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A NEW JEWELFLOWER (*STREPTANTHUS*, BRASSICACEAE) FROM MARIN COUNTY, CALIFORNIA, USA

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ABSTRACT

Streptanthus anomalus D.L.Smith, A.Arthur, & R.E.Preston is a newly described species growing on serpentine soils in the vicinity of Mount Burdell in Marin County, CA. Floral morphology and other characters indicate that this taxon is most closely related to the *S. glandulosus* complex, but the bracted inflorescence is unlike that found in any other member of that complex. This very rare serpentine endemic, restricted to two known populations, merits recognition as a species of conservation concern.

Key Words: California, endemism, floristics, rare species, serpentine, taxonomy.

The genus *Streptanthus* Nutt. currently consists of about 35 species in western North America, with the primary center of diversity in California (Al-Shehbaz 2010), although the circumscription of infrageneric and intraspecific taxa is likely to change in the near future as new findings based on DNA data become available (Cacho et al. 2014). The genus is well-known as the subject of many ecological studies, especially with respect to edaphic endemism (Kruckeberg 1951; Reeves et al. 1981; Boyd et al. 1994; Strauss and Cacho 2013). The common name "jewelflower" stems from the brightly colored sepals, which vary among species from green, to bright yellow, to white, to pink, to a deep reddish-purple.

In May 2011, during a rare plant survey of a property in Marin County, Aaron Arthur encountered a jewelflower population with wine-red sepals that initially struck him as possibly one of several subspecies of *Streptanthus glandulosus* Hook. that occur in that region. However, the plants did not key well using The Jepson Manual (Buck et al. 1993), Marin Flora (Howell et al. 2007), or A Flora of Sonoma County (Best et al. 1996) and individuals did not fit the taxonomic descriptions in The Jepson Manual.

In May 2012, Doreen Smith also encountered an unfamiliar jewelflower in the same general area, although these plants had yellow sepals. Plants in both populations were characterized by deep yellow, ovate leaves and bracts that stood out distinctly from the surrounding grassland. Because the most distal bracts subtended the proximal one or two flowers, the plants most closely resembled *S. tortuosus* Kellogg and keyed fairly well to that species in most recent treatments of *Streptanthus* (Rollins 1993; Buck et al. 1993; Al-Shehbaz 2010, 2012).

The authors sent photographs to several *Streptanthus* authorities for help with identifying the plants, and the general consensus was that these populations had characteristics of both *S. tortuosus* and *S. glandulosus* and probably represented an unusual form of *S. tortuosus*. However, photographs of the plants posted online as *S. tortuosus* at the CalPhotos website (https://calphotos.berkeley.edu/flora/) came to the attention of the lead author, who immediately recognized that the plants were not *S. tortuosus*, based on his extensive experience with the floral morphology and pollination biology of that species (Preston 1991, 1994). A subsequent visit to one of the populations confirmed that this was a distinctive new taxon, and samples of the flowers, leaves, and seeds were collected for further analysis. Dissection of the flowers indicates that the plants are closely related to members of *Streptanthus* section *Euclisia* Kruckeberg and Morrison, which consists of *S. glandulosus* and its multiple subspecies. Members of section *Euclisia* have carinate sepals, upper stamens with connate filaments (filaments of lower stamens not connate) and much smaller or sterile anthers, a round, flat stigma, and flattened siliques that are glabrous or hispid. Because the bracted inflorescence is unique among section *Euclisia*, the new taxon is recognized at species rank.

This remarkable new species, growing in close proximity to a large suburban population and in a well-traveled area, adds to the growing list of floristic surprises found "in our backyards" (Ertter 2000).

Taxonomic Treatment

Streptanthus anomalus D.L.Smith, A.Arthur, & R.E.Preston, sp. nov. (Figs. 13).—Type: USA, California, Marin Co., Mt. Burdell, County open space, 25 May 2015, *Doreen L. Smith s.n.* (holotype: CAS1202615).

Allied with *Streptanthus glandulosus* Hook., but differs by having conspicuous ovate, deeply clasping distal leaves that bract the inflorescence below or above the proximal flower.

Plants annual. **Stems** erect, simple to branched, lower stems and leaves with stiff, bulb-based hairs, reddish-tinged, 1.5–4.0(–6) dm tall. **Leaves** rosetted basally, basal blades oblanceolate, dentate, margins ciliate, faces with scattered short, stiff hairs, 3–5 cm long; proximal cauline leaves clasping, oblong, dentate, margins ciliate, 3–4 cm long; basal and lower cauline leaves generally deciduous by flowering; distal leaves deeply clasping, ovate, entire to distally dentate, glabrous, turning yellow by flowering, 1–2.5 cm long, 0.5–2 cm wide. **Flowers** divaricately ascending to horizontally spreading, ± secund, pedicels 2–3 mm long. **Sepals** yellow or purple, medially keeled, tips obtuse, erect, glabrous or with short bristles, 6 mm long. **Petals** exserted, base yellow, blades brown to purple with white margins, 7–9 mm long. **Stamens** in three unequal pairs, ± exserted, anthers of the lateral stamens larger than those of the lower stamens, upper stamens with fused filaments, sterile anthers. **Siliques** straight to arcuate, glabrous or with sparse, short, stiff bristles, 4–7 cm long, 3–4 mm wide. **Seeds** 30–40, 2 mm long, 1.75 mm wide, narrowly winged all around.

Paratypes: USA, California, **Marin Co.**, San Antonio Creek watershed, north side of greater Mt. Burdell Ridge, 07 Aug 2011, *A. Arthur 10* (CAS1204602); Mt. Burdell Open Space, 21 June 2015, *R. E. Preston 3006* (DAV). [Note: We were unable to locate any prior or additional specimens.]

Etymology

The specific epithet "anomalus" alludes to the anomalous possession of bracted inflorescences that led to the initial hypothesis that this was an odd form of *S. tortuosus*. We suggest "Mount Burdell jewelflower" as the common name for this species.

Phenology and Reproductive Biology

Streptanthus anomalus is an annual species that germinates in response to winter rains and forms rosettes during the early spring. The plants bloom from mid-May through mid-June. Sepal color is polymorphic, being wine-red in one population and bright yellow in the other population (Fig. 2). Sepal color is generally uniform within *Streptanthus* populations, but in some species, sepal color can vary among subspecies or even among populations (Hoffman 1952; Kruckeberg 1957a; Kruckeberg et al. 1982; Kruckeberg and Morrison 1983; Dolan and LaPré 1989; Boyd et al. 2009; Mayer and Beseda 2010). Leaf morphology changes substantially as the plants develop (Figs. 1, 3). The basal rosette leaves are sessile, oblong, with dentate margins, and hirsute with bulb-based trichomes. Leaves developing distally become oblong, are clasping at the base, and are less hairy than basal leaves. The upper leaves are ovate, deeply clasping, with entire to dentate margins, and are glabrous. The leaf teeth are often tipped with orange hydathodes, which contrast strongly with the dark green of the leaves. These colored structures are found in other serpentine-endemic *Streptanthus* species and appear to be egg-mimics of Pierid butterflies that reduce the level of oviposition and subsequent herbivory (Shapiro 1981).

Streptanthus species are self-compatible, but predominantly outcrossing, requiring pollinator visits for seed set due to a combination of protandry and spatial separation of the anthers and stigmas (Rollins 1963; Preston 1991, 1994; Dieringer 1991). In *S. anomalus*, however, the sepals, petals, and stamens remain erect, so that there is relatively little spatial separation of the anthers and stigmas (Fig. 2), which may indicate some level of self-pollination. Kruckeberg (1957b) reported a similar floral morphology for *S. glandulosus* subsp. *niger* (Greene) Al-Shehbaz, M.S.Mayer & D.W.Taylor, observing that the anthers remain included in the mouth of the corolla, so that the stigma picks up pollen from them as the pistil elongates, and concluding that the flowers were self-pollinating. Unopened flowers (n = 7) and mature siliques (n = 29) were collected in the field on June 21, 2015 (vouchered by *Preston 3006*). Pollen counts were determined following the methods in Preston (1985), and ovule and seed number were determined from dissection of the siliques. The lateral anthers of *S. anomalus* average 37,533 pollen grains per anther, and the lower anthers average 16,000 pollen grains per anther, for a total of 107,066 pollen grains per flower. With an average of 35.3 ovules per ovary, the pollen-ovule ratio is 3,033, which is at the low end of the range for allogamous species in the Brassicaceae and comparable to that for *S. glandulosus* (3,800) (Preston 1985). Strongly outcrossing species in the family, such as *Streptanthus tortuosus,* have a much higher pollen-ovule ratio (5,000–10,000) than *S. anomalous* (Preston 1985; 1994). Seed set in *S. anomalus* was relatively high (mean = 84.9%, range = 55.4–100%). By contrast, seed set in open-pollinated *S. tortuosus* populations averaged 70.7% (range = 61.7–77.3%, six populations) (R. Preston, unpublished data).

Distribution and Ecology

Streptanthus anomalus is known from only two small populations in the vicinity of Mount Burdell, in Marin County. The plants grow in grassy openings in

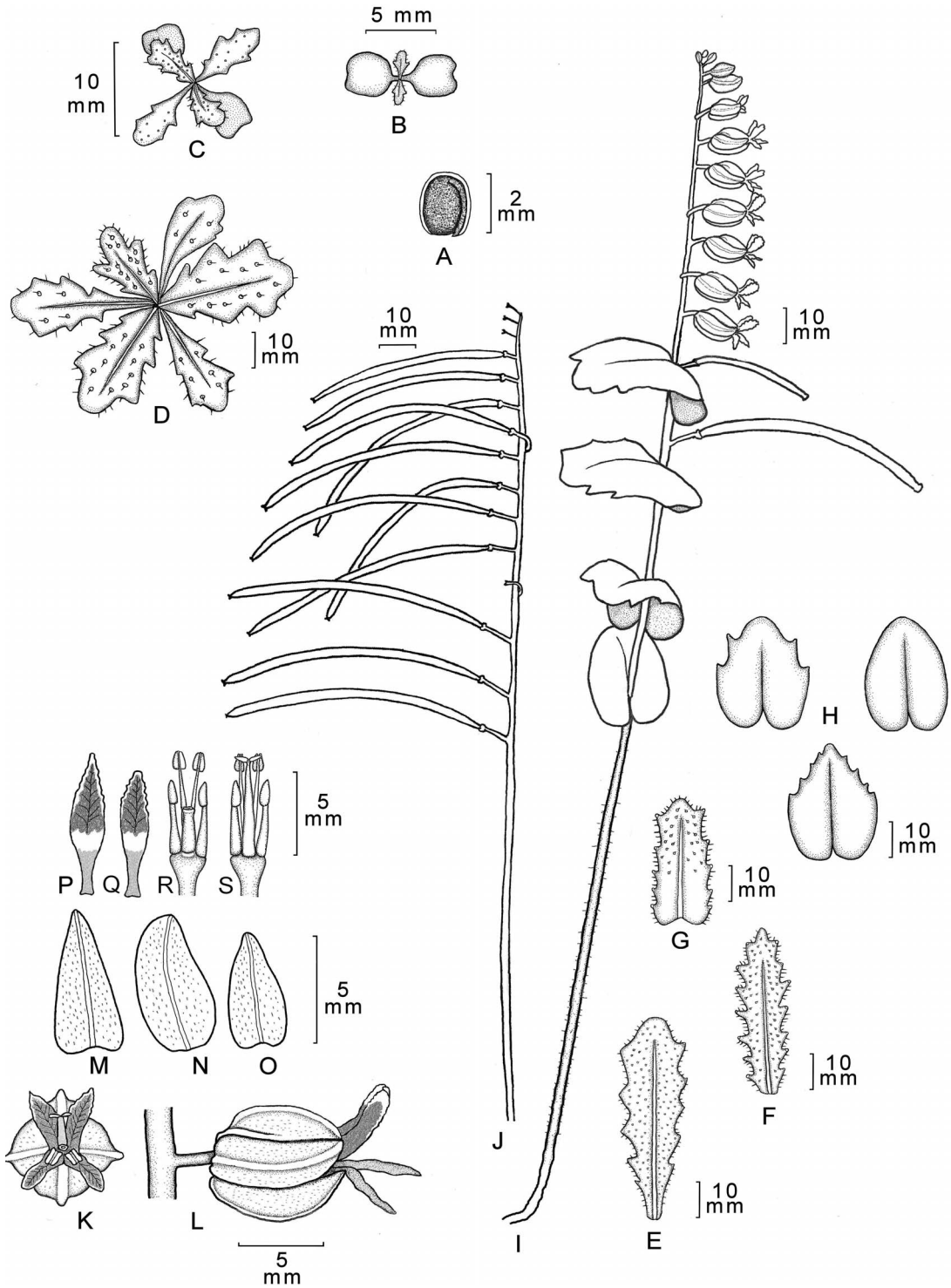

FIG. 1. Illustration of *Streptanthus anomalus*. A. Mature seed with narrow wing. B–C. Seedlings. B. Cotyledons and first leaves. C. Four-leaf stage. D. Basal leaf rosette. E–H. Stem leaves. E. Basal leaf. F. Lower cauline leaf. G. Upper cauline leaf. H. Bracting leaves, showing leaf margin variation. I. Habit at anthesis. J. Mature siliques. K–J. Flower at anthesis. K. Frontal view. L. Lateral view. Sepals. M. Abaxial sepal. N. Lateral sepal. O. Adaxial sepal. P–Q. Petals. P. Adaxial petal. Q. Abaxial petal. R–S. Stamens. R. Adaxial stamens removed to show ovary. S. Adaxial view of stamens showing connate adaxial stamens with vestigial anthers. From live material, vouchered by *Preston 3006*.

FIG. 2. Inflorescence, flowers, and fruits of *Streptanthus anomalus*. Upper left: wine-red-flowered morph. Upper middle: yellow-flowered morph. Upper right: close-up of flowers, showing the relative position of petals, anthers, and the stigma. Lower: inflorescence, showing the bracts and developing siliques.

oak woodlands (Fig. 4) on serpentine soils, between 50 and 115 m in elevation. The ridgeline supporting the northern population is mapped as Henneke stony clay loam (Kashiwagi 1985). These soils are dark rocky clays, formed from residuum weathered from serpentinite. The soil supporting the southern population is mapped as Montara clay loam, which also formed in material weathered from serpentinitic rocks (Kashiwagi 1985). Both soils are shallow, only 20 to 50 cm deep above serpentinite bedrock, and outcrops are common.

Associated species include *Quercus agrifolia* Née, *Quercus durata* Jeps., *Umbellularia californica* (Hook. & Arn.) Nutt., *Festuca microstachys* Nutt., *F. idahoensis* Elmer, *Elymus multisetus* (J.G.Sm.) Burtt-Davy, *Koeleria macrantha* (Ledeb.) Schult., *Triteleia laxa* Benth., *Brodiaea elegans* Hoover, *Sisyrinchium bellum* S.Watson, *Eriogonum luteolum* Greene var. *caninum* (Greene) Reveal, *Eriogonum nudum* Benth., *Leptosiphon androsaceus* Benth., *Eschscholzia californica* Cham., *Chlorogalum pomeridianum* (DC.) Kunth, *Antirrhinum vexillocalyculatum* Kellogg, *Gilia capitata* Sims subsp. *capitata*, *Acmispon brachycarpus* (Benth.) D.D.Sokoloff, *Hemizonia congesta* DC., *Lessingia ramulosa* A.Gray, *Achillea millefolium* L., *Monolopia major* DC., and *Madia exigua* (Sm.) A.Gray. In addition to *S. anomalus* and *Eriogonum luteolum* var. *caninum*, two other rare serpentine endemic species are present in the serpentine grasslands at Mount Burdell Open Space Preserve, *Fritillaria liliacea* Lindl. and *Hesperolinon congestum* (A.Gray) Small.

FIG. 3. Leaves of *Streptanthus anomalus*. Lower right: basal rosette. Left: lower and middle cauline leaves. Upper right: upper cauline leaves.

TAXONOMIC CONSIDERATIONS

Because *Streptanthus anomalus* possesses characteristics of both *S. glandulosus* and *S. tortuosus* (Table 1), this poses questions about its relatedness to both species and whether it might have had a hybrid origin. In the most recent phylogenetic analysis of the genus *Streptanthus* and its allies (Cacho et al. 2014), the *S. glandulosus* complex (=*Streptanthus* section *Euclisia*) is part of a clade that is basal to the clade containing the Tortuosus Alliance, which includes *S. tortuous*, *S. diversifolius* S.Watson, *S. farnsworthianus* J.T.Howell, and *S. fenestratus* (Greene) J.T.Howell, all of which have bracted inflorescences. The relative position of these two clades in the phylogenetic tree indicates a substantial divergence time between them, with the

FIG. 4. Habitat for *Streptanthus anomalus* at the ecotone between oak woodland and grassland. The serpentine soils are shallow, with scattered rock outcrops.

TABLE 1. COMPARISON OF SIX CHARACTERS IN *STREPTANTHUS GLANDULOSUS*, *S. ANOMALUS*, AND *S. TORTUOSUS*.

	S. glandulosus	*S. anomalus*	*S. tortuosus*
Pubescence	Proximal stems and leaves bristly-hairy	Proximal stems and leaves bristly-hairy	Glabrous throughout
Basal Rosette	Absent	Present	Present
Basal Leaf Morphology	Oblanceolate, dentate	Oblanceolate, dentate	Spatulate, entire to distally dentate
Distal Leaves	Lanceolate to lance-linear, not bracting proximal flowers	Ovate, bracting proximal 1–2 flowers	Round to oblong-ovate, bracting proximal 1–2 flowers
Flowers	Bilateral, sepals strongly keeled	Bilateral, sepals strongly keeled	Weakly bilateral, sepals not or weakly keeled
Upper Stamens	Filaments connate, anthers sterile	Filaments connate, anthers sterile	Filaments free, anthers fertile

S. glandulosus complex diversifying in the Coast Ranges and the Tortuosus Alliance diversifying primarily in the Sierra Nevada. Because reproductive isolation between *Streptanthus* species is strongly correlated with the divergence time between them (Christie and Strauss 2018), a recent hybrid origin of *S. anomalus* seems highly unlikely.

As noted in the introduction, the floral morphology of *S. anomalus* is consistent with members of *Streptanthus* section *Euclisia*. In contrast, flowers of *S. tortuosus* are less strongly zygomorphic, all stamens are free to the base, and all anthers are fertile. Floral character differences, which may have evolved as prezygotic barriers to hybridization, are also strongly correlated with divergence time (Christie and Strauss 2018). Because *S. anomalus* possesses the floral morphology of *Streptanthus* section *Euclisia,* it is best regarded as a member of that section. The strongly dentate proximal leaves and hispid leaves and stems of (Fig. 3), also shared with *Streptanthus* section *Euclisia*, but not with *S. tortuosus*, also support this relationship.

Streptanthus section *Euclisia* currently consists of between seven and nine subspecies of *S. glandulosus* that differ from one another in perianth color, degree of pubescence, and orientation of the flowers and fruits (Al-Shehbaz 2010, 2012; Mayer and Beseda 2010). All the subspecies have lanceolate to lance-linear cauline leaves, and none have distal leaves that are bracting the proximal flowers of the inflorescence. The distinctly-different bracted inflorescence found in *S. anomalus* (Figs. 1, 2), which is its most anomalous and distinguishing feature, supports its recognition at species rank. Future research of *S. anomalus* should focus on understanding whether its morphology represents convergence or a homoplastic loss in the rest of *Streptanthus* section *Euclisia*.

CONSERVATION STATUS

Streptanthus anomalus is extremely rare and localized, with a combined total of less than 1,500 individuals in both populations. The northern larger population is located on private land within a conservation bank, although it is subject to disturbance by grazing cattle. The southern smaller population is secured within the Mount Burdell Open Space, although it is also subject to disturbance by grazing cattle. In 2015, cattle trampling churned up a substantial portion of the southern population when soils were quite soggy from a prior rain event, and in 2018, we observed that only a few viable siliques remained after cattle grazing had occurred. Grazing is often used as a management tool to reduce the cover of alien grasses and potentially reduce the level of competition with native species. Grazing may increase native species richness on sites with serpentine soils (Safford and Harrison 2001; Harrison et al. 2003, but see Harrison 1999), but it may also have direct adverse effects on native species that offset the benefits of reduced competition (Kimball and Schiffmann 2003). The adverse effects of cattle grazing we observed indicate a need for a more focused grazing prescription in the areas where *S. anomalus* is present.

Applying the NatureServe ranking criteria (Faber-Langendoen et al. 2012), the species would likely warrant global (G) and State (S) ranks of 1 (Critically Imperiled — at very high risk of extinction due to extreme rarity [often 5 or fewer populations], very steep declines, or other factors). We recommend a California Rare Plant Rank of 1B.1 (Rare or Endangered in California and elsewhere, seriously threatened in California) in the California Department of Fish and Wildlife (CDFW) Special Plants list (CDFW 2018) and the California Native Plant Society (CNPS) Inventory of Rare and Endangered Plants (CNPS 2018).

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