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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 orminio glabra; caules erecti simplices vel ramose, 2-20 cm alti; folia pauca, plerumque basalia crassa subtus purpurea, supra viridia, 3-4 cm longa; folia inferiora orbiculata vel obovata, saliente crenata, petioles 1 cm longa; folia superiores sessilia, lineari-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, ascendentes; 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 orbiculate 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 exserted, equal, recurved, white, 2 mm long. Stamens in three pairs, upper pair 7-8 mm long, filaments exserted, connate to the apex, anthers reduced, reflexed at anthesis, middle pair connate ⅓ 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 sabina Douglas, Arctostaphylos viscosa C. Parry, Quercus durata Jepson, Streptanthus morrisonii subsp. elatus F. W. Hoffman, Mimulus brachiatus Pentell, Minuartia douglasii Torrey and A. Gray, and Epilobium minutum Lehman.

Several rare serpentine endemics occur near Three Peaks, including Hymenocallis halii (D. D. Keck) B. G. Baldwin, Cryptantha plicata Lindley, Hesperolinon spergulatum 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 LaPre collected several species of Streptanthus in the vicinity of Three Peaks for their biochemical genetic studies of the S. morrisonii complex (Dolan and LaPre 1989). They referred to Neilson’s report of the undescribed plant in their unpublished consultants’ report (Dolan and LaPre 1987). They speculated that it might be related to Streptanthus bathrochopus 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 jewel flower near Three Peaks that they believed was related to S. brachialus 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 secondary inflorescence, its zig-zag stem, overall yellow color (especially its leaves), greenish-yellow calyx, more connivent sepals and later flowering appears, based on morphological features, to be most similar to S. brachialus.

Although similar in size and habit, other morphological attributes separate S. bathrochopus from S. vernalis. In addition, like S. breweri var. hesperidis, S. bathrochopus flowers later than S. vernalis. Furthermore, the only known colonies of S. bathrochopus 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 resembles those of the annual S. vernalis initially, but as S. morrisonii grows, its basal leaves become longer, wider, and spathulate. They are also mottled purple/brown adaxially. These leaf features are not seen in S. vernalis.

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 Buta 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 the 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 pterid butterfly egg mimesis 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. bathrochopus 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>
<thead>
<tr>
<th>Attributes</th>
<th>S. vermis</th>
<th>S. morrisonii subsp. elatus</th>
<th>S. breweri var. hesperidii</th>
<th>S. brachyopus</th>
<th>S. brevifrons</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flowering period</td>
<td>Annual, March-May</td>
<td>Annual, May-July</td>
<td>Annual, May-July</td>
<td>Biennial, May-June</td>
<td>Biennial, May-June</td>
</tr>
<tr>
<td>Plant height</td>
<td>2-20 cm</td>
<td>Less than 4 dm</td>
<td>5-18 cm</td>
<td>2-6 dm</td>
<td>2-6 dm</td>
</tr>
<tr>
<td>Habit</td>
<td>Usually simple, or rachned from below</td>
<td>Simple or branched below</td>
<td>Racemose, lax</td>
<td>Generally branched below</td>
<td>Discreetly racemose, bractate or not</td>
</tr>
<tr>
<td>Inflorescence</td>
<td>Racemose, sometimes second</td>
<td>Racemose, often second</td>
<td>Purple-mottled above, obovate, less than 5 cm long, lobed</td>
<td>Discrete racemose, bractate to or not</td>
<td>Obovate, toothed above middle, thick, 1.5-4 cm, purple below, mottled-purplebrown above</td>
</tr>
<tr>
<td>Leaf, basal</td>
<td>Orbicular, apically crenate, green above, purple below, apical teeth orangetipped, succulent, 3-4 cm, petiole 1 mm</td>
<td>Purple-mottled above, purple below, oblancoate, thick, toothed above middle, 3-5 cm long</td>
<td>Entire to coarsely dentate, obovate, less than 5 cm long</td>
<td>Purple-mottled above, obovate, lobed, petiole 1-2.5 cm long</td>
<td>Racemose, lax</td>
</tr>
<tr>
<td>Leaf, cauline</td>
<td>Narrowly lanceolate, entire, sessile, orange-tipped to 1-2 mm</td>
<td>Narrowly lanceolate, entire, sessile, clapping short</td>
<td>Lower clasping, upper generally lanceolate, entire</td>
<td>Sessile, lanceolate, entire</td>
<td>Lower clasping, upper generally lanceolate, entire</td>
</tr>
<tr>
<td>Pedicel length</td>
<td>1-2 mm</td>
<td>Biradial, glabrous</td>
<td>Biradial, glabrous</td>
<td>Biradial, glabrous</td>
<td>Biradial, glabrous</td>
</tr>
<tr>
<td>Calyx</td>
<td>Up to 7 mm, yellowish</td>
<td>Up to 7 mm, yellowish</td>
<td>4-7 mm, greenish yellow</td>
<td>4 mm, green or purple, white recurved, glabrous tips</td>
<td>4 mm, green or purple, white recurved, glabrous tips</td>
</tr>
<tr>
<td>Sepal</td>
<td>White, strongly reflexed, 2 mm</td>
<td>White, lightly veined with purple, 9 mm, undulate margins</td>
<td>6-8 mm, whitish or purple-veined</td>
<td>White with purple mid-vein, 6-7 mm</td>
<td>Upper white or purple veined, lower light purple, 7-9 mm</td>
</tr>
<tr>
<td>Petal</td>
<td>Three pairs, upper pair broadly connate, exerted, recurved, middle, inserted, fused to middle, bottom pair free, inserted</td>
<td>Three pairs, upper pair broadly connate, exerted, recurved, middle and lower pairs inserted</td>
<td>Three pairs, upper pair broadly connate, exerted, recurved, middle and lower pairs inserted</td>
<td>Three pairs, upper pair broadly connate, exerted, recurved, middle and lower pairs inserted</td>
<td>Three pairs, upper pair broadly connate, exerted, recurved, middle pair fused at base, lower pair free</td>
</tr>
<tr>
<td>Stamens</td>
<td>Three, upper pair broadly connate, exerted, recurved, middle, inserted, fused to middle, bottom pair free, inserted</td>
<td>Ascending or spreading, up to 2-11 cm, curved, narrowed between seeds</td>
<td>Arcuate spreading, 2.5-3 cm</td>
<td>Ascending, narrowed between seeds, 5-7 cm</td>
<td>Arcuate spreading, 2.5-3 cm</td>
</tr>
<tr>
<td>Silique</td>
<td>Erect, up to 4-5 cm, torulose</td>
<td>Winged at the end</td>
<td>Not winged</td>
<td>Wing weak</td>
<td>Brown, winged</td>
</tr>
<tr>
<td>Seed</td>
<td>Orange, winged</td>
<td>Winged at the end</td>
<td>Not winged</td>
<td>Wing weak</td>
<td>Brown, winged</td>
</tr>
</tbody>
</table>
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), phosphoglucoseisomerase (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 clearly indicates that S. vernalis is not S. batrachopus or S. brachiatius, 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 Sokal [1973]) yielded two distinct branches, placing S. vernalis with S. morrisonii subsp. elatus. Streptanthus brachiatius 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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