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A NEW SPECIES OF *STREPTANTHUS* (BRASSICACEAE) FROM THREE PEAKS IN LAKE COUNTY, CALIFORNIA

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ABSTRACT

Streptanthus vernalis is a newly described species inhabiting serpentine rock outcrops in the Three Peaks area in Lake County, California. Morphological and allozyme data indicate that this taxon is related to the *S. morrisonii* complex.

Key Words: *Streptanthus*, serpentine, endemism, new species, allozyme analysis.

In the 1970s and 1980s, botanical researchers who were developing information about the distribution of *Streptanthus morrisonii* F.W. Hoffman subsp. *elatus* F.W. Hoffman observed an undescribed jewelflower near Three Peaks in Lake County, California, USA. Their findings were not published. In this paper, we describe and name this jewelflower and provide the findings of allozyme analysis that indicate the relationship of the new species to morphologically similar species in the region.

SPECIES TREATMENT

Streptanthus vernalis Richard O'Donnell and Rebecca Dolan, sp. nov.—TYPE: USA, California, Lake Co., serpentine talus and gravel less than 0.4 km northeast of Three Peaks, Lake County, California, along an abandoned fire trail between White Point and McGuire Peak. UTM 10 537004E 4282565N (WGS84/NAD83). USGS Detert Reservoir Quad. 610 m elevation. *Richard O'Donnell s.n.* (Holotype: JEPS). Collected May 1, 2004.

Herba annua omnino glabra; caules erecti simplices vel ramose, 2–20 cm alti; folia pauca, plerumque basalia crassa subtu purpurea, supra viridia, 3–4 cm longa; folia inferiora orbiculata vel obovata, saliete crenata, petioles 1 cm longa; folia superiora sessilia, lineri-lanceolata, integra; flores erecti; sepala 6–7 mm longa, viridia apicibus patentibus acutis; petala valde exserta, alba, 2 mm longa; stamina trisericata, superiorum filamentis 7–8 mm longis, connatis; siliquae 4–5 cm longae, erectae, torulosae, ascendentis; semina alata.

Annual. Stem erect, simple or branched, 2–20 cm tall. Leaves few, mostly basal, thick, purple beneath, green above, 3–4 cm long, lower leaves orbicular to obovate, saliently crenate, petioles 1 cm long, upper leaves sessile, linear lanceolate, entire. Flowers erect. Sepals green, tips reflexed, 6–7 mm

long. Corolla flask-shaped. Petals well exerted, equal, recurved, white, 2 mm long. Stamens in three pairs, upper pair 7–8 mm long, filaments exerted, connate to the apex, anthers reduced, reflexed at anthesis, middle pair connate ½ of length, lower pair free. Stigma entire. Silique 4–5 cm long, ascending, torulose. Seeds orange, winged.

Streptanthus vernalis is found in serpentine talus and gravel less than a quarter of a mile northeast of Three Peaks, Lake County, California, along an abandoned fire trail between White Point and McGuire Peak. Plants in the vicinity of the small colony include *Cupressus sargentii* Jepson, *Pinus sabiniana* Douglas, *Arctostaphylos viscida* C. Parry, *Quercus durata* Jepson, *Streptanthus morrisonii* subsp. *elatus* F. W. Hoffman, *Mimulus brachiatus* Pennell, *Minuartia douglasii* Torrey and A. Gray, and *Epilobium minutum* Lehm.

Several rare serpentine endemics occur near Three Peaks, including *Harmonia hallii* (D. D. Keck) B. G. Baldwin, *Cryptantha hispidula* Brand, *Triteleia peduncularis* Lindley, *Hesperolinon spergulinum* A. Gray, and *Solidago guiradonis* A. Gray. Three Peaks is most notable as the type locality for *Streptanthus morrisonii* subsp. *elatus*, discovered there by Freed Hoffman in 1952.

MORPHOLOGY

Neilson first reported an undescribed *Streptanthus* in an unpublished consultant's report (Neilson 1977). He referred to this undescribed taxon as a diminutive variety of the generally much taller *S. morrisonii* subsp. *elatus* and noted that it was fairly common in the vicinity of Three Peaks, an observation we have not been able to confirm. His research also located two herbarium specimens at the Dudley Herbarium (DS) and the California Academy of Sciences (CAS) that he believed were this plant, one of which was labeled *S. morrisonii* subsp. *elatus*. The herbarium specimens indicated

to him that the plant was also to be found north of Three Peaks, near Middletown.

Dolan and LaPrè collected several species of *Streptanthus* in the vicinity of Three Peaks for their biochemical genetic studies of the *S. morrisonii* complex (Dolan and LaPrè 1989). They referred to Neilson's report of the undescribed plant in their unpublished consultants' report (Dolan and LaPrè 1987). They speculated that it might be related to *Streptanthus batrachopus* J. Morrison, known, then and still, from only two sites in Marin County, but they did not develop the speculation further. In the mid-1980s, Steve Edwards and Chris Thayer also observed a small, yellow-flowered jewelflower near Three Peaks that they believed was related to *S. brachiatus* Hoffman (Edwards personal communication).

As shown above, different observers of the undescribed jewelflower in the area adjacent to Three Peaks came to different conclusions about its relationship to other *Streptanthus* species, but all recognized it as unique. Their observations warrant examination. Table 1 compares the morphological attributes of the new species with those of the three others, plus *S. breweri* var. *hesperidis* Jepson.

The comparisons show that all of the species share some characters but that the new species shares few characters with any single one of them. *S. vernalis* has a unique combination of morphological traits. While *S. breweri* var. *hesperidis* resembles *S. vernalis* in stature, branching habit and second inflorescence, its zig-zag stem, overall yellow color (especially its leaves), greenish-yellow calyx, more connivent sepals and later flowering period set it apart from *S. vernalis*. Although similar in size and habit, other morphological attributes separate *S. batrachopus* from *S. vernalis*. In addition, like *S. breweri* var. *hesperidis*, *S. batrachopus* flowers later than *S. vernalis*. Furthermore, the only known colonies of *S. batrachopus* are separated from *S. vernalis* by about 160 km.

Streptanthus vernalis appears, based on morphological features, to be most similar to *S. morrisonii* subsp. *elatus*. They resemble each other in sepal and petal color, and some basal leaf attributes. They also often have a second inflorescence, arranged in a spiral around the main stem: a feature they share with *S. breweri* var. *hesperidis*. On the other hand, *S. morrisonii* subsp. *elatus* is biennial while *S. vernalis* is annual. In addition, the shape of the basal leaves of *S. morrisonii* in its flowering year resemble those of the annual *S. vernalis* initially, but as *S. morrisonii* grows, its basal leaves become longer, wider, and spatulate. They are also mottled purple/brown adaxially. These leaf features are not seen in *S. vernalis*. In addition, the plants exhibit substantial differences in height, habit, and flowering period.

Streptanthus morrisonii and *Streptanthus vernalis* also differ in vestiture of their calyces. *Streptanthus morrisonii* is comprised of three subspecies,

all of which are tall and branched from about the top third of the main stem, not also from the base as in *S. vernalis*. The calyces of *S. morrisonii* vary from glabrous to villous. The calyces of *S. morrisonii* subsp. *elatus* alone vary with respect to vestiture. At Three Peaks the calyces of *S. morrisonii* subsp. *elatus* that we have observed are glabrous (although Nielson found specimens at Three Peaks that were visibly hispidulous), while less than a mile to the east, in an area Nielson is unlikely to have visited due to the extremely difficult terrain, the calyces of the subspecies are usually hispidulous. The calyces of *S. morrisonii* subsp. *elatus* in Butts Canyon are vested with sparse but longer hairs. (Buds from each of these variants of *S. morrisonii* subsp. *elatus* were used in the allozyme analysis.) In contrast, the calyces of *S. vernalis* are uniformly glabrous.

Abaxially the basal leaves in all of the species discussed herein are more or less purple. Most of the species we have compared to *S. vernalis* also have purple/brown mottling on the upper surfaces of their basal leaves, while *S. vernalis* has no mottling.

The tips of the basal leaf teeth and the tips of the cauline leaves are orange in *S. vernalis* as they are in *S. morrisonii* subsp. *elatus*. These may have the same function as the non-green callosities on the marginal teeth of *S. glandulosus* Hooker, which are believed to function as pierid butterfly egg mimics to deter butterfly ovipositing and subsequent predation (Shapiro 1981).

The flowering periods of the jewelflowers compared to *S. vernalis* herein begin after *S. vernalis* has begun to set seed, with little or no overlap. Differences in seasonal flowering period, even as small as 2 weeks, can contribute significantly to the reproductive isolation of a species (Levin 1971). The early flowering period of *S. vernalis* is probably an effective barrier to gene exchange with any of its neighbors. In addition, *S. morrisonii* subsp. *elatus* and *S. vernalis* may be facultatively autogamous, a condition that increases the probability that they do not exchange genes. Some degree of autogamy is indicated by the enclosure of the two pairs of fertile stamens within the calyx, supertending the short post-like stigma. Dissection of the flower reveals that the stigma is virtually buried in pollen that rains down upon it from the four anthers immediately above it. At one time, the pair of vestigial infertile anthers well exerted from the calyx possibly functioned as agents of pollen dispersal; the atrophy of these organs may indicate selection for facultative self-pollination. The genus contains other autogamous species: *S. batrachopus* and *S. niger* E. Greene (Kruckeberg 1957, 1984).

ALLOZYME ANALYSIS

Morphology, as is often the case, is not the last word in species delimitation. Genetic data for mem-

TABLE 1. MORPHOLOGICAL COMPARISON OF FIVE *STREPTANTHUS* SPECIES. Data are from Hickman (1993), Hoffman (1952), and Personal Observations of *Streptanthus vernalis* over three seasons.

Attributes	<i>S. vernalis</i>	<i>S. morrisonii</i> subsp. <i>elatus</i>	<i>S. breweri</i> var. <i>hesperidis</i>	<i>S. batrachopus</i>	<i>S. brachiatus</i>
Flowering period	Annual, March–May	Biennial, May–July	Annual, May–July	Annual, May–July	Biennial, May–June
Plant height	2–20 cm	Up to 12 dm	Less than 4 dm	5–18 cm	2–6 dm
Habit	Usually simple, or rancbed from below	Remotely branched	Simple or branched below	Simple or branched from base	Generally branched below
Inflorescence	Racemose, sometimes secund	Racemose, often secund	Racemose, often secund, zig-zag	Racemose, lax	Discretely racemose, bracteate or not
Leaf, basal	Orbicular, apically crenate, green above, purple below, apical teeth orange-tipped, succulent, 3–4 cm, petiole 1 mm	Purple-mottled above, purple below, oblanceolate, thick, toothed above middle, 3–5 cm long	Entire to coarsely dentate, obovate, less than 5 cm long	Purple-mottled above, obovate, lobed, petioled 1–2.5 cm long	Oblanceolate, toothed above middle, thick, 1.5–4 cm, purple below, mottled-purple/brown above
Leaf, cauline	Narrowly lanceolate, entire, sessile, orange-tipped	Narrowly lanceolate, entire, sessile, clasping	Lower clasping, upper generally lanceolate, entire	Sessile, auriculate clasping, linear-lanceolate, entire	Sessile, narrowly ovate, serrate, upper lanceolate
Pedicle length	1–2 mm	Short	Short, if any	2–3 mm	1 mm
Calyx	Biradial, glabrous	Biradial, glabrous or hispidulous	Biradial, glabrous	Biradial, glabrous, strongly narrowed at tip	Biradial, glabrous
Sepal	6–7 mm, green, yellow toward tips	Up to 7 mm, yellowish	4–7 mm, greenish yellow	4 mm, green or purple, white recurved, glabrous tips	Yellow to light purple, 6–9 mm
Petal	White, strongly reflexed, 2 mm	White, lightly veined with purple, 9 mm, undulate margins	6–8 mm, whitish or purple-veined	White with purple mid-vein, 6–7 mm	Upper white or purple veined, lower light purple, 7–9 mm
Stamens	Three pairs, upper pair broadly connate, exserted, recurved, middle, inserted, fused to middle, bottom pair free, inserted	Three pairs, upper pair broadly connate, exserted, recurved, middle and lower pairs inserted	Three pairs, upper pair broadly connate, exserted, recurved, middle and lower pairs inserted	Three pairs, upper pair broadly connate, exserted, recurved, middle and lower pairs inserted	Three pairs, upper pair broadly connate, exserted, recurved, middle pair fused at base, lower pair free
Silique	Erect, up to 4–5 cm, torulose	Erect to spreading, up to 7.5 cm, torulose	Ascending or spreading, 2–11 cm, curved, narrowed between seeds	Arcuate spreading, 2.5–3 cm	Ascending, narrowed between seeds, 5–7 cm
Seed	Orange, winged	Winged at the end	Not winged	Brown, winged	Wing weak

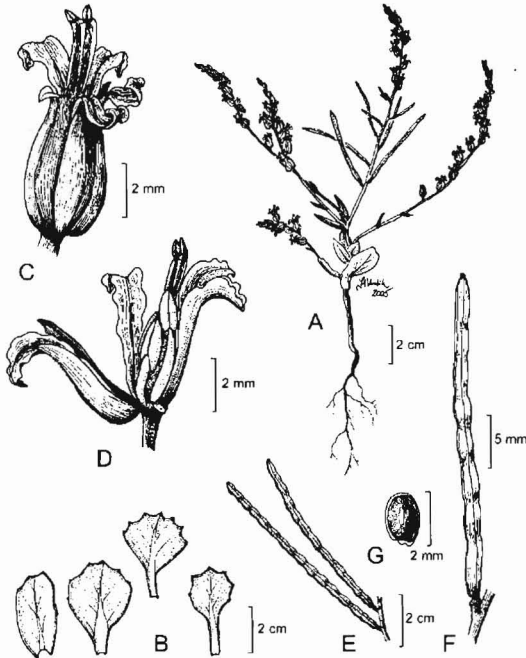


FIG. 1. *Streptanthus vernalis*. A. Habit; B. Leaf variations; C. Flower; D. Flower dissected open; E. Fruits; F. Fruit; G. Seed.

bers of the *Streptanthus morrisonii* complex has been shown to be incongruent with morphological data (Dolan 1995). Consequently, we conducted allozyme analysis of *S. vernalis* to test its genetic relationship to the species we compared morphologically.

Fresh buds of *S. vernalis* and suspected related species were assayed for allozymes following the procedures of Dolan (1995). With the exception of *Streptanthus batrachopus* buds, which were collected from San Geronimo Ridge in Marin County, the buds used in the analysis were collected from populations within 5 miles of Three Peaks. Data were analyzed using GDA (Lewis and Zaykin 2001).

Clear, repeatedly resolvable bands were obtained from 8–14 individuals per taxa for alcohol dehydrogenase (ADH), phosphoglucose isomerase (PGI) and Esterase (EST). Fifteen apparent alleles were detected. All taxa had banding patterns consistent with diploidy. *Streptanthus vernalis* exhibited a second EST locus not detected in the other taxa. *Streptanthus breweri* var. *breweri* A. Gray and *S. batrachopus* had an apparent duplicated PGI locus. Absence of these loci in other taxa was scored as an identical character state, indicated by use of a single absent allele designation.

Allozymes revealed *S. vernalis* is genetically distinct from related taxa (Fig. 2). Although only a small number of plants were sampled, the analysis

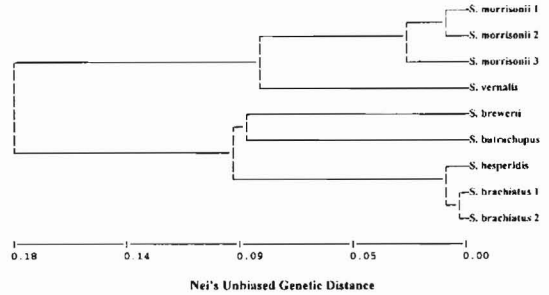


FIG. 2. Cluster diagram of genetic distance between *Streptanthus vernalis* and related taxa based on allozymes. *S. morrisonii* subsp. *elatus* was sampled from 3 different sites, *S. brachiatus* from 2.

clearly indicates that *S. vernalis* is not *S. batrachopus* or *S. brachiatus*, and appears to be most closely allied with *S. morrisonii*.

Cluster analysis (based on Nei's [1978] unbiased genetic distance values clustered by the UPGMA method of Sneath and Sokol [1973]) yielded two distinct branches, placing *S. vernalis* with *S. morrisonii* subsp. *elatus*. *Streptanthus brachiatus* and *S. breweri* var. *hesperidis* cluster closely in a second branch that also shows a close genetic relationship between *S. breweri* var. *breweri* and *S. batrachopus*.

IMPLICATIONS FOR *STREPTANTHUS* TAXONOMY

Streptanthus vernalis has a unique combination of traits. Its four white petals, the lower pair delicately tinted light yellow in the midvein area, do not exhibit the pronounced color dimorphism of *S. breweri* and *S. morrisonii*, the lower petals of which are typically and clearly purplish or brownish. In addition, *S. vernalis* is an annual, the evidence for which is that no resting rosettes among the flowering population have been observed for four seasons of close monitoring. Its annual life form, typical of section *Hesperides*, distinguishes *S. vernalis* from *S. morrisonii elatus*, a biennial as are the other members of the section *Biennes*. The allozyme evidence and the morphology of *S. vernalis* indicate a close relationship with *S. morrisonii*. Thus, *S. vernalis* appears to confound the previously recognized boundaries between the section *Biennes* and *Hesperides*. The sectional assignment of *S. vernalis*, if not the entire taxonomy of both sections, warrants further study.

CONCLUSION

Evidence from comparative morphology and genetic analysis indicate that *S. vernalis* is a new species of *Streptanthus*. It is likely related to the *S. morrisonii* complex.

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