supported clade (BS = 100; PP =1.00) with several other *Monardella* taxa that are not associated with the *Monardella odoratissima* species complex. Appendix 1 contains information for all samples included in analyses for this study.

Taxonomy—Morphologically, the *Monardella ovata* species complex forms a cohesive group of taxa with relatively large leaves (average 20 × 6 mm for the genus), distinct petioles, short hairs (generally ≤ 0.2 mm), a sparse pubescence on the stems and leaves, and large bracts (≥ 10 × 5 mm) (Table 1). The species complex occurs from the Cascade and Klamath Ranges of Oregon south into the North Coast Range of California, southeast to the central Sierra Nevada Range, and eastward in scattered mountain ranges of the Great Basin Desert in California, Oregon, and Nevada including the Modoc Plateau and its associated mountain ranges such as the Warner Mountains (Fig. 1). It should be noted that at least a portion of the distributions of several additional perennial *Monardella* taxa occur within the distribution of the *M. ovata* species complex but are morphologically and/or genetically distinct from it, specifically: *M. beneolens* Shevock, Ertter, and Jokerst; *M. follettii* (Jeps.) Jokerst; *M. linoides* A.Gray subsp. *anemonoides* (Greene) Elvin and A.C.Sanders; *M. linoides* A. Gray subsp. *sierrae* Elvin and A.C.Sanders; *M. purpurea* Howell subsp. *purpurea*; *M. reflexa* Howell; *M. sheltonii* Torr. ex Durand; *M. siskiyouensis* Hardham; *M. stebbinsii* Hardham and Bartel; and *M. villosa* Benth. subsp. *subserrata* (Greene)

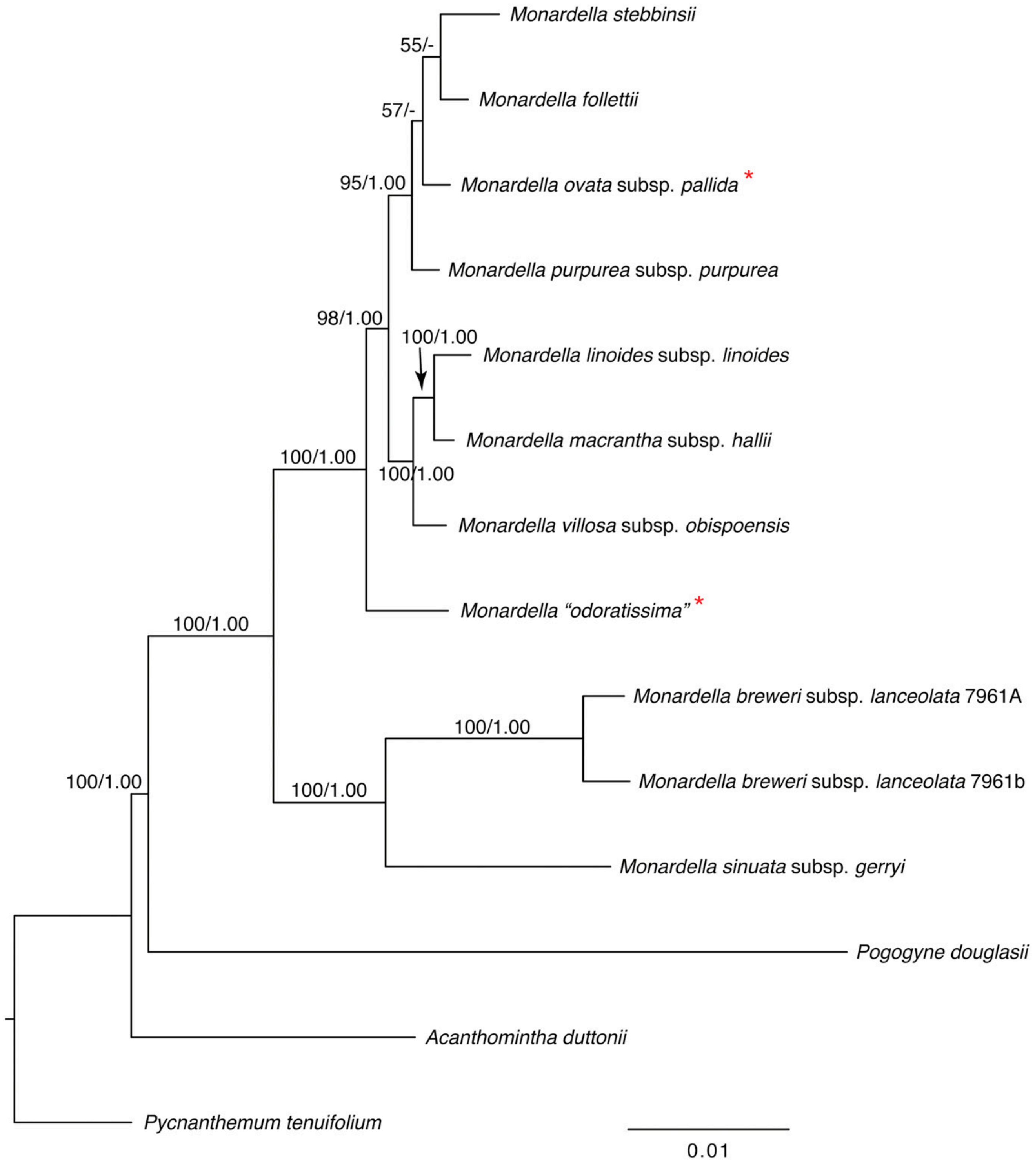

FIG. 3. Maximum likelihood tree with ML bootstrap and posterior probability (> 0.70) values indicated on branches. Asterisks indicate taxa that are part of the *Monardella odoratissima* species complex s.l. (in the historical sense). The *Monardella* "*odoratissima*"* accession is from Ouray County, Colorado, and has previously been named *Madronella oblongifolia* Rydb. The taxonomy of this entity will be addressed in a future publication. The *Monardella ovata* subsp. *pallida** collection is from Nevada County, California and has previously been recognized as *M. odoratissima* subsp. *pallida*.

Epling (=*M. villosa* subsp. *villosa*, misapplied). Some putative introgressant specimens have been collected between *M. linoides* subsp. *sierrae* and both *M. ovata* and *M. rubella*, as well as between *M. ovata* and both *M. linoides* subsp. *anemonoides* and *M. purpurea* subsp. *purpurea*.

The *M. odoratissima* species complex s.s. (including *M. odoratissima* and *M. nervosa*), forms a cohesive group of taxa with small leaves (generally ≤ 20 × 6 mm; with the exception of *M. odoratissima* Benth. subsp. *discolor* (Greene) Epling and *M. nervosa* Greene) that are sessile or have indistinct petioles, longer trichomes on the stems and bracts (generally ≥ 0.3 mm), a moderate to dense pubescence on the stems and leaves, and small bracts (≤ 10 × 5 mm). The *M. odoratissima* species complex s.s. only occurs in central and northeastern

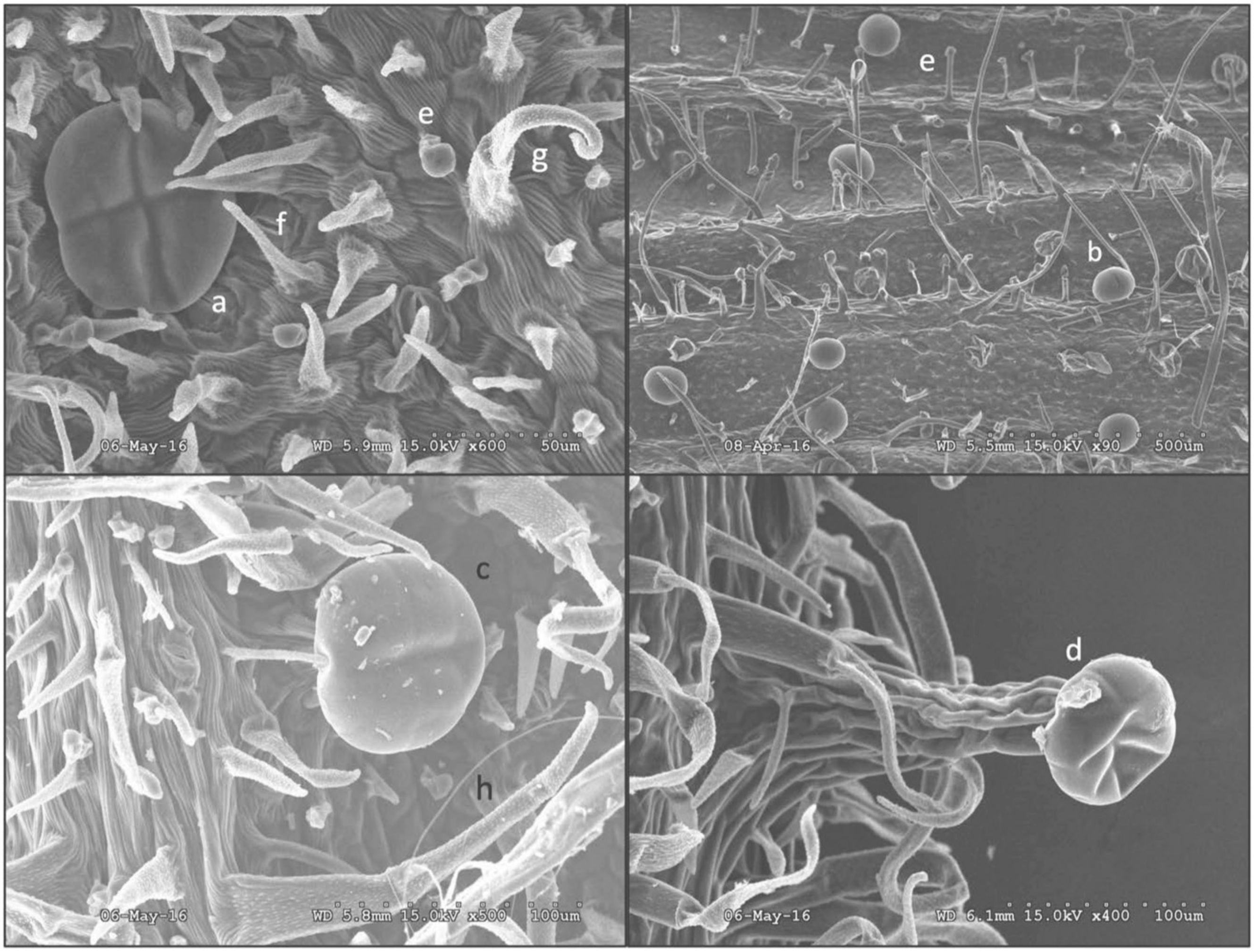

FIG. 4. Basic trichome types in *Monardella*. A. Multiseriate multicellular (MSMC) sunken. B. MSMC sessile. C. MSMC subsessile. D. MSMC stalked. E. Uniseriate (US) capitate. F. Unicellular (UC). G. Uniseriate bicellular (USBC). H. Uniseriate multicellular (USMC). Bottom left image: after Elvin et al. (2019). Images taken by Mark A. Elvin with assistance from Sherwin Carlquist.

Washington, adjacent southern British Columbia, and along the southern banks of the Columbia River in central northern Oregon. Molecular data (i.e. nrDNA, cpDNA, NGS) also support the assertion that *M. odoratissima* s.l. (as previously recognized) is not monophyletic (Fig. 3) and that *M. odoratissima* s.s. (i.e. plants from Washington and the immediate vicinity) is not the closest relative of taxa within the *M. ovata* species complex (Liu et al. 2016; Drew et al. 2018). Therefore, *M. odoratissima* does not occur in the California Floristic Province or anywhere else within the range of *Monardella* outside of Washington and its immediate vicinity (e.g. Idaho, Nevada, Oregon) and the name *M. odoratissima* has been misapplied to various species in these regions since the mid-1800s (Gray 1876, 1878; Coulter 1885; Epling 1925; Jepson 1925, 1943; Peck 1941, 1961; Abrams 1951; Munz 1959, 1974; Kartesz 1988; Jokerst 1993; Sanders et al. 2012).

Plants in the *M. ovata* species complex are neither consistent with the type of *M. odoratissima* (1826, *Douglas s.n.*; K [barcode] 000248489!) nor with any of the associated taxa in the *M. odoratissima* species complex s.s. (e.g. *M. odoratissima* subsp. *odoratissima*, *M. odoratissima* subsp. *discolor*, *M. nervosa*). To help remedy this, we offer the combinations below.

TAXONOMIC TREATMENT OF THE MONARDELLA OVATA GREENE SPECIES COMPLEX

1. MONARDELLA OVATA Greene, Pittonia 5: 82. 1902. *Madronella ovata* (Greene) Greene, Leafl. Bot. Observ. Crit. 1: 169. 1906. *Monardella odoratissima* Benth. var. *ovata* (Greene) Jeps., Man. Fl. Pl. Calif. 882. 1925. TYPE: USA. California. Siskiyou Co., "…from near Sisson, California," June 1897, *H. E. Brown 381* (holotype, US-299244!; isotypes, CAS-26176!, DS-129363!, MO-114272!, NY [barcode] 00429345!, P [barcode] 00737805). Table 1. Figures 5, 6.

Monardella californica Gand., Bull. Soc. Bot. France, lxv. 67, in clavi. 1918, syn. nov. TYPE: USA. California. [Nevada Co.], Mount Lola, *P. B. Kennedy 173* (holotype, LY [barcode] 0018958 [digital image!]).

Monardella tortifolia Gand., Bull. Soc. Bot. France, lxv. 67, in clavi. 1918, syn. nov. TYPE: USA. Oregon. Klamath Co., eastern Cascade Mountains, 30 June 1902, *W. C. Cusick 2846* (holotype, LY [barcode] 0018956 [digital image!]; isotypes, ORE-78314!, VT-s.n.!).

Distribution and Ecology—*Monardella ovata* s.l. (including all of its subspecies and 'morphotypes') has a north-south distribution from the southern Cascade Range in central western

TABLE 1. Comparison of characters between taxa in the *Monardella ovata* species complex taxa and *Monardella odoratissima* subsp. *odoratissima*.

Monardella Taxa / Characters (mm unless otherwise noted)	*M. ovata* subsp. *ovata*	*M. ovata* subsp. *pallida*	*M. ovata* subsp. *lenmaniae*	*M. modocensis*	*M. rubella*	*M. odoratissima* subsp. *odoratissima*
Stem length (cm)	20–28	25–35	20–30	16–21	20–25	25–40
Internode length	30–53	30–45	30–53	35–45	24–45	7–20
Stem pubescence density	Moderate–dense	Moderate–dense	Sparse	Sparse–moderate	Sparse–moderate	Dense
Stem trichomes: MSMC capitate	Subsessile	Stalked	None	Stalked	Stalked and subsessile	Subsessile
Stem trichome type: longest US	0.1–0.2	0.1–0.2	0.3–0.6	0.1–0.2	0.1–0.2	0.3–0.4
Leaf length	28–36	30–40	18–43	16–25	25–30	10–19
Leaf width	6.5–11.5	8–12	7.5–13	4.8–8.5	6–7.5	3–4.5
Petiole length	3–8	5–11	1.5–8	1.5–3.5	3–4.5	0–1
Leaf pubescence density: adaxial	Sparse–moderate	Subglabrous–sparse	Sparse	Dense	Sparse–moderate	Dense
Bract length	13–15	6.5–7	10.5–15.5	6.2–12	12–15	8–11
Bract width	3.5–6.5	3.5–4.5	6.5–9	6–9.2	5.5–9	3–6
Bract trichomes: adaxial: longest US	~0.2	0.3–0.6	0.1–0.2	0.2–0.4	0.1–0.2	0.6–1.0
Calyx length	7–8	5.5–6.5	7.5–9.5	8–9.5	8–10	7–8
Calyx trichome type: MSMC capitate	None	Stalked and sessile	Stalked and sessile	Stalked	Subsessile	None
Calyx trichome type: longest US	0.3–0.6	0.2–0.4	0.2–0.4	0.2–0.4	0.3–0.6	0.1–0.2
Calyx teeth pubescence density	Moderate–dense	Dense–very dense	Dense–very dense	Moderate	Moderate	Moderate–dense

Oregon to the southern Sierra Nevada Range in central eastern California. It also occurs within the Klamath Range (including the Siskiyou Mountains) of southwestern Oregon and northeastern California and the North Coast Range of northwestern California (Fig. 1). In addition, a few specimens that fit within the circumscription of *M. ovata* s.l. were collected from the Modoc Plateau region of northeastern California and central southern Oregon. The area within the geographical boundaries of *M. ovata* s.l. (Figs. 1, 2) has considerable ecological and geological diversity. *Monardella ovata* s.l. is associated with multiple vegetation, soil, and ecological habitat types, but it commonly occurs in lithosolic openings of montane and coniferous forests where it tends to occur in mesic microsites of an overall xeric niche, such as in the cracks of boulders and interstitial spaces of rocky outcrops. It generally occurs in the middle to upper elevations within its geographic distribution.

Notes—*Monardella odoratissima* does not occur within either the California or Great Basin Floristic Province, and by extension does not occur in California or in Nevada, Oregon, Idaho, or Utah (Drew et al. 2018; Elvin et al. 2019). *Monardella odoratissima* is nearly restricted to Washington. Most of the specimens from California (and adjacent western Oregon and western Nevada) that were historically labeled as *M. odoratissima* (Jepson 1925, 1943; Munz 1959, 1974; Kartesz 1988; Jokerst 1993; Elvin and Sanders 2009; Sanders et al. 2012; CCH 2019) form a cohesive group that is neither consistent with the type of *M. odoratissima* nor any of its associated species or subspecies (e.g. *M. odoratissima* subsp. *discolor*, *M. nervosa*). *Monardella ovata* is the oldest name at the specific rank available (Greene 1901) that matches the set of characters and fits within the circumscription of these specimens.

Monardella ovata s.l. has a surprisingly similar general habit and appearance throughout its range and is perhaps the "quintessential" perennial *Monardella*. It has a single glomerule per main stem of moderate size (generally 13–24 mm wide). The bracts range from lanceolate to ovate, are of moderate size, sparsely to moderately (occasionally ± densely) pubescent, and usually pale to dark purple, although occasionally green(ish). The leaves are generally large (18–40(–49) × 6.5–13 mm), have distinct petioles 1–8 mm long, and are sparsely to moderately pubescent. The stems are generally 20–30 cm long (well within the standard range of 10–45 cm for the genus) and have a sparse to ± dense pubescence with trichomes generally shorter than 0.25 mm, but rarely with trichomes 0.3–0.6 mm.

Even though plants within *M. ovata* have a similar habit and gestalt, they still contain a considerable amount of diversity; this diversity is especially apparent among some of the smaller, less conspicuous characters (Table 1). *Monardella ovata* presents a good example of the cryptic diversity that occurs throughout the genus. Taxonomic diversity within *M. ovata* is either currently recognized (e.g. *M. ovata* subsp. *pallida* [=*M. odoratissima* subsp. *pallida* (in part)], see below), has been previously, but is not currently recognized (e.g. *M. ovata*), has been published but never received general acceptance (e.g. *M. tortifolia* Gand., *M. californica* Gand.), or has neither been recognized or published.

The diversity within *M. ovata* appears to be mostly allopatric and corresponds with disparate and specific floristic ecoregions. Several of the various forms within *M. ovata* have discrete differences and contain a punctuated gradient separating them from other *M. ovata* forms; hence, we are opting to recognize those at the subspecific level. However, other *M. ovata* forms are often distinct but seem to be less morphologically diagnosable and differ from each other incrementally as opposed to having discrete character delimitations. We choose not to name these 'morphotypes' at the subspecific level at this time for two main reasons: first, there are numerous intermediate specimens between them, and second, the morphotypes don't appear to have sufficiently developed reproductive isolating mechanisms. While some characters within these *M. ovata* morphotypes tend to intergrade and have intermediate character states (e.g. leaf length, leaf

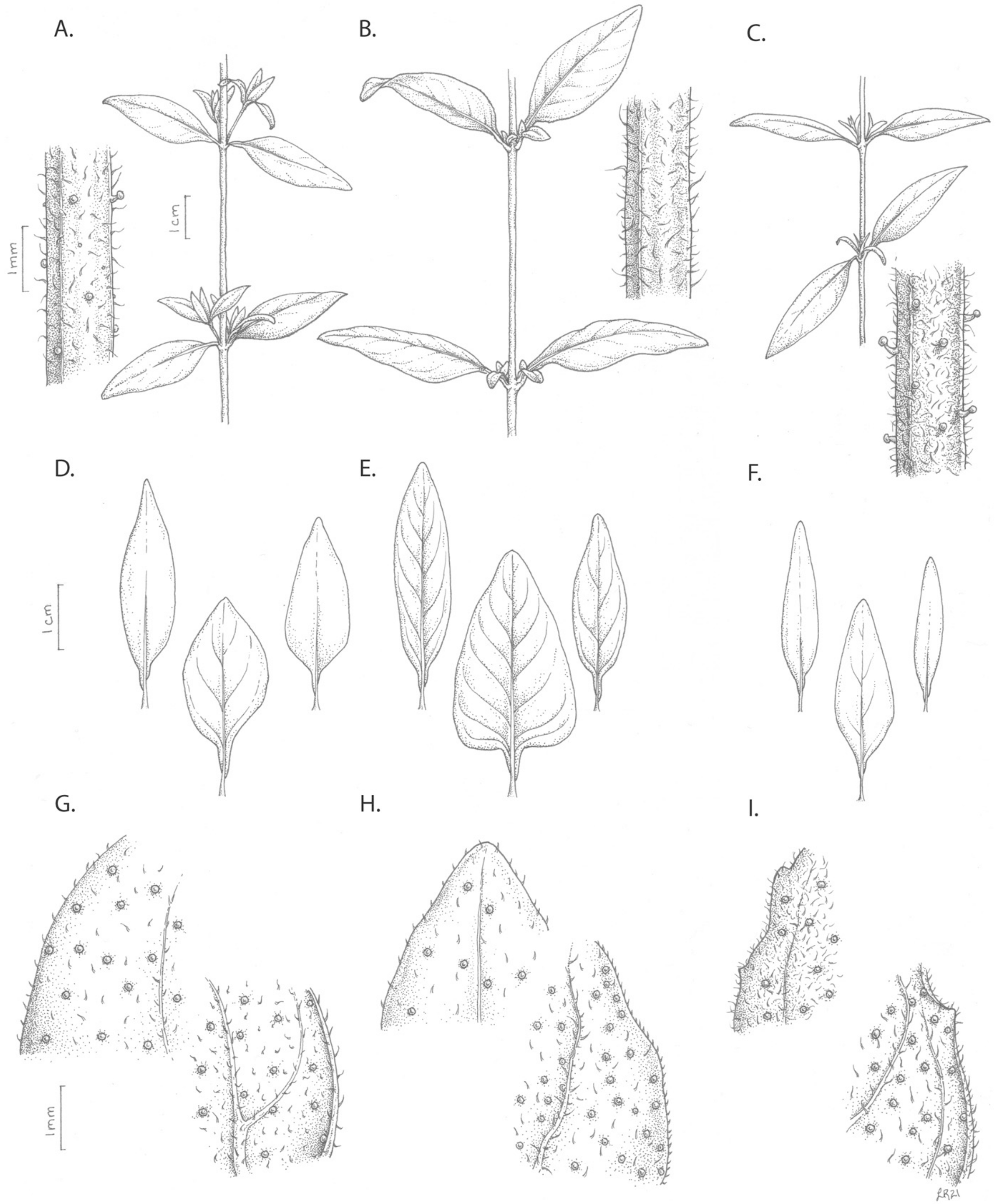

FIG. 5. Comparison of stem and leaf characters between *M. ovata* Green subsp. *ovata* (left), *M. ovata* subsp. *lenmaniae* Elvin, R.B.Kelley, and B.T.Drew (center), and *M. ovata* subsp. *pallida* (A.Heller) Elvin, R.B.Kelley, and B.T.Drew (right). Top (A–C): Stem internodes and stem pubescence/trichomes (inset). Middle (D–F): Leaf variation (three) including petioles. Bottom (G–I): Leaf pubescence/trichomes (left: adaxial face; right: abaxial face). A–B drawn from *M. A. Elvin 8067 and B. T. Drew* (LA); C from *M. A. Elvin 8630B and B. T. Drew* (LA); D–E from *M. A. Elvin 8067 and B. T. Drew* (LA); F–J from *M. A. Elvin 8351 and B. T. Drew* (LA); K–O from *M. A. Elvin 8091A and B. T. Drew* (LA). All figures drawn by Lesley Randall.

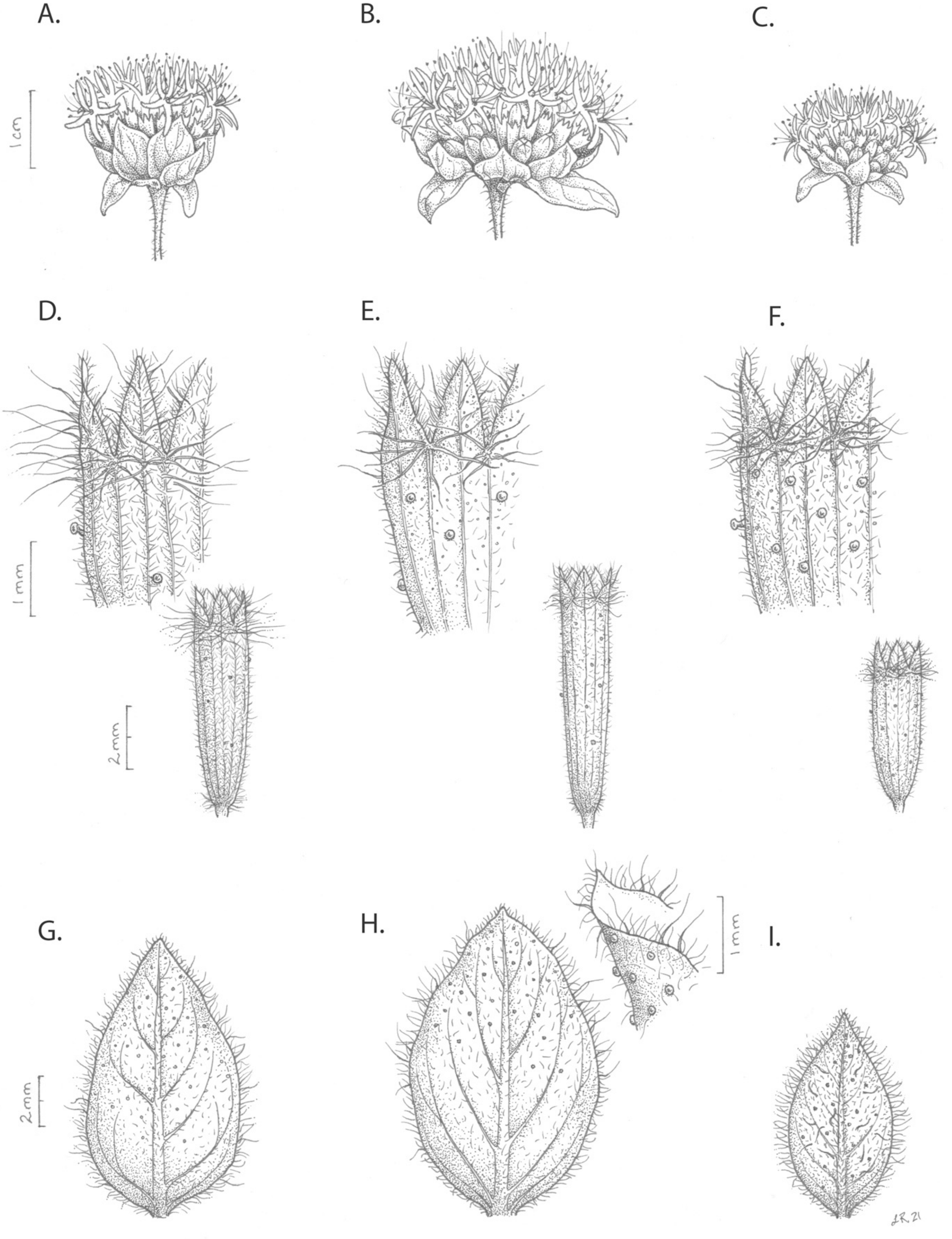

FIG. 6. Comparison of inflorescence and floral characters between *M. ovata* Green subsp. *ovata* (left), *M. ovata* subsp. *lenmaniae* Elvin, R.B.Kelley, and B.T.Drew (center), and *M. ovata* subsp. *pallida* (A.Heller) Elvin, R.B.Kelley, and B.T.Drew (right). Top (A–C): Glomerule. Middle (D–F): Calyx and calyx pubescence/trichomes (inset). Bottom (G–I): Abaxial face of glomerule bract (with an inset for *M. ovata* subsp. *lenmaniae* bract pubescence/trichomes). A drawn from *M. A. Elvin 8067 and B. T. Drew* (LA); B–C from *M. A. Elvin 8067 and B. T. Drew* (LA); D from *M. A. Elvin 8630B and B. T. Drew* (LA); E–G from *M. A. Elvin 8325C and B. T. Drew* (LA); H–I from *M. A. Elvin 8351 and B. T. Drew* (LA); J from *M. A. Elvin 8627A and B. T. Drew* (LA); K–M from *M. A. Elvin 8094 and B. T. Drew* (LA). All figures drawn by Lesley Randall.

width), other characters are more distinct between them (e.g. trichome types on the stems, leaves, bracts, and calyces). Characters frequently used for other genera (e.g. corolla color) can vary within each morphotype and are often not useful for taxonomic delimitation in *Monardella*. For example, although rare, the corolla color of *M. ovata* can vary from nearly white to deep lavender within a single population.

Monardella ovata s.l. contains several morphotypes that do not fit within the circumscription of the recognized subspecies discussed below, but still fit within the broad circumscription of *M. ovata*. Each of the following regions contain unrecognized diversity and the plants contain fairly consistent character states, but they are each perhaps not distinct enough to be recognized as named taxa. The morphotypes occur in the following distinct regions: A) southern Cascade Range, of central western Oregon (e.g. *H. L. Chambers 8372* [OSC!], *B. Powne 192* [OSC!]); B) Klamath Lakes region, of the southern Cascade and the eastern Klamath Range (e.g. *M. tortifolia*, *W. C. Cusick 2846* [LY [digital image!], ORE!, VT!]); C) northern Sierra Nevada Range, north of Mount Lola (e.g. *M. californica*, *P. B. Kennedy 173* [LY [digital image!]], *M. A. Elvin 8131 and B. T. Drew* [LA!]); D) southern Klamath Range, of southwestern Oregon (e.g. *L. Leach 2356* [ORE!], *J. Rasey 19* [ORE!]; E) North Coast Range, of northwestern California from near Yolla Bolly and the Trinity Alps (e.g. *L. Kellogg 89* [WTU!], *M. Strull 21* [UCR!]); F) western and southern Sierra Nevada Range, that generally have medium sized, moderately colorful bracts (e.g. *J. D. Jokerst 3016B* [CHSC!], *J. R. Shevock 2240* [CAS!], *I. L. Wiggins 6887* [WS!]); G) central-eastern Sierra Nevada Range, in the higher elevations that generally have small colorful bracts (e.g. *M. A. Elvin 9853 and J. M. André* [LA!], *9850* [LA!], *C. W. Sharsmith 3710* [WS!]); and H) southeastern Sierra Nevada Range, in the lower elevations that generally have medium sized colorful bracts (e.g. *M. A. Elvin 9851 and J. M. André* [LA!], *M. A. Elvin 9856* [LA!]; 12 July 1935, *C. C. Epling s.n. and W. Robison* [LA-62597!]) (see Fig. 2 for approximate distributions of these morphotypes). Plants within each of the aforementioned regions are more consistent morphologically with each other than with plants in morphotypes from other regions or from *M. ovata* subsp. *ovata*. *Monardella ovata* s.l. plants within each of these regions have slight (and consistent) differences from *M. ovata* subsp. *ovata* but tend to intergrade more from one morphotype to another than would be expected from a species or subspecies. While the plants in each of these regions are fairly distinct and each may warrant recognition as a subtaxon of *M. ovata*, we are not separating them out as distinct taxa at this time because we cannot confidently verify that each of these morphotypes fits all of the categories that we used to determine whether an entity is worthy of distinct taxonomic recognition. Specifically, we consider a taxon worthy of formal recognition if it: 1) possesses a unique set of characters that differentiate it from other taxa and intermediate, introgressant, or hybrid individuals between them are absent or uncommon; 2) typically occurs within a distinct ecological niche or edaphic condition; 3) has a distinct geographic range relative to other *Monardella* taxa; and 4) is generally reproductively isolated. In some cases, there are a limited number of intermediate, introgressant, or hybrid individuals between these morphotypes, in other cases there are numerous putative intermediate or introgressant individuals. Each morphotype has a different ecological niche and/or edaphic preference. They each have a distinct geographic range. However, it is unclear if they each are reproductively isolated as evidenced by their numerous intermediate/introgressant individuals. The above mentioned morphotypes appear to be diverging from *M. ovata* subsp. *ovata* and the other recognized subspecies, which may represent incipient speciation, but we do not believe that they have diverged sufficiently to be recognized as independent and discrete named taxa at this time. This is not unexpected because *Monardella* is a relatively young genus, with a crown age estimated at about 3.5–8.8 MYA (Liu et al. 2016; Drew et al. 2018; Hays et al. 2019). Based on this, *M. ovata* exemplifies the recent divergences and rapid radiations within *Monardella* in general as well as ongoing evolution of the genus.

We include the previously published, but rarely recognized, *M. californica* as a synonym under *M. ovata*, within the 'northern Sierra Nevada Range' morphotype. The type specimen for *M. californica* (*P. B. Kennedy 173* [LY!]) fits within the range of variability for *M. ovata* s.l., but not within *M. ovata* subsp. *ovata* or either of the other two *M. ovata* subspecies (discussed below). While specimens consistent with *M. californica* occupy an exclusive and distinct geographic range, they do not have 1) a set of nonoverlapping characters from other *M. ovata* morphotypes/subspecies, 2) occur under unique edaphic conditions, and 3) appear to be reproductively isolated from other morphotypes/subspecies within *M. ovata*. Plants that conform with *M. californica* primarily occur in the vicinity of Mount Lola in the northern Sierra Nevada Range to the Modoc Plateau (Fig. 2). They differ from *M. ovata* subsp. *ovata* by generally having smaller glomerules (11–15 mm) and leaves that contain sessile MSMC capitate trichomes. *Monardella* plants in this geographic region fit within the range of gross morphological characters of *M. ovata* s.l., but do not fit within the range of gross morphological and trichome characters of *M. ovata* subsp. *ovata*. Therefore, we hereby recognize *M. californica* as a synonym of *M. ovata* s.l., but not of *M. ovata* subsp. *ovata*.

We likewise include *M. tortifolia* as a synonym within *M. ovata* s.l. The type specimen of *M. tortifolia* (*W. C. Cusick 2846* [LY!]) fits within the broad range of variability of *M. ovata* s.l., but not within the circumscriptions of *M. ovata* subsp. *ovata* or either of the other two *M. ovata* subspecies (discussed below). Plants that conform with *M. tortifolia* primarily occur in Klamath County of southern Oregon. The plants of this morphotype differ from *M. ovata* subsp. *ovata* by having stems that contain short (0.15–0.25 mm) US trichomes (i.e. nonglandular trichomes) as the longest trichomes in what is best described as a moderately dense pubescence, and the stems on these plants generally, but not always, lack MSMC capitate trichomes. *Monardella* plants in this area fit within the broad range of characters for *M. ovata* s.l. in gross morphological and trichome characters, but not within those of *M. ovata* subsp. *ovata*. Thus, we hereby recognize *M. tortifolia* as a synonym of *M. ovata* s.l., but not of *M. ovata* subsp. *ovata*. We do not discuss the morphotypes identified above from each of these regions further in this manuscript, other than to say that there is likely additional unrecognized/cryptic diversity that currently resides within *M. ovata* s.l. that requires further research.

1a. *Monardella ovata* Greene subsp. *ovata*. Table 1. Figures 5, 6.

Distribution and Ecology—*Monardella ovata* subsp. *ovata* has a fairly broad distribution ranging from the southern Cascade Range in central western Oregon southward through the Klamath Range (including the Siskiyou Mountains) to the northwestern Sierra Nevada Range in California (Figs. 1, 2). *Monardella ovata* subsp. *ovata* commonly occurs in lithosolic openings of montane and coniferous forests where it tends to occur in the mesic microsites of an overall xeric niche. It has been collected at elevations from approximately 1500 to 2700 m.

Notes—*Monardella ovata* subsp. *ovata* is distinct within *Monardella ovata* s.l. in having stems that contain subsessile MSMC capitate trichomes, glomerules and bracts that are generally intermediate in size between the other two recognized *M. ovata* subspecies (see below), bracts that are sparsely to moderately pubescent on the abaxial surface (vs. moderately to densely pubescent for other *M. ovata* subspecies), and calyx tubes that lack MSMC capitate trichomes (vs. having them in the other *M. ovata* subspecies). *Monardella ovata* subsp. *ovata* occurs primarily on the western slopes of the northern Sierra Nevada Range and extends north and west to the Cascade Range in central Oregon. Generally, *M. ovata* subsp. *ovata* has a distinct, mostly non-overlapping geographic range relative to the other *M. ovata* subspecies, but some portions of its range do overlap with the formerly named *M. odoratissima* subsp. *pallida* ([= *M. ovata* subsp. *pallida*], see below); in the northwestern Sierra Nevada and southeastern Cascade Range and with the new *M. ovata* subspecies described below in the eastern Siskiyou Mountains and southwestern Cascade Range (Figs. 1, 2). However, even within these areas of overlap, the different taxa each have separate ecological and elevational distributions that result in separate micro-geographic distributions.

Selected Additional Specimens Examined—**USA.** —CALIFORNIA: Butte Co., *V. Oswald 817* (CHSC!); Shasta Co., *A. Eastwood 770* (GH!), *Gillett 305* (ID [digital image!]); Siskiyou Co., *A. S. Barclay 1318* (MSC!), *M. A. Elvin 8291* (LA!, NEBK!), *A. A. Heller 8018* [type location] (MSC!); Tehama Co., *G. K. Helmkamp 6911* (UCR!). —OREGON: Jackson Co., *K. L. Chambers 4333* (OSC!), *M. A. Elvin 8630* (LA!, NEBK!), 02 September 2010, *A. Golub-Tse s.n.* (SRP-45368!), *G. B. Straley 8141* (V!); Klamath Co., *E. I. Applegate 3714* (WILLU!), *Mrs. M. F. Small 102* (ORE!), *A. N. Steward 6424* (OSC!).

1b. ***Monardella ovata*** Greene subsp. ***lenmaniae*** Elvin, R.B.Kelley, and B.T.Drew, subsp. nov. TYPE: USA. California. Siskiyou Co., Greyback Road at the California/Oregon state line, 07 July 2016, *M. A. Elvin 8351 and B. T. Drew* (holotype, LA!; isotypes, CIC!, GH!, JEPS!, K!, LY!, MO!, NDG!, NEBK!, NY!, OSC!, UCR!, US!, UTC!, V!, VT!). Table 1. Figures 5, 6, 7.

Diagnosis—*Monardella ovata* Greene subsp. *lenmaniae* Elvin, R.B.Kelley, and B.T.Drew is similar to *Monardella ovata* Greene subsp. *ovata* but differs from it by having stems that lack multiseriate multicellular capitate trichomes, leaves with lower length-to-width ratios, larger glomerules, and bracts that are wider and have lower length-to-width ratios.

Description—Caespitose (± rhizomatous) to tufted perennial to subshrub, 20–30(–56) cm tall. **Stems** woody at base; primary stems thick (1.3–1.5 mm diam); secondary stems rare, 3–15 cm, ascending, generally forming in lower to middle nodes, very rarely in upper nodes, thinner (0.4–0.8 mm diam); green, sparsely pubescent with the following main types of trichomes: (1) MSMC capitate (not present to very rare), (2) uniseriate multicellular (USMC) straight and spreading to recurved 0.3–0.6 mm (rare), (3) USBC recurved reflexed to ascending 0.1–0.2 mm (frequent), and (4) UC straight spreading 0.02–0.06 mm (abundant); internodes 30–53(–150) mm. **Leaves** (middle to upper cauline) 18–43(–85) × 7.5–13(–38) mm, lanceolate to narrowly ovate, with L:W ratios 2.3–3.3:1, entire, distinctly petiolate, petiole 1.5–8(–15) mm, base obtuse, decurrent, apex acute to narrowly obtuse, pale to medium green (appearing dull to glaucous), abaxially sparsely pubescent with the following main types of trichomes: (1) MSMC capitate sunken (frequent), (2) USBC–USMC spreading 0.1–0.3 mm (occasional), and (3) UC spreading, 0.02–0.06 mm (frequent), adaxially sparsely pubescent with the following main types of trichomes: (1) MSMC capitate sunken (occasional to frequent), (2) USMC curved flexuose 0.2–0.3(–4) mm (occasional to frequent), (3) USBC curved 0.1 mm (frequent), (4) UC spreading 0.04–0.06 mm (occasional to frequent). **Inflorescence** a terminal glomerule on primary stems, usually solitary, rarely a modified cyme with 1–3 axillary glomerules per main stem; flowers in terminal glomerules, glomerules on primary stems 25–28 mm wide, glomerules on axillary stems smaller when present; glomerule bracts 10.5–15.5 × (3.1–)6.5–9 mm, +/− equaling the calyces, green to purple-tinged, ovate to narrowly ovate, entire, ciliate, with L:W ratios 1.4–2.3(–4.1):1, apices widely acute to obtuse, mucronulate; abaxially moderately to densely pubescent with the following main types of trichomes: (1) MSMC capitate stalked (occasional to frequent), (2) MSMC capitate subsessile (very rare to occasional), (3) USTC thick-walled appressed to ascending 0.1–0.25 mm (frequent to common), and (4) UC spreading to ascending less than 0.1 mm (occasional to frequent); bract margins densely pubescent with the following main types of trichomes: (1) USMC thick-walled 1.0–1.4 + mm (rare to occasional, mostly near apex), (2) USMC thick-walled 0.6–1.0 mm (occasional to frequent), (3) USMC 0.3–0.6 mm (rare), (4) USBC thin-walled 0.1–0.2 mm (rare), and (5) UC less than 0.1 mm (very rare to rare). **Flowers** with the calyx 7.5–9.5 mm; calyx tube green, moderately to densely pubescent with the following main types of trichomes: (1) MSMC capitate stalked (rare to occasional), (2) MSMC capitate (sub)sessile (rare to occasional), (3) UC capitate 0.02–0.04 mm (frequent to common), (4) USTC spreading to ascending 0.2–0.4 mm (frequent to common), and (5) USBC spreading to ascending 0.1–0.2 mm (occasional to frequent), calyx teeth 0.96–1.14 × 0.64–0.90 mm with L:W ratios of 1.16–1.50:1, green-tinged-purple to purple, very densely pubescent (much more so than the calyx tube) with the following main types of trichomes: (1) UC capitate 0.02–0.04 mm (occasional to frequent, only on tooth face), (2) USMC thick-walled 0.6–1.0 + mm (occasional), (3) USMC thick-walled 0.3–0.6 mm (frequent to common), and (4) US thin-walled 0.1–0.25 mm (occasional); corolla 14–18 mm, generally pale whitish-purple to bright lavender, pale bluish-purple, but occasionally purple, corolla tube exserted 0–1.0 mm beyond calyx teeth, moderately to densely pubescent with the following main types of trichomes: (1) MSMC capitate sessile trichomes (rare to occasional), (2) USBC reflexed 0.1–0.2 (frequent), and (3) US less than 0.1 mm (rare to occasional), corolla lobes 3.5–5.5 mm long, very slightly elliptical, apices obtuse-rounded, (sub)glabrous with the following main types of trichomes: (1) MSMC (sub)sessile (rare, only located at the apex); stamens exserted beyond corolla lobes 0–2 mm, lavender with some stramineous markings, glabrous; pistil 15–21 mm, style dark stramineous, (sub)glabrous, stigma exserted 0–3 mm beyond anthers, stigma widely bifurcated, 0.2–0.8 mm long for each fork. **Fruit** a nutlet [no fruit on any available specimen]. **Flowering** June to September. **Elevation** 750–2000 m.

Distribution and Ecology—*Monardella ovata* subsp. *lenmaniae* has a narrow distribution and occurs almost entirely within the Klamath-Siskiyou Mountains of northwestern California

FIG. 7. Habit of *Monardella ovata* Greene subsp. *lenmaniae* Elvin, R.B.Kelley, and B.T.Drew. Figure drawn by Lesley Randall.

and southwestern Oregon (Figs. 1, 2). The northernmost *M. ovata* subsp. *lenmaniae* collection was taken approximately 40 km north of the California state line (near "Stone Chair" in the mountains approximately 11 km east of the Pacific Ocean) and the southernmost collection approximately 80 km south of the Oregon state line (near Mount Eddy approximately 135 km east of the Pacific Ocean). We estimate the area of occurrence of *M. ovata* subsp. *lenmaniae* to be approximately 8000 km^2.

Monardella ovata subsp. *lenmaniae* has been collected from areas with stony soils, dry slopes, rocky ridges, and in rock outcrops on north-facing slopes within the otherwise mesic coastal mountain ranges of northern California and southern Oregon. Specimen labels indicate that it has been collected from loose sandy granite-loam, quartz diorite, limestone, and serpentine soils. There is a high correlation between the locations of georeferenced specimens of this taxon with geologic units mapped predominantly as serpentinite type base rock (Jennings et al. 1977; Walker and MacLeod 1991; CCH 2019; CPNWH 2019). None of the other *M. ovata* subspecies or morphotypes correlate with serpentine to the extent of *M. ovata* subsp. *lenmaniae*. We expect *M. ovata* subsp. *lenmaniae* to occur in additional similar habitats and similarly specialized edaphic conditions within its range. Associated species include *Calocedrus decurrens* (Torr.) Florin (Cupressaceae), *Abies concolor* (Gordon and Glend.) Lindl. ex Hildebr. and *Pseudotsuga menziesii* (Mirb.) Franco (Pinaceae), *Festuca californica* Vasey (Poaceae), *Sedum* spp. (Crassulaceae), *Quercus* spp. (Fagaceae), *Arctostaphylos* spp. (Ericaceae), *Orthocarpus cuspidatus* Greene subsp. *copelandii* (Eastw.) T.I.Chuang and Heckard (Orobanchaceae), and *Eriogonum compositum* Douglas ex Benth. (Polygonaceae).

Etymology—The epithet *lenmaniae* refers to and honors the noted Los Angeles environmental advocate Susan Lenman, who grew up in a log cabin built by her Swedish immigrant father in a remote portion of Quebec, Canada where she developed her love of nature and conservation. She is honored here for her dedication to advancing environmental awareness in Southern California. The epithet was chosen by her husband, Daniel Gottlieb, as a celebration of their love and her passion for conservation, after winning the naming rights in an environmental fund-raising auction by the California Native Plant Society to support conservation efforts for California native plants. Gottlieb requested "Susan Lenman's monardella" to be the common name for this taxon.

Notes—*Monardella ovata* subsp. *lenmaniae* is similar to the other taxa in *M. ovata* in general habit and gestalt. *Monardella ovata* subsp. *lenmaniae* is distinct among the taxa in *M. ovata* because it is generally less pubescent and lacks the subsessile to stalked MSMC capitate trichomes found on the stems of its sister taxa. It also has generally larger leaves; larger, wider, and more colorful bracts; and larger glomerules.

Monardella ovata subsp. *lenmaniae* is separated from *M. ovata* subsp. *ovata* primarily by its stems that lack subsessile MSMC capitate trichomes (vs. having that type of trichome on the stem for subsp. *ovata*), leaves that have slightly lower L:W ratios (2.3–3.3:1 vs. (2.6–)3.2–3.5:1) and have USMC 0.2–0.3 mm trichomes adaxially as the longest (vs. UC 0.06–0.1 mm), larger glomerules (25–28 vs. 19–22 mm), slightly larger calyces (7.5–9.5 vs. 7–8 mm) with stalked and sessile MSMC capitate trichomes (vs. lacking MSMC capitate), and wider bracts (6.5–9 vs. 3.5–6.5 mm). These two taxa have mostly parapatric geographic distributions (Figs. 1, 2). Their ranges overlap in a small region near the southeastern corner of Josephine County, Oregon and the northwestern corner of Siskiyou County, California. Several putative introgressant specimens have been taken from the areas of sympatry, e.g. *L. E. Detling 4347* (ORE!), *R. H. Whittaker SS 359-S* (WS!), *B. Wilson 6353* (ORE!) as well as from areas in Siskiyou and Trinity Counties, California where their ranges are contiguous, but not sympatric, e.g. *A. A. Heller 8774* (PH!), *I. L. Wiggins 13578* (WS!).

While some gross morphological characters overlap between these two taxa (e.g. leaf length and width, petiole length, bract length), other characters exhibit mostly nonoverlapping ranges (e.g. bract width, glomerule width). However, the separation between the two taxa is more distinct/evident in traits involving trichomes (e.g. trichome type, location, and abundance). The differences in the types, locations, and abundance of trichomes on the structures of each taxon are consistent throughout their respective ranges. Therefore, these differences represent a distinct separation between these two taxa. Based on the separation of geographic ranges, differences in gross morphological characters, and distinct differences in trichome types and abundances, *M. ovata* subsp. *lenmaniae* may warrant recognition at the specific level; however, we are being conservative and describe it as a subspecies of *M. ovata* at this time.

Monardella ovata subsp. *lenmaniae* is separated from *M. ovata* subsp. *pallida* (see below) primarily by its stems that lack stalked MSMC capitate trichomes (vs. having that type of trichome on the stems for subsp. *pallida*); leaves with lower L:W ratios (2.3–3.3:1 vs. 3.25–3.75:1) and that lack stalked MSMC capitate trichomes abaxially (vs. having that type of trichome abaxially); glomerules that are larger (25–28 vs. 12–25 mm); calyces that are longer (7.5–9.5 vs. 5.5–6.5(–7) mm); calyx teeth that have USMC trichomes 0.6–1.0 + mm as the longest (vs. 0.3–0.6 mm); and bracts that are longer (10.5–15.5 vs. 6.5–10 mm), wider 6.5–9 vs. 3–8 mm), and lack sunken MSMC capitate trichomes abaxially (vs. having that type of trichome abaxially). They have allopatric distributions (Figs. 1, 2) and occur in different ecological regions (Sanders et al. 2012; Griffith et al. 2016). We are not aware of any specimens that represent hybrid, introgressant, or ambiguous specimens between these two taxa.

Monardella ovata subsp. *lenmaniae* is separated from the partially sympatric *M. purpurea* subsp. *purpurea* by having stems that are erect (vs. decumbent to ascending for *M. purpurea* subsp. *purpurea*), sparsely pubescent (vs. subglabrous to ±sparsely pubescent), and have USMC trichomes 0.3–0.6 mm as the longest (vs. 0.06–0.1 mm); internodes that are longer (30–53 vs. 10–25 mm); leaves that have USMC trichomes 0.2–0.3 mm as the longest (vs. 0.02–0.04 mm); glomerules that are larger (25–28 vs. 15–25 mm); bracts that are wider (6.5–9 vs. 5–7 mm); and calyces that are longer (7.5–9.5 vs. 6–8 mm) and lack MSMC capitate trichomes (vs. having that type of trichome on the calyx). The distribution of *M. ovata* subsp. *lenmaniae* is sympatric with much of that of *M. purpurea* subsp. *purpurea*. Approximately half of its distribution (~4300 km^2) overlaps with that of *M. purpurea* subsp. *purpurea*. *Monardella purpurea* subsp. *purpurea* tends to have a more coastal and valley distribution, while *M. ovata* subsp. *lenmaniae* has more of a montane distribution that runs from the coastal mountains to interior mountains (Figs. 1, 2). In their area of sympatry, they occur in different ecological niches. We have seen two specimens that represent putative hybrid individuals from within their area of sympatry, e.g. *M. E. Peck 8934* (WILLU!), 11 Aug 1993, *R. Brainerd s.n.* (ORE-185922!). Some *M. ovata* subsp. *lenmaniae* specimens were previously determined to be

M. purpurea subsp. *purpurea*, e.g. *D. E. Breedlove 699* (SBBG!), *P. Zika 13265* (OSU!), *S. Stefanovic 98–50* (WTU!).

***Paratypes*—USA.** —California: Del Norte Co., *E. Lee 1117* (LA!); Siskiyou Co., *A. A. Heller 12105* (GH!, PH!, US!, WTU!), *A. A. Heller 12230* (GH!, PH!, WTU!), *C. L. Hitchcock 5213* (GH s.n.!, JWT in WTU!, UTC!, WTU!), *J. D. Jokerst 3431* (CHSC!), *L. R. Short 104* (USFS in RM!), *J. M. Tucker 3785* (LA!). —Oregon. Curry Co., *P. Zika 13265 and V. Stansell* (ORE!); Josephine Co., *V. L. Crosby 814* (OSC!), *L. E. Detling 6720* (WTU!, ORE!), *L. E. Detling 6733* (ORE!), *M. A. Elvin 8325* (LA!, NEBK!), *C. L. Hitchcock 5162* (WTU!), *5182* (JWT in WTU!, WS!, UTC!), *T. Howell 1250* (MSC!), *D. C. Ingram 1141* (USFS in RM!), *L. Leach 2932* (ORE!), *M. E. Peck 5542* (WILLU, JWT in WTU!), *M. E. Peck 8360* (WILLU!), *M. E. Peck 16468* (WILLU!), 11 Aug 1928, *F. Snipe s.n.* (OSC-36363!), 26 July 1986, *V. Stansell s.n.* (ORE-170658!), *S. Stefanovic 98–50* (WTU!), *R. H. Whittaker SS 221* (WS!).

1c. ***Monardella ovata*** Greene subsp. ***pallida*** (A.Heller) Elvin, R.B.Kelley, and B.T.Drew, comb. et stat. nov. Basionym: *Monardella pallida* A.Heller, Muhlenbergia 1: 36. 1904. *Madronella pallida* (A.Heller) A.Heller, Muhlenbergia 1: 138. 1906. *Monardella odoratissima* Benth. subsp. *pallida* (A.Heller) Epling, Ann. Missouri Bot. Gard. 12: 66. 1925. Type: USA. California. Nevada Co., ridge near lower end of Donner Lake (south side), 17 July 1903, *A. A. Heller 6959* (holotype, BKL [barcode] 00000841 [digital image!]; isotypes, DOV-15467 [digital image!], DS-23565!, DS-129367 [digital image!], G, GH-1363!, IND-47217 [digital image!], K [barcode] 000910794!, MSC-71023!, MO-114281!, NY [barcode] 00429346 [digital image!], P [barcode] 00737806, PH-507124!, POM-19719!, RM-46584!, UC-58425 [digital image!], UC-58425!, US-735622!, US-467362!, WS-22947!, WTU-80966!, YU-1932). Table 1. Figures 5, 6.

Distribution and Ecology—*Monardella ovata* subsp. *pallida* occurs in the northern and central Sierra Nevada, southern Cascade, and eastern Klamath Ranges in California (Placer, Nevada, Sierra, Plumas, Shasta, and Siskiyou Counties) extending into the eastern portion of the Klamath Range in southwestern Oregon (Jackson and Klamath Counties) (Figs. 1, 2). *Monardella ovata* subsp. *pallida* commonly occurs in lithosolic openings of montane and coniferous forests where it tends to occur in mesic microsites of an overall xeric niche. It generally has been collected at elevations from approximately 1600 to 2800 m. Comparatively, *M. ovata* subsp. *pallida* has a more southerly/lower distribution than that of *M. ovata* subsp. *ovata*, i.e. when these two taxa occur within the same general area or on the same mountain, *M. ovata* subsp. *pallida* occurs at lower elevations and, correspondingly, occurs in different (generally less xeric) ecological conditions. For example, both subspecies occur on Mount Ashland and Mount Shasta. In both cases *M. ovata* subsp. *pallida* occurs lower on each mountain and has an earlier peak blooming period than that of *M. ovata* subsp. *ovata*, which is a common ecological response in plants when they occur at different elevation gradients.

Notes—*Monardella ovata* subsp. *pallida* is distinct from other subspecies and morphotypes within *M. ovata* in having stalked MSMC capitate trichomes on the stems, glomerules that are smaller, bracts that are noticeably more inconspicuous (i.e. smaller and drabber), calyces that are shorter, and corollas that are paler/lighter. It has an essentially distinct allopatric geographic distribution from the other *M. ovata* subspecies, but the western portion of its distribution overlaps slightly ($\sim$3800 km^2) with that of *M. ovata* subsp. *ovata*. However, even within the area of overlap, they have separate ecological and elevational distributions that result in separate micro-geographic distributions. Putative introgressant specimens between these two subspecies have been taken, e.g. *M. A. Elvin 8288* (LA!, NEBK!), *8628* (LA!, NEBK!), *L. P. Janeway 2104* (CHSC!), 16 June 1932, *P. L. Johannsen s.n.* (USFS in RM!), *M. Ownbey 2182* (UTC!).

***Selected Additional Specimens Examined*—USA.** —California: Alpine Co., *J. C. Johnson 135* (WS!); Amador Co., *H. J. Oosting 2178* (RM!); Butte Co., *A. A. Heller 12860* (WTU!); El Dorado Co., *A. A. Heller 12186* (GH!, WTU!), *G. K. Helmkamp 10817* (UCR!); Lassen Co., 28 July 1894, *M. S. Baker s.n.* (RM-4180!); Mono Co., *H. Mozingo 79–84* (RENO!); Nevada Co., *L. Ahart 8970* (CHSC!); Placer Co., *M. A. Elvin 8091* (LA!, NEBK!); Plumas Co., *L. Constance 2317* (GH!, RM!, UC, UTC!, WS!); Shasta Co., 17 July 1935, *C. C. Epling s.n.* (LA-62601!); Sierra Co., *M. A. Elvin 8122* (LA!, NEBK!); Siskiyou Co., *M. A. Elvin 8280* (LA!, NEBK!), *R. Tofsrud 1757* (UTC!), *C. B. Wolf 5993* (RM!); Tehama Co., 16 July 1935, *C. C. Epling s.n.* (LA-54268!, LA in UC-2035959, LA in UC-2035960). —Nevada: Washoe Co., *Archer 5440* (PH!). —Oregon: Jackson Co., *M. A. Elvin 8627* (LA!, NEBK!); Lake Co., *A. N. Steward 7467* (OSC!, PH!, V!). Co. unknown, *Canby s.n.* (GH s.n.!).

2. Monardella modocensis Greene, Pittonia 4: 321. 1901. *Madronella modocensis* (Greene) Greene, Leafl. Bot. Observ. Crit. 1: 169. 1906. Type: USA. California: Modoc Co. timbered hillside, 02 July 1893, *M. S. Baker s.n.* (lectotype, designated here, NDG-16539 [digital image!]; isolectotype, UC-25496 [digital image!]). Table 1.

Distribution and Ecology—*Monardella modocensis* occurs primarily in northeastern California and central-southern Oregon (Fig. 1) with most collections from the Modoc Plateau ecoregion of the Great Basin Floristic Province, but a few collections falling within the southeastern portion of the Cascade Range ecoregion of the California Floristic Province (Baldwin et al. 2012). It has also been collected from the Warner Mountains in both northeastern California and central-southern Oregon. Specimen labels indicate that it occurs in lithosolic openings or exposed areas such as rocky slopes, flats, roadcuts, rock outcrops, and talus slopes, that are essentially mesic microsites within an otherwise xeric habitat. It has been reported from lateral moraines, lava, loose white sand, shallow sand, stony loam, gravelly shallow loam, and dry sandy loose rock type soil associations. It has been collected at elevations between approximately 1200 and 2550 m. Associated species include *Abies magnifica* A.Murray bis and *Pinus jeffreyi* A.Murray bis (Pinaceae), *Festuca idahoensis* Elmer (Poaceae), *Phacelia* spp. (Hydrophyllaceae), and *Purshia tridentata* (Pursh) DC. and *Rosa* spp. (Rosaceae).

Notes—The *Monardella* plants from northeastern California and southern-central Oregon that formerly had the name *M. odoratissima* subsp. *glauca* misapplied that occur within the Modoc Plateau ecoregion of the Great Basin Floristic Province (Fig. 1) fit within the circumscription of another previously described taxon: *Monardella modocensis*, with its type from Modoc County, California.

For the past approximately 100 yr, many *Monardella* plants throughout western North America have been called or labeled *M. glauca* Greene (as either *M. glauca*, *M. odoratissima* subsp. *glauca*, or *M. odoratissima* Benth. var. *glauca* (Greene) H.St.John), presumably because they had large colorful bracts and the vestiture was pale or glaucous in appearance (Epling 1925; Jepson 1925, 1943; Peck 1941, 1961; Abrams 1951; Davis 1952; Munz 1959, 1974; St. John 1963; US Department of Agriculture, Soil Conservation Service 1982; Cronquist et al. 1984; Kartesz 1988; Jokerst 1993, 2002; Elvin and Sanders 2009; Sanders et al. 2012; CCH 2019; CPNWH 2019; IMRHN 2019; NANSH 2019; SEINet 2019). However, these plants do not fit within the circumscription of *M. odoratissima* subsp. *glauca* (*M. glauca*); therefore, that name has been misapplied to them. By examining additional characters beyond gross morphology (particularly trichome morphology), it is evident that most of the plants throughout the western United States (formerly misapplied to *M. glauca* [=*M. odoratissima* subsp. *glauca*]) are not *M. glauca* and in fact require different or novel names to be applied to them.

Monardella glauca is a narrow endemic with a distribution limited to the interface of the southern edge of the Blue and Wallowa Mountains and the northern edge of the Owyhee Uplands ecoregion (Albert and Chipman 2015) in eastern Oregon near the town of Drewsey and, therefore, does not occur in California, Nevada, Idaho, Wyoming, Utah, Colorado, New Mexico, or Arizona. It is distinguished from all other *Monardella* taxa by containing ascending USMC trichomes on its stem (vs. solely recurved or spreading in all other *Monardella* taxa). We know of no other *Monardella* that has ascending trichomes on the stem making this species unique in that respect for the genus.

Monardella modocensis has a general habit and gross morphology that is similar to other perennial *Monardella* taxa in California, Nevada, and Oregon. However, *M. modocensis* has a unique geographic distribution and a unique set of fine morphological characters. *Monardella modocensis* is similar to other species in the *M. ovata* species complex based on its large leaves; distinct petioles; sparse pubescence including short USMC trichomes and MSMC capitate trichomes on the stems, leaves, and calyces; and other gross morphological characters (e.g. bract size and color). *Monardella modocensis* is generally distinguished from other species in the *M. ovata* species complex by having stems that are short to moderately tall (16–21 cm), sparsely to moderately pubescent with stalked MSMC capitate trichomes, and short USMC trichomes (up to 0.2 mm long); long internodes (35–45 mm); leaves that are distinctly petiolate (1.5–3.5 mm), large (16–25 × 4.8–8.5 mm), sparsely to moderately pubescent abaxially and moderately to densely pubescent adaxially, possess sunken MSMC capitate trichomes, and lack US capitate trichomes; main bracts that are large (6.2–12 × 6–9.2 mm), colorful (purple to lavender), sparsely to moderately pubescent, and possess stalked MSMC capitate trichomes; and calyces that are long (8–9.5 mm), possess stalked MSMC capitate trichomes, and lack US capitate trichomes.

Monardella modocensis is similar to *M. ovata* subsp. *ovata* in that it has large leaves with distinct petioles and large bracts and the same general gestalt. It differs from *M. ovata* subsp. *ovata* primarily in having stalked MSMC capitate trichomes on the stems, bracts, and calyces and in having larger calyces (8–9.5 vs. 7–8 mm in *M. ovata* subsp. *ovata*). *Monardella modocensis* primarily occurs outside of the California Floristic Province in the Modoc Plateau subregion of the Great Basin Floristic Province (Baldwin et al. 2012). Most of the distribution of *M. modocensis* falls within the US Geological Survey's level III ecoregion classified as the Eastern Cascades Slopes and Foothills, with some of it occurring within the Northern Basin and Range ecoregion (Bryce et al. 2003; Thorson et al. 2003; Griffith et al. 2016). These two taxa have allopatric distributions separated by approximately 50 km and the crest of the Sierra Nevada Range (Fig. 1). We are not aware of any specimens that represent hybrid, introgressant, or ambiguous specimens between these two taxa.

Monardella modocensis is similar to *M. ovata* subsp. *pallida* in that they both have large leaves, distinct petioles, and the same general gestalt. It is separated from *M. ovata* subsp. *pallida* primarily by having shorter stems (16–21 vs. 25–35 cm for subsp. *pallida*), smaller leaves (16–25 × 4.8–8.5 vs. 30–40 × 8–12 mm) that only have sunken MSMC capitate trichomes abaxially (vs. having sunken and stalked MSMC capitate trichomes abaxially), shorter petioles (1.5–3.5 vs. 5–11 mm), larger bracts (6.2–12 × 6–9.2 vs. 6.5–7 × 3.5–4.5 mm) that possess stalked MSMC capitate trichomes abaxially (vs. having sunken and sessile MSMC capitate trichomes abaxially), and longer calyces (8–9.5 vs. 5.5–6.5 mm) that lack US capitate trichomes (vs. having that type of trichome). They have allopatric distributions (Fig. 1) and occur in different ecological regions and floristic provinces (Bryce et al. 2003; Thorson et al. 2003; Baldwin et al. 2012; Griffith et al. 2016).

Greene (1901) described *M. modocensis* from "… specimens taken by Mr. Milo S. Baker in Modoc Co., 1893. It was distributed by myself [E. L. Greene], from near Yreka in 1876, under n. 910 [NDG!], and Mr. Sonne obtained it near Verdi, Nevada." Greene did not designate any single specimen as the "type", nor did he indicate any specific herbarium where the "type" resided. Therefore, collections that fit within the parameters of those collections listed above must be relegated to syntype status. Making this more complicated, some of the syntype specimens do not fit within the circumscription of *M. modocensis*, but instead fit within the circumscriptions of other taxa. We hereby exclude *E. L. Greene 910* (NDG!) and all Sonne collections "near Verde, Nevada" from syntype status under *M. modocensis* because they represent different taxa. *E. L. Greene 910* (NDG!) was collected near the type location for *M. ovata* and based on its set of characters it represents *M. ovata* subsp. *ovata*. All Sonne collections from "near Verdi" (Verdi, Nevada, the type location for *M. rubella*) that we have examined represent *M. rubella*. Because no single type was designated for *M. modocensis* by Greene (1901) in his protologue or any other botanists in any other publication since then (e.g. Epling 1925, Abrams 1951), we believe the 02 July 1893, *M. S. Baker s.n.* (NDG-16539!) specimen is the most representative from among the remaining syntypes used by Greene to develop his concept of *M. modocensis*; we hereby designate *M. S. Baker s.n.* (NDG-16539!) as the lectotype for *M. modocensis*.

***Syntypes*—USA.** —California: Modoc Co., 1893, *M. S. Baker s.n.* (DS-23556); 20 June 1893, *M. S. Baker s.n.* (UC-25509 [digital image!]); 02 July 1893, *M. S. Baker s.n.* (NDG-16539 [digital image!], UC-25496 [digital image!]); 08 July 1893, *M. S. Baker s.n.* (PH-1113669!, NDG-200 [digital image!], UC-25490 [digital image!]).

***Syntypes Excluded*—USA.** —California: Siskiyou Co. *E. L. Greene 910* (NDG-16521 [digital image!]). —Nevada: [Washoe Co.], [20 May 1888], *C. F. Sonne s.n.* [*19*] (NDG-16547 [digital image!], UC-104677 [digital image!], UC-193932 [digital image!]).

***Paratypes*—USA.** —California: Modoc Co., 1893, *M. S. Baker s.n.* (DS-23556); 20 June 1893, *M. S. Baker s.n.* (UC-25509 [digital image!]); 08 July 1893, *M. S. Baker s.n.* (PH-1113669!, NDG-200 [digital image!], UC-25490 [digital image!]).

***Selected Additional Specimens Examined*—USA.** —California: Lassen Co., *E. A. Bourdo Jr. 25365* (MSC!), *G. A. Fischer F-225* (USFS in RM!), *G. A. Fischer F-274* (USFS in RM!), *J. T. Howell 11888* (LA!), *L. R. Short S-467* (USFS in RM!); Modoc Co., *M. Ownbey 2150* (UTC!, WS!, WTU!), *L. S. Smith 1046 ½* (USFS in RM!), *L. S. Smith 1419* (USFS in RM!). —Nevada: Washoe Co., *H. L. Mason 12345* (WS!).

3. *Monardella rubella* Greene, Pittonia 5: 84. 1902. *Madronella rubella* (Greene) Greene, Leaflets Bot. Obs. 1: 169. 1906. Type: USA. Nevada. [Washoe Co.], Verdi, [20 May 1888], *C. F. Sonne s.n.* [*19*] (lectotype, designated here, NDG-16547 [digital image!]; isolectotypes, UC-104677 [digital image!], UC-193932 [digital image!]). Table 1.

Distribution and Ecology—*Monardella rubella* occurs along the California/Nevada border region in the mountains on the eastern slopes of the northern and central Sierra Nevada Range and in the mountains and foothills at the western edge of the Great Basin Desert (Fig. 1). It has been collected from Lassen County, California and Washoe County, Nevada south to Inyo County, California and Mineral County, Nevada. Specimen labels indicate that it occurs in lithosolic openings that are often rocky areas such as slopes, flats, roadcuts, and rock outcrops. It has been reported from granitic, volcanic, metavolcanic, moist sandy loam, bare tuffaceous, and talus soil associations, which represent more mesic microsites within otherwise xeric habitats. It has been collected at elevations from approximately 1200 to 3050 m. Associated species include *Pinus albicaulis* Englem. and *P. contorta* Loudon (Pinaceae), *Artemisia* spp., *Ericameria* spp., *Erigeron aphanactis* (A.Gray) Greene, and *Eriophyllum lanatum* (Pursh) J.Forbes (Asteraceae), *Lupinus* spp. (Fabaceae), *Castilleja* spp. (Orobanchaceae), *Penstemon* spp. (Plantaginaceae), and *Cercocarpus ledifolius* Nutt. (Rosaceae).

Notes—The *Monardella* plants formerly referred to as *M. odoratissima* subsp. *glauca* within the distinct geographic area along the interface zone of the eastern Sierra Nevada Range and the western edge of the Great Basin Desert (Fig. 1) fit within the circumscription of the previously described *Monardella rubella*, with its type from Verdi, Nevada.

Monardella rubella is distinguished primarily by its large leaves, distinct petioles, large colorful main bracts, and sparse to moderate pubescence on the stems and leaves. Some distinguishing characteristics for *M. rubella* consist of having stems that are tall (20–25 cm), sparsely to ± densely pubescent with stalked and subsessile MSMC capitate trichomes and short USMC trichomes (up to 0.25 mm long), but lacking US capitate trichomes; long internodes (24–45 mm); leaves that are distinctly petiolate (3–4.5 mm), large (25–30 × 6–7.5 mm), moderately to densely pubescent abaxially and sparsely to moderately pubescent with sunken MSMC capitate trichomes adaxially and lacking US capitate trichomes adaxially; main bracts that are large (12–15 × 5.5–9 mm), colorful (purple to lavender), and subglabrate to sparsely pubescent with stalked and subsessile MSMC capitate trichomes; and calyces that are long (8–10 mm), possess subsessile MSMC capitate trichomes, and lack US capitate trichomes. Putative hybrid specimens with other taxa have been collected from areas where they are adjacent to or overlap with *M. linoides* A. Gray subsp. *sierrae* Elvin and A.C.Sanders, e.g. *J. M. André 15062* (GMDRC!, UCR!), *K. Y. Kiew 13* (V!) and *M. ovata* subsp. *pallida*, e.g. *W. H. Baker 17023* (WTU), *C. B. Wolf 5468* (WTU!).

Monardella rubella is similar to *M. ovata* subsp. *ovata* in that they both have large leaves, distinct petioles, large bracts, and the same overall gestalt. It is separated from *M. ovata* subsp. *ovata* primarily by having stems that possess both subsessile and stalked MSMC capitate trichomes (vs. having only subsessile MSMC capitate trichomes for *M. ovata* subsp. *ovata*), leaves that are narrower (6–7.5 vs. 6.5–11.5 mm) with higher L:W ratios (4–4.2:1 vs. (2.6–)3.2–3.5:1) and USMC trichomes adaxially 0.1–0.25 mm as the longest (vs. 0.06–0.1 mm), shorter petioles (3–4.5 vs. 3–8 mm), smaller glomerules (15–20 vs. 19–22 mm), wider bracts (5.5–9 vs. 3.5–6.5 mm) with generally lower L:W ratios (1.7–2.2:1 vs. 1.6–3.7:1), longer calyces (8–10 vs. 7–8 mm), and calyx tubes that lack USMC trichomes 0.1–0.25 mm (vs. having them). They have allopatric distributions separated by approximately 65 km and the crest of the Sierra Nevada Range (Fig. 1), and they occur in different ecoregions and floristic provinces (Bryce et al. 2003; Baldwin et al. 2012; Griffith et al. 2016). We are not aware of any specimens that represent hybrid, introgressant, or otherwise ambiguous specimens between these two taxa.

Monardella rubella is similar to *M. ovata* subsp. *pallida* in that they both have large leaves, distinct petioles, and the same general gestalt. It is separated from *M. ovata* subsp. *pallida* primarily by having stems that possess both subsessile and stalked MSMC capitate trichomes (vs. having only stalked MSMC capitate trichomes for *M. ovata* subsp. *pallida*); leaves that have shorter petioles (3–4.5 vs. 5–11 mm), are smaller (25–30 × 6–7.5 vs. 30–40 × 8–12 mm) with higher L:W ratios (4–4.2:1 vs. 3.25–3.75:1), and only possess sunken MSMC capitate trichomes abaxially (vs. having sunken and stalked MSMC capitate trichomes abaxially); larger bracts (12–15 × 5.5–9 vs. 6.5–7 × 3.5–4.5 mm) that possess subsessile and stalked MSMC capitate trichomes abaxially (vs. having sunken and sessile MSMC capitate trichomes abaxially); and longer calyces (8–10 vs. 5.5–6.5 mm) that lack US capitate trichomes (vs. having that type of trichome). They have parapatric (although contiguous) distributions (Fig. 1) and occur in different ecological regions and floristic provinces (Bryce et al. 2003; Baldwin et al. 2012; Griffith et al. 2016). There are a number of putative hybrid specimens from areas on the eastern slopes of the Sierra Nevada range, e.g. *J. M. André 10604* (GMDRC!, UCR!), *A. A. Heller 10345* (RENO!), *C.B. Wolf 5468* (WTU!).

Monardella rubella is similar to *M. modocensis* in that they both have large leaves, distinct petioles, large bracts, and the same overall gestalt. It is separated from *M. modocensis* primarily by having stems that are generally longer (20–25 vs. 16–21 cm for *M. modocensis*) and that possess subsessile and stalked MSMC capitate trichomes (vs. having only subsessile MSMC capitate trichomes), leaves that are longer (25–30 vs. 16–25 mm) with higher L:W ratios (4–4.2:1 vs. 2.5–3.7:1), glomerules that are slightly larger (15–20 vs. 12–18 mm), bracts that are longer (12–15 vs. 6.2–12 mm) and possess subsessile and stalked MSMC capitate trichomes abaxially (vs. having only stalked MSMC capitate trichomes abaxially), and calyces that possess subsessile MSMC capitate trichomes (vs. stalked MSMC capitate trichomes). They have parapatric distributions (Fig. 1) and occur in different ecoregions and floristic provinces (Bryce et al. 2003; Thorson et al. 2003; Baldwin et al. 2012; Griffith et al. 2016). There are several putative hybrid specimens from areas where these two taxa are contiguous, e.g. *J. T. Howell 11888* (LA!), *L. S. Lewis 40593* (RM!), *L. R. Short S-467* (USFS in RM!).

In describing *M. rubella*, Greene (1902) did not list any single specimen or collection as the "type" nor did he declare a specific herbarium where the "type" resided; therefore, it is necessary to designate a lectotype. Greene merely stated, "Known only as sent me many years since, from near Verdi, Nevada, by Mr. C. F. Sonne" (Greene 1902). No date or collection number is mentioned in the protologue (Greene 1902). Thus, all C. F. Sonne collections from "near Verdi" must be considered as syntypes for *M. rubella*, regardless in which herbarium they reside. Making matters more difficult, in his description of *M. modocensis* (Greene 1901) the previous year, Greene cited a specimen (possibly specimens) that had been distributed to him from C. F. Sonne from "near Verdi, Nevada." It is unknown whether *C. F. Sonne s.n.* [*19*] (NDG-16547!) is the same specimen that Greene intended as the type for *M. modocensis* or whether he intended to use one of the two duplicates at UC as the type for *M. modocensis*. Therefore, it seems possible, if not likely, that Greene inadvertently cited the same specimen to describe both of these species. Or, he might have purposely changed his mind regarding the determination for this specimen. Unfortunately, he did not explain himself regarding this apparent error.

We know that Greene did not annotate *C. F. Sonne s.n.* [*19*] (NDG-16547!) as *M. modocensis*. But he did annotate that specimen as *M. rubella*, which changed the determination for that specimen from the original label determination of *M. odoratissima* (presumably made by C. F. Sonne). Of particular note, is that Greene did not label this specimen as "type". Because no single type was designated by Greene (1902) or anyone else in another publication since then (e.g. Epling 1925), we believe the *C. F. Sonne s.n.* [*19*] (NDG-16547!) specimen is the one most likely to have been used by Greene to develop his concept of *M. rubella*. We hereby designate the *C. F. Sonne s.n.* [*19*] specimen at NDG (NDG-16547!) as the lectotype for *M. rubella* and the two specimens at UC (UC-104677! and UC-193932!) as isolectotypes.

***Syntypes*—USA.** —NEVADA: Washoe Co., [20 May 1888,] *C. F. Sonne s.n.* [*19*] (NDG-16547 [digital image!], UC-104677 [digital image!], UC-193932 [digital image!]).

***Selected Additional Specimens Examined*—USA.** —CALIFORNIA: Alpine Co., *C. G. Albertus 309* (USFS in RM!), *G. K. Helmkamp 14007* (UCR!), *15297* (UCR!); El Dorado Co., *G. K. Helmkamp 16722* (UCR!); Inyo Co., *J. M. André 11831* (GMDRC!, UCR!), *R. Bayer CA-726* (RM!), *P. A. Munz 12656* (WTU!); Lassen Co., *J. M. André 19692* (UCR!); Madera Co., *H. K. Sharsmith 4540 A* (V!); Mono Co., *A. M. Alexander 1841* (UTC!, WTU!), *B. Ertter 3904* (UTC!), *C. McMillan 125* (USFS in RM!), *M. J. Williams 83–141–1* (RENO!, RM!, UTC!); Plumas Co., *A. C. Barrett B-48* (USFS in RM!), *F. C. Vasek 750710–29* (UCR!); Sierra Co., *S. B. Doten 37* (RENO [2]!); Tuolumne Co., *T. C. Wells 642* (V!), *I. L. Wiggins 8128* (WTU!). —NEVADA: Douglas Co., *J. Bair 83* (RENO!); Lyon Co., *B. O. Moore 847* (RENO!), *B. O. Moore 867* (RENO!); Mineral Co., *A. Pinzl 11730* (SRP!), *P. Train 4203* (RENO!); Washoe Co., *J. T. Howell 48952* (RENO!), *J. T. Howell 49035* (RENO!), 11 June 1897, *M. E. Jones s.n.* (UTC-11500!), *P. B. Kennedy 781* (RENO!, RM!), 02 August 1912, *P. P. Kennedy s.n.* (US-509633!), 12 August 1912, *P. P. Kennedy s.n.* (RENO-10492!), *O. Reifschneider 14* (RENO!).

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AUTHOR CONTRIBUTIONS

MAE was the primary author of the manuscript, primary author of the new species description, and assisted with producing the maps. RBK participated in writing the manuscript, analyzing the data, and producing the maps. BTD participated in writing the manuscript, analyzing the data, producing the maps, and was the primary author for producing and analyzing the genetic data.

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Appendix 1. Samples included in the molecular analyses.

Ingroup: *Monardella stebbinsii*, *B. T. Drew 684A*, NEBK, SAMN26199936. *Monardella follettii*, *B. T. Drew 682C*, NEBK, SAMN26199937. *Monardella ovata* subsp. *pallida*, *L. Ahart 8970B*, NEBK, SAMN26199939. *Monardella purpurea* subsp. *purpurea*, *B. T. Drew 693E*, NEBK, SAMN26199938. *Monardella linoides* subsp. *linoides*, *M. A. Elvin 7899*, NEBK, SAMN26199940. *Monardella macrantha* subsp. *hallii*, *M. A. Elvin 7897*, NEBK, SAMN26199949. *Monardella villosa* subsp. *obispoensis*, *M. A. Elvin s.n.*, NEBK, SAMN26199941. *Monardella odoratissima*, *S. Liu 44*, NEBK, SAMN26199942. *Monardella breweri* subsp. *lanceolata*, *M. A. Elvin 7961A*, NEBK, SAMN26199943. *Monardella breweri* subsp. *lanceolata*, *M. A. Elvin 7961B*, NEBK, SAMN26199944. *Monardella sinuata* subsp. *gerryi*, *M. A. Elvin 7575A*, NEBK, SAMN26199945.

Outgroup: *Pogogyne douglasii*, *H. Forbes s.n.*, NEBK, SAMN26199946. *Acanthomintha duttonii*, *H. Forbes s.n.*, NEBK, SAMN26199947. *Pycnanthemum tenuifolium*, *B. T. Drew 665*, NEBK, SAMN26199948.