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RESURRECTION OF *ORTHOCARPUS ERIANTHUS* VAR. *GRATIOSUS* AND ITS TRANFER TO *TRIPHYSARIA* (OROBANCHACEAE)

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ABSTRACT

Orthocarpus erianthus var. *gratiosus* from the near-coast region of northwestern California and adjacent southwestern Oregon is resurrected and assigned to the genus *Triphysaria* as ***Triphysaria eriantha* subsp. *gratiosa*** (Jeps. & Tracy) Egger, **comb. nov.** Range maps and a key to the subspecies of *T. eriantha* are presented, as well as photographs to aid in their field identification.

The taxonomic entity *Orthocarpus erianthus* var. *gratiosus* Jeps. & Tracy was first proposed by W.L. Jepson and J.P. Tracy (Jepson 1925, p. 941), which they distinguished from other forms of the species primarily by the unique coloration of the inflated lobes of the abaxial lip of the corolla, in which the middle lobe is yellow, while the two lateral lobes are a strongly contrasting white. The *gratiosus* form was subsequently accepted in several floras and treatments (Keck 1927, 1951; Peck 1941; Munz and Keck 1959; Smith and Sawyer 1988; Smith and Wheeler 1990-1991), spanning over five decades. It was also mentioned by name and photographically documented in the popular literature (e.g., Eastman 1991).

However, Chuang and Heckard (1991) transferred several *Orthocarpus* species, including *O. erianthus* Benth., to *Triphysaria* Fischer & Meyer, a move later supported by phylogenetic studies (e.g., Tank et al. 2009). In the same paper, Chuang and Heckard also reduced *O. erianthus* var. *gratiosus* to synonymy (without comment) under their new combination, *Triphysaria eriantha* subsp. *rosea* (A. Gray) Chuang & Heckard. However, two years later (Chuang and Heckard 1993), they transferred the synonymy of var. *gratiosus* to *T. eriantha* subsp. *eriantha*, where it has remained in subsequent treatments, including that of *Triphysaria* in the Flora of North America North of Mexico (Zacharias 2019).

It is likely that the 1991 placement of var. *gratiosus* in subsp. *rosea* was due to an error during page setting (M. Wetherwax 2024, pers. comm.). However, its synonymy under subsp. *rosea* is still indicated in the International Plant Names Index and related internet sites, such as Plants of the World Online. As a result of this confusion, some specimens of var. *gratiosus* have since been synonymized under *T. eriantha* subsp. *rosea*, while many others are now listed under subsp. *eriantha*. This is especially true for online regional specimen catalogues, such as the California Consortium of Herbaria and the Consortium of Pacific Northwest Herbaria. To our knowledge, no authors have published a justification for the synonymy of the long-accepted var. *gratiosus* under either subsp. *rosea* or subsp. *eriantha*. While the largely separate ranges and lack of morphologically introgressive intermediates suggests that the three subspecies of *T. eriantha* might be better treated at the species level, genetic and morphological studies of the entire genus are ongoing, and we prefer to maintain the nomenclatural

stability the genus has achieved in the last three decades until a comprehensive revision of *Triphysaria* can be presented. The goal of this paper is more limited.

Studies of *Triphysaria* by Egger over several decades confirm the earlier treatment of *Orthocarpus erianthus* var. *gratiosus* as a morphologically distinctive form of the species with an essentially parapatric range and justifiably worthy of nomenclatural recognition, while also supporting its placement in the resurrected genus *Triphysaria*. Since it has no published name in *Triphysaria*, we propose the following new combination, as well as rank, in accordance with the present nomenclature assigned to that genus and followed in all recent treatments cited above.

Triphysaria eriantha subsp. **gratiosa** (Jeps. & Tracy) J.M. Egger, **comb. et stat. nov.** *Orthocarpus erianthus* Benth. var. *gratiosus* Jeps. & Tracy, Manual of the Flowering Plants of California 941. 1925. **TYPE: USA. California.** Humboldt Co.: Sand hills, Eureka, Humboldt Bay, 18 May 1901, *J.P. Tracy 2035* (holotype: JEPS, Fig. 3).

The only other known herbarium specimen labeled as *Tracy 2035* is at UC (Fig. 4), but it is not regarded as part of the type gathering. Tracy's original label, as well as detailed annotations by Tracy and by D.D. Keck in 1926 indicate that the UC sheet contains a single specimen of a hybrid between *Orthocarpus erianthus* var. *gratiosus* and *O. pusillus* Benth., the latter now identified as *Triphysaria pusilla* (Benth.) Chuang & Heckard. We concur in this identification. Tracy's annotation on the UC sheet states that "This was found growing in a patch of *O. pusillus*, near where *O. erianthus* var. *gratiosus* also grew abundantly."

Representative specimens examined. California. Del Norte Co.: W side of Hwy 101, Crescent City Beach, 23 May 1941, *Van Deventer s.n.* (HSC); near Fort Dick, 4 May 1961, *Van Deventer s.n.* (HSC), 19 May 1962, *Rockwell 62-0093* (FSC); Kellogg Ranch, 30 Apr 1939, *Van Deventer s.n.* (HSC); N of Lake Earle, 30 Apr 1939, *Van Deventer 315* (JEPS); Pacific Shores near Lake Talawa, 1 Jun 1967, *Hobart s.n.* (HSC); dunes W of Smith River, 7 Jun 1977, *Thiers 37621* (SFSU). Humboldt Co.: Vicinity of Garberville, Jun 1887, *Marshall 468* (HSC), 8 May 1927, *Tracy 7984* (UC), 1 May 1932, *Tracy 9888* (JEPS); Ryan's Slough Hill, near Eureka, 2 Jun 1898, *Tracy 229* (WTU); near Bucksport, region of Humboldt Bay, 9 Apr 1899, *Tracy 136* (JEPS), 1 May 1904, *Tracy 15322* (JEPS, WTU, US), 30 May 1911, *Tracy 3207* (UC), 12 May 1912, *Tracy 3633*, 24 Apr 1927, *Tracy 7946* (JEPS), 14 May 1944, *Tracy 17465* (JEPS); Humboldt Bay, 1 May 1901, *Chandler 1142* (GH, JEPS, UC); Bear River Ridge, 10 Jun 1942, *Harris 1474* (GH, MUHW, NCSC, RSA-POM, TENN, UBC, UC, WTU); sand dunes of Ocean Beach at Humboldt Bay, 14 Apr 1901, *Tracy 1020* (UC), 24 Apr 1904, *Tracy 2019* (GH, UC, US); Kneeland Prairie, 10 Jun 1906, *Tracy 2477* (UC); Little River Beach, 30 May 1917, *Tracy 4805* (JEPS[2]); Eureka, 24 Apr 1904, *Tracy 2035* (UC), 26 Apr 1924, *Jones s.n.* (RSA-POM), Apr 1927, *Hutchinson s.n.* (SBBG); S Fork of Eel River, Phillipsville, 24 Apr 1921, *Tracy 5473* (UC); terraces near Petrolia (Mattole Valley), 10 May 1932, *Tracy 9947* (UC); sand dunes at Samoa, Humboldt Bay, 3 Apr 1941, *Tracy 16805* (JEPS, WTU); along road to Patrick Point State Park, 28 Jul 1941, *Peirson 13107* (RSA); dunes, Samoa Peninsula, 25 Apr 1954, *Rose 54014* (RSA), 24 Apr 1966, *Braa 9* (FSC), 16 Apr 1971, *Nelson 382* (HSC), 24 May 1975, *Montalvo 275* (HSC), 25 Mar 1978, *Pava 22* (SFSU), 2 Apr 1980, *Stopher 45* (CHSC), 29 Mar 2002, *Pickart 17* (HSC); 1 mi W of Petrolia, 18 Jun 1950, *Tracy 18765* (UC); near Fairhaven, Samoa Peninsula, 19 Apr 1960, *Winter s.n.* (HSC), 1 May 1963, *Woodside 21* (HSC), 2 Mar 1963, *Forester 26* (HSC), 19 May 1964, *Francis 45* (HSC), 9 May 1979, *Miller 5-115* (HSC); 0.5 mi off the Samoa road, 7.5 mi SW of Arcata, 11 May 1963, *Vernimen 54* (RSA); U.S. 101 at the Little River turnoff, 12 May 1965, *Thurman 669* (UC); 4.4 mi S of Samoa, 8 Apr 1965, *Thurman 626* (HSC, RSA); 1 mi W of McKinleyville, past the end of Murray Rd, 14 May 1965, *Hawks 56* (HSC); End of Murray Rd, W of Hwy 101, 9 Apr 1975, *Specht 124* (HSC); North Spit of Humboldt Bay, 4 Jun 1976, *Sorenson s.n.* (HSC), 11 Apr 1984, *Janeway 729* (CHSC); E of Samoa Drag Strip, 16 Apr 1979, *York 231* (SCC); Elk River Wildlife Area,1 May 1982, *Newton 2487* (HSC); coastal prairie, N of Inglenook Fen, ca. 5

mi N of Fort Bragg, 28 May 1983, Wheeler 3403 (HSC); W of Eureka, ca. 3 mi S of Samoa Bridge, 18 Apr 1985, *Straley 3466* (UBC); Samoa Boat Ramp County Park, 16 Apr 1998, *Oswald 8916* (CHSC); before McNutt Gulch on Mattole Rd, 40.34504 -124.32524, 1 Apr 2011, *Wheeler 264* (BLMAR); U.S. Hwy 101 ca. 9.5 mi S of Garberville, just N of Mendocino Co. line, 24 Mar 2016, *Halse 9683* (CHSC, RENO, SRP); Lost Coast. Mattole Road, ca. 10 km NW of Petrolia, 4 Apr 2021, *Giblin 8039* (WTU). Mendocino Co.: S Fork of Eel River, near Humboldt-Mendocino county line, near Piercy, 14 Apr 1929, *Tracy 8535* (JEPS, UC); South Fork of Eel River at the Humboldt-Mendocino county line, 3 Apr 1941, *Tracy 16832* (JEPS, WTU); in Piercy, *Pendell 162* (UC); along CA Hwy 271, ca. 0.25 mi NW of Piercy exit from U.S. Hwy 101, on E bluffs above S. Fk. Eel River, 16 Apr 2003, *Egger 1264* (WTU); jct of CA Hwy 271 and U.S. Hwy 101, ca. 1 mi N of Piercy exit and just S of Humboldt/Mendocino County line, on both sides of Hwy 101, 16 Apr 2003, *Egger 1265* (WTU); margins of U.S. Hwy 101, ca. 0.5 mi. S of Humboldt/Mendocino county line, on E side of Hwy 101, 16 Apr 2003, *Egger 1267* (WTU[3]). **Oregon.** Coos Co.: near Bandon, 15 May 1938, *Bradley 133* (WTU), 28 May 1967, *Godfrey 79* (SOC), 6 May 1993, *Helmcamp s.n.* (UCR); Two miles S of Bandon, 31 May 1953, *Bergin s.n.* (HPSU); ca. 8 km N of Langlois, 1 km N of Croft Lake, 14 May 1979, *Sundberg 452* (OSC-ORE); Bullards Beach State Park; Hwy 101 N of Bandon, 26 Apr 1986, *Bridges 38* (LINF); near mouth of Fourmile Creek, 28 Apr 1997, *Newhouse 97-016* (OSC); Bullard's Bay State Park, across bay from Bandon, open sandy flats along road to lighthouse, T28S, R14W, Sec. 18, SW1/4, 17 May 2001, *Chambers 6294* (OSC, WTU). Curry Co.: Port Orford, 23 Jun 1919, *Peck 8477* (OSC-WILLU, WTU), 4 May 1932, *Oshanic s.n.* (OSC); mouth of the Winchuck River, 15 Jul 1919, *Peck 8847* (OSC-WILLU), 22 Apr 1984, *Berg 533* (HSC, OSC); mouth of Rogue River, Gold Beach, 15 May 1923, *Ingram 2179* (SOC[2]); sandy field, Pistol River, 18 May 1929, *Henderson 10270* (OSC-ORE); Pistol River Sand Dunes, 11 Jun 1929, *Leach 2546* (OSC-ORE); beach N of Brookings, May 1932, *Zeller s.n.* (OSC), 15 mi S of Gold Beach, 20 May 1933, (SBBG); 1 May 1972, *Hansen 1588* (HPSU); sandy bank, Pistol River, 26 Mar 1936, *Peck 18883* (OSC-WILLU, WTU); near mouth of Pistol River, 21 Jun 1936, *Thompson 12821, 12824* (WTU); Agate Beach, Port Orford, 27 Apr 1940, *Rogers s.n.* (OSC); Port Orford, 11 Jun 1940, *Baker1802* (ID); coastal strand, Gold Beach, 6 May 1951, *Balls 16457* (WTU); Doyle's Ranch, N side Rogue River, along Squaw Creek, 6 May 1951, *Balls 16467* (WTU); Brookings, Del Norte Filtration Plant, May 1967, *Coleman s.n.* (SOC); "beach area," 7 May 1967, *Phillips 176* (SOC); Oregon-California state line at coast, 7 May 1967, *Kuhl 90* (SOC); Gold Beach, sandy field at edge of airport, 27 Apr 1975, *Johnston 3024* (OSC); Gold Beach, along Jerry's Flat Road ca. 0.5 mi E of its junction with U.S. Hwy 101, 29 May 2005, *Halse 6732* (OSC).

Distribution and ecology. Aside from the consistent differences in corolla coloration, a significant factor in resurrecting and retaining subsp. *gratiosa* is its largely parapatric distribution (Figures 1–2). This conclusion is supported by the herbarium specimens cited above, numerous posts of photographic observation on the iNaturalist website, and our own field studies. While subsp. *gratiosa* more closely resembles the typical form of *Triphysaria eriantha* in coloration, its ecology is more like that of subsp. *rosea*. *Triphysaria eriantha* subsp. *eriantha* is a common element of the California flora from Santa Barbara and Kern counties northward, from near the coast to about 1000 meters elevation on the western slopes of the Sierra Nevada, throughout the coastal ranges and the San Joaquin and Sacramento valleys, while becoming less common to the north and reaching its northern limit in Jackson and Josephine counties in southwestern Oregon. Occasional plants occur beyond the core area, usually as waifs. While subsp. *eriantha* is often found in near-coastal situations, it is rarely found on the immediate coast.

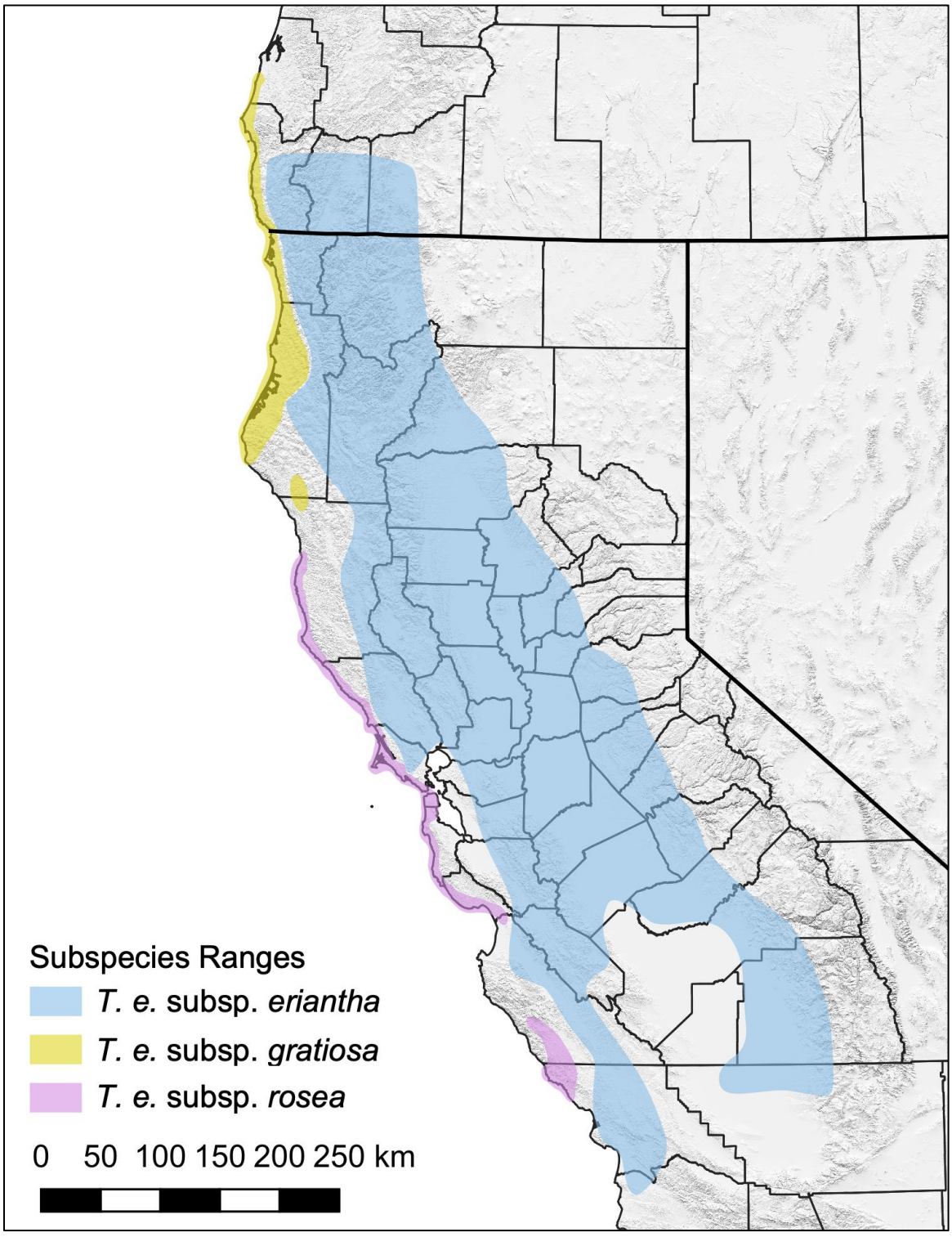

Figure 1. Approximate ranges of the subspecies of *Triphysaria eriantha* in California and southwestern Oregon.

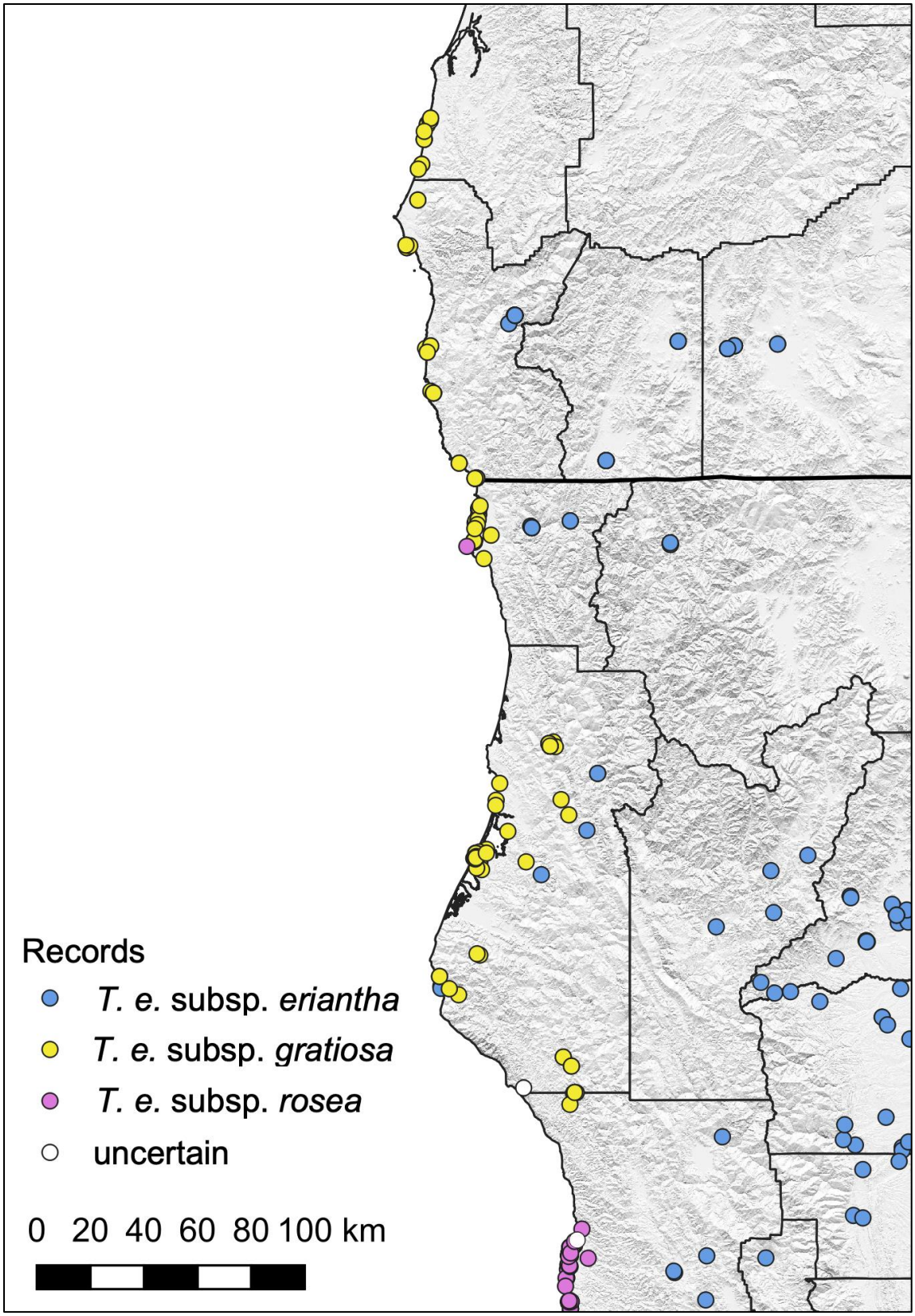

Figure 2. Distribution records of the subspecies of *Triphysaria eriantha* in northwestern California and southwestern Oregon. Data points represent both herbarium specimens and verified field images from the iNaturalist website.

Conversely, both subsp. *rosea* and subsp. *gratiosa* occur in greatest numbers on sandy bluffs, flats, low dunes, and hills on or close to the immediate coast and are rarely found more than 15–20 kilometers inland. Subspecies *rosea* is found from San Luis Obispo County sporadically in appropriate habitat northward to the Fort Bragg region of Mendocino County. Occasional waifs are recorded elsewhere. In contrast, subsp. *gratiosa* essentially replaces subsp. *rosea* to the north, extending from extreme northern Mendocino County northward in appropriate habitat to coastal Oregon, where it apparently reaches its northern limit in the vicinity of Bandon in Coos County. In addition to its primarily coastal distribution, subsp. *gratiosa* is also found in a few meadowy or roadside situations away from the immediate coast, especially in the vicinity of Garberville, Humboldt County, south to Piercy in northern Mendocino County. In Oregon, subsp. *gratiosa* is strictly coastal.

While there are a few valid reports of subsp. *rosea* within the range of *Triphysaria eriantha* subsp. *gratiosa*, other reports and annotations prove to be false, due to the nomenclatural confusion discussed above and the occurrence of atypical color morphs discussed below. In addition, the examination of herbarium sheets can result in significant confusion from the effects of drying on the color or the corollas. While the more deeply pigmented specimens of subsp. *rosea* usually retain hints of their color when dried, in all three subspecies, the white- and/or yellow-colored flowers almost always dry to a dull off-white, completely masking the distinctive color patterns that distinguish them as key characters in the field. This phenomenon was noted first by Keck (1927), "In the older herbarium specimens of this variety (*gratiosus*) the lower lip appears uniform in color. In the field the plants are decidedly distinct from var. *typicus*."

Identification of the subspecies of *Triphysaria eriantha*. Living or freshly collected specimens of all three subspecies are readily identified using the key below. Older, dried specimens are more problematic, but descriptive notes added to the labels by the collector can be helpful, as well as the location of the collection. Some older specimens remain difficult to place with certainty. All three subspecies can vary greatly in height, number of stems, and angle of branching from the base. Plants found in open habitats on the immediate coast are usually clumped and the stems are often produced from the base at divaricate angles, while those found inland tend to be considerably taller and emerge upright or at an ascending angle. In our experience, none of the three subspecies occurs in mixed populations with other subspecies.

Key to the subspecies of *Triphysaria eriantha*

1. Corollas mostly pale to deep rose-pink or purple, or the abaxial lip white, fading to rose-pink; plants mostly limited to the coastal and near-coastal regions of central California ..... subsp. **rosea**
1. Corollas mostly yellow or yellow with the two lateral lobes of the abaxial lip white; plants of western California and southwestern Oregon but largely absent from the range of subsp. *rosea*.

    2. Abaxial lobes of the corollas entirely pale to bright yellow; plants widespread in western California and adjacent southwestern Oregon, mostly away from the immediate coast ..... subsp. **eriantha**
    2. Abaxial lobes of the corollas with the central lobe yellow and the lateral lobes white; plants limited to the coastal and near-coastal regions from northern Mendocino Co., California, north to southern Coos Co., Oregon ..... subsp. **gratiosa**

As an aid to field identification, images of each subspecies of *Triphysaria eriantha* are presented below. Subspecies *gratiosa* is seen in Figures 5-9, subsp. *eriantha* in Figures 10-13, and subsp. *rosea* in Figures 14-17. All field photos below are by Egger except where noted. Many more images of *Triphysaria* are found on the first author's Flickr site (Egger 2024).

Rare color variants in *Triphysaria eriantha*. The occurrence of rare and sporadic color variants can be confusing in assigning them to a given subspecies and have resulted in incorrect identifications in a few cases. One such variant of subsp. *eriantha* has been recorded a few times in recent years in photos from northern Napa County and adjacent southern Lake County, as well as from Tuolumne County, California on the iNaturalist and CalFlora websites. Several of these images are presented in Figures 12–13. These mostly reddish-orange forms vary somewhat in shade but are alike in that all three corolla lobes are the same shade within an individual plant, as is the yellow in the typical plants of this subspecies. In contrast, similarly rare color forms are known for subsp. *gratiosa* from the Samoa Peninsula on the west side of Humboldt Bay. An example of that form, shown in Fig. 9, preserves the color pattern of this subspecies in that the central lobe of the abaxial lip is orange-red, while the lateral lobes are rose-purple. The fact that the rare color variants follow the same pattern in the distribution of color on the three lobes of the abaxial lip of both subsp. *gratiosa* and subsp. *eriantha* also suggests support for their treatment as separate taxa. At least some reports of subsp. *rosea* from areas north on Mendocino County are attributable to variants like that seen in Fig. 9.

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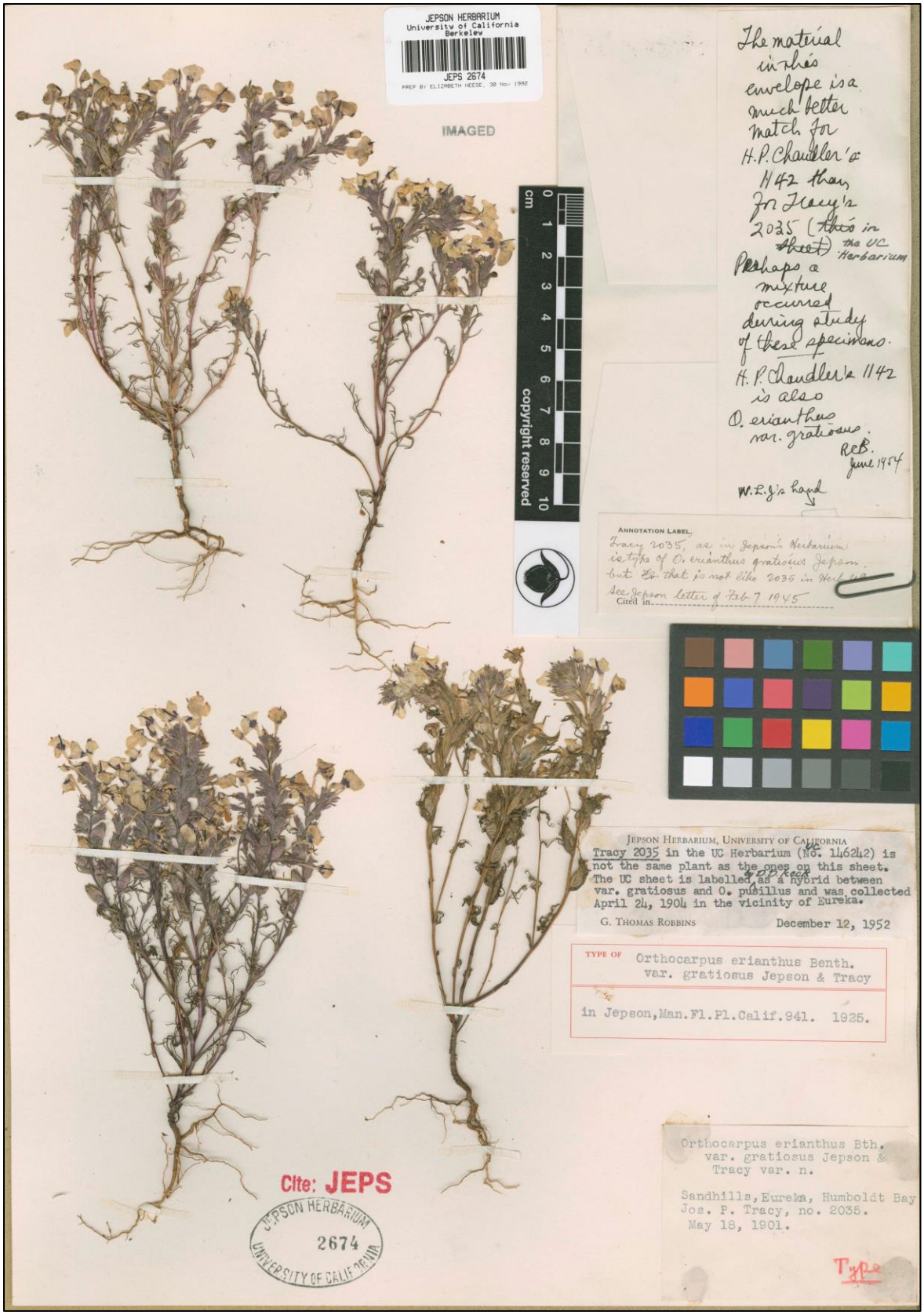

Figure 3. Holotype of *Orthocarpus erianthus* var. *gratiosus*, *Tracy 2035* (JEPS).

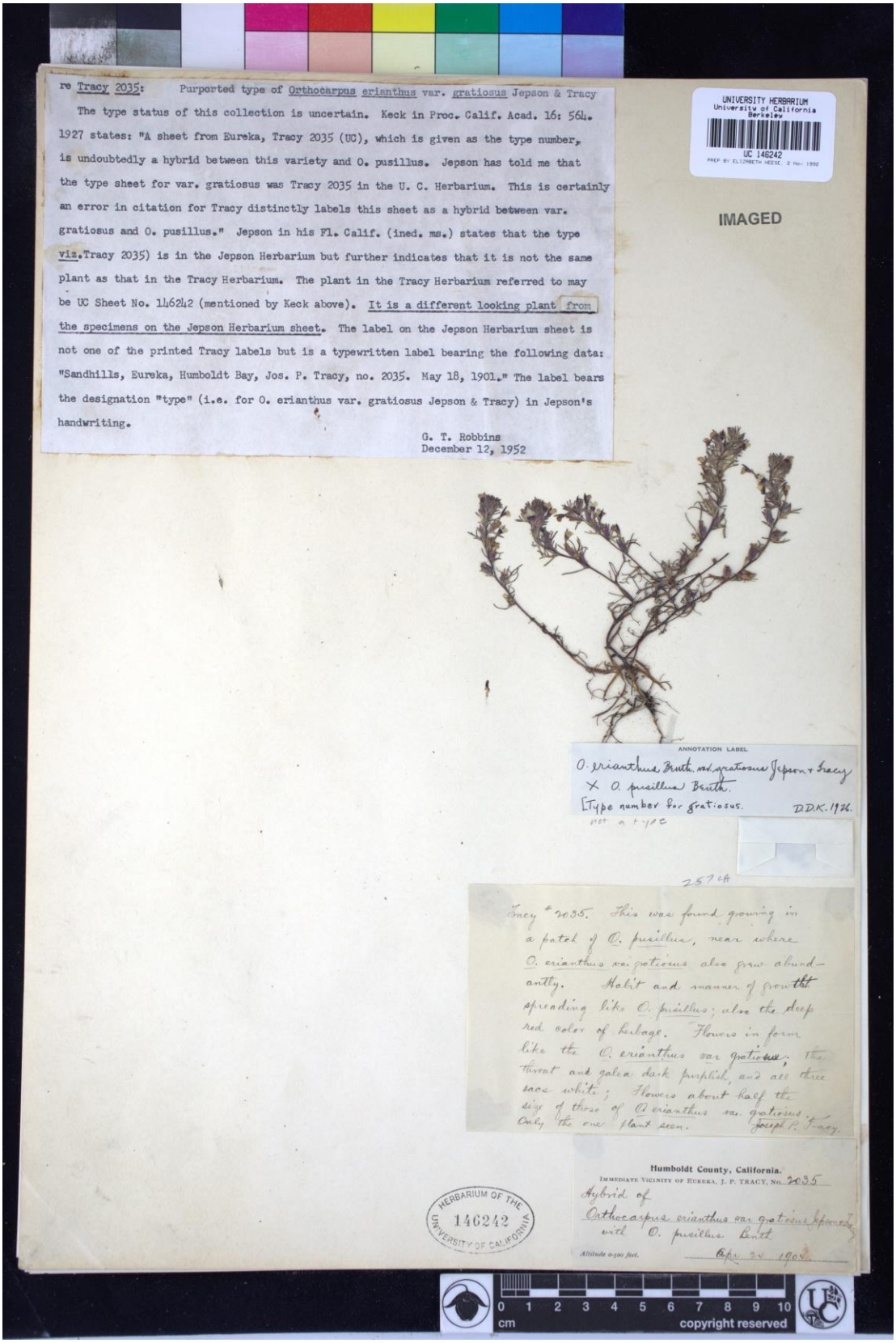

Figure 4. The UC sheet of *Tracy 2035*, with notes by Tracy and (later) Keck explaining why this is not part of the type collection of *Orthocarpus erianthus* var. g*ratiosus*.

Figure 5. *Triphysaria eriantha* subsp. *gratiosa*, inland growth form, near South Fork Eel River, north of Piercy, Mendocino Co., California, 16 Apr 2003.

Figure 6. *Triphysaria eriantha* subsp. *gratiosa*, inland growth form, near South Fork Eel River, north of Piercy, Mendocino Co., California, 16 Apr 2003.

Figure 7. *Triphysaria eriantha* subsp. *gratiosa*, inland growth form, near South Fork Eel River, north of Piercy, Mendocino Co., California, 16 Apr 2003.

Figure 8. *Triphysaria eriantha* subsp. *gratiosa,* coastal growth form, Tolowa Dunes State Park, Del Norte Co., California, 12 May 2023. Photo by Don Hollander, used with permission.

Figure 9. *Triphysaria eriantha* subsp. *gratiosa*, coastal growth form, typical plants with a remarkable color variant plant, near Samoa Field Airport, Samoa Peninsula, Humboldt Bay, Humboldt Co., California, 3 May 2023. Photo by Claudia Voigt, used with permission. Note the central corolla lobe is orange-red, while the two lateral lobes are rose-purple, preserving the general bicolored pattern characteristic of subsp. *gratiosa*.

Figure 10. *Triphysaria eriantha* subsp. *eriantha*, adjacent to White River Road just S of its easternmost crossing of the Kern-Tulare Co. line, Greenhorn Mountains, Kern Co., California, 30 Mar 2016.

Figure 11. *Triphysaria eriantha* subsp. *eriantha*, adjacent to White River Road just S of its easternmost crossing of the Kern-Tulare County line, Greenhorn Mountains, Kern Co., California, 30 Mar 2016.

Figure 12. *Triphysaria eriantha* subsp. *eriantha*, typical form with rare color variant, Zim Zim Falls area, Lake Co., California. Photo by Ken-ichi Ueda, used with permission.

Figure 13. *Triphysaria eriantha* subsp. *eriantha*, rare color morphs. Upper: Zim Zim Falls area, 13 Apr 2019, Napa Co., California. Photo by Ken-ichi Ueda. Lower: SE of New Melones Lake, Tuolumne Co., California, 9 Apr 2018. Photo by Charles Russell. Both photos used with permission.

Figure 14. *Triphysaria eriantha* subsp. *rosea*, rose-pink coastal morph, near Pt. Reyes Lighthouse, Marin Co., California, 14 Apr 1992.

Figure 15. *Triphysaria eriantha* subsp. *rosea*, white coastal morph. Upper: Pt. Reyes Microwave Site, Marin Co., California, 14 Apr 1992; lower: San Bruno Mountain, San Mateo Co., California, 3 Apr 2018.

Figure 16. *Triphysaria eriantha* subsp. *rosea*, white inland morph, near Wagon Caves, Santa Lucia Range, Monterey Co., California, 17 Apr 2019.

Figure 17. *Triphysaria eriantha* subsp. *rosea*, white and rose-purple inland morphs, near Wagon Caves, Santa Lucia Range, Monterey Co., California, 17 Apr 2019.