BRODIAEA SANTAROSAE (THEMIDACEAE), A NEW RARE SPECIES FROM THE SANTA ROSA BASALT AREA OF THE SANTA ANA MOUNTAINS OF SOUTHERN CALIFORNIA

Tom Chester
1802 Acacia Lane, Fallbrook, CA 92028
tom@tchester.org

Wayne Armstrong
Life Sciences Department, Palomar College, 1140 West Mission Road,
San Marcos, CA 92069

Kay Madore
The Nature Conservancy, Santa Rosa Plateau Ecological Reserve, 22115 Tenaja Road,
Murrieta, CA 92562

Abstract

Brodiaea santarosae (Themidaceae) is a new species from southwest Riverside County and immediately-adjacent Miller Mountain of San Diego County, CA. It is easily distinguished from other *Brodiaea* species in southern California by its large flowers and distinctive, variable staminodes; morphological analysis revealed 11 total differentiating characteristics. *Brodiaea santarosae* occurs only on or very close to the 8–11 million-year-old Santa Rosa Basalt. It has the smallest range of the southern California *Brodiaeas*, with just four known populations occupying only a small portion of a ~40 km² area, plus a fifth small population disjunct by 11 km.

It has been speculated that the *B. santarosae* population is a hybrid swarm between *B. filifolia* and *B. orcuttii,* based solely on the appearance of the staminodes and filaments in selected flowers. This speculation was rejected due to the lack of sympatry between the three taxa and because specimens of *B. santarosae* have numerous characteristics that are not intermediate between the claimed parent taxa. In contrast, intermediate characteristics were seen in F1 specimens of *B. filifolia* X *B. orcuttii* discovered in San Marcos, CA, the only location where those species overlap.

We also report extensions to the length characteristics for both *B. filifolia* and *B. orcuttii* and demonstrate that two populations of *B. filifolia* previously thought to be hybrids are consistent with other *B. filifolia* populations.

Resumen

Brodiaea santarosae (Themidaceae) es una nueva especie del sudoeste del Condado de Riverside y del monte Miller inmediato-adyacente en el Condado de San Diego, CA. Es distinguido fácilmente de las otras especies de *Brodiaea* del Sur de California por sus flores grandes y staminodes variables y distintivos; el análisis morfológico reveló 11 totales que distinguen características. *Brodiaea santarosae* ocurre solamente en o muy cerca del Santa Rosa Basalt de 8–11 millones de años de antigüedad. Tiene la gama más pequeña de las *Brodiaeas* del Sur de California, con apenas cuatro poblaciones conocidas ocupando solamente una porción pequeña de un área de ~40 km², más una quinto población pequeña disjunta por 11 kilómetros.

Se ha especulado que la población de *B. santarosae* es un enjambre híbrido entre *B. filifolia* y *B. orcuttii*, basados solamente en el aspecto de los staminodes y de los filamentos en flores seleccionadas. Esta especulación fue rechazada debido a la carencia de sympatry entre los tres taxa y porque los especímenes de *B. santarosae* tienen características numerosas que no sean intermedias entre los taxa demandados del padre. En contraste, las características intermedias fueron consideradas en los especímenes F1 del *B. filifolia* X *B. orcuttii* descubierto en San Marcos, CA, la única localización donde esas especies se traslapan.

También divulgamos extensiones a las características de la longitud para *B. filifolia* y *B. orcuttii* y demostramos que dos poblaciones del *B. filifolia* pensaron previamente para ser híbridos son constantes con otras poblaciones del *B. filifolia*.

Key Words: Basalt, *Brodiaea*, California, endemic, Peninsular Ranges, Santa Ana Mountains, Santa Rosa Basalt, Santa Rosa Plateau.

We describe here a new species of *Brodiaea* that has previously been collected by at least six different botanists and variously determined as *B. orcuttii* (E. Greene) Baker, *B. filifolia* S. Watson, or a hybrid between the two (see paratype specimens cited below, as well as Boyd et al. 1992, 1995).

The confusion stems from the remarkable variation in the staminodes in this species. About 10% of the flowers of this species have no staminodes and long filaments, superficially resembling the flowers of *B. orcuttii*. Approximately another 5–10% have short recurved filiform staminodes and shorter filaments, superficially resembling the flowers of *B. filifolia*. The majority of the flowers have longer staminodes and variable-length filaments, which in the absence of quantitative analysis appeared to be hybrids between those taxa.

The recognition of this new species came from a research program of the first two authors on hybrids of various *Brodiaea* species in southern California, combined with the discovery by the third author of a large accessible population of this new species. Analysis of that population revealed that it was not consistent with any previously-known southern California *Brodiaea* species, nor did it seem consistent with a hybrid swarm between any of those species.

This discovery came in time to survey many of the relevant *Brodiaea* populations in Riverside and San Diego Counties during the 2006 season. During that survey, we found three specimens from San Marcos that appear to be true hybrids between *B. filifolia* and *B. orcuttii*. These specimens were valuable in confirming that this new species was not of hybrid origin.

We were able to obtain and analyze enough fresh specimens from enough populations to determine that this entity warranted recognition as a new species that is distinguished from *B. filifolia* and *B. orcuttii* by at least 11 separate characteristics. This new species has the smallest range of the southern California *Brodiaeas* and is found only on or very close to the 8–11 million-year-old Santa Rosa Basalt.

Our analysis also showed that two populations of *B. filifolia* previously thought to be hybrids are consistent with other *B. filifolia* populations. This adds two protected populations of *B. filifolia* to the list in U.S. Fish and Wildlife Service (2004). These populations were omitted from that list since hybrids are not as important as pure populations for the conservation of the species.

Species Description and Distribution

Brodiaea santarosae T. Chester, W. Armstrong & K. Madore, sp. nov. (Fig. 1)

Differt a *B. filifolia* filamenta 2.4–8.2 mm. Differt a *B. orcuttii* staminodia praesens in 90% de flores, acuminatus, 0–7 mm; perianthii tubi 6.0–11.3 mm; anthera 5.4–8.9 mm; ovaria 3.5–8.2 mm; et styli (includens stigmata) 10.5–17.0 mm.

Geophyte; glabrous; *corm* 15–25 mm high, 25–31 mm wide, producing cormlets at the sides; *leaves* 2–4, basal, linear, appearing before the inflorescence; *inflorescence* scapose, 1–2 scapes per corm, scape 8.8–36 cm, umbellate; *flowers* 2–6 in terminal umbels, erect on pedicels 18–107 mm long and 1.1–1.9 mm wide at distal end; *bracts* at base of umbel, scarious, 6.5–11 mm; *corolla* blue-purple, campanulate, base 2.0–3.9 mm wide, tube 6.0–11.3 mm, lobes 6, ascending, 15.4–29.5 mm; *ovary* green, 3.5–8.2 mm; *style* including stigma 10.5–17.0 mm, stigma 3-lobed, with one lobe usually slightly above the other two, distal end of stigma from 3.0 mm below to 1.4 mm above distal end of anthers; *anthers* barely exserted from corolla tube, filaments 2.4–8.2 mm, anther sacs 5.4–8.9 mm; *staminode* present in 90% of flowers, white to lavender, tapered to tip, free portion 0.0–7.0 mm, usually variable in length within individual flowers; *fruit* loculicidal capsule, with perianth tube becoming thin and sometimes splitting at fruit maturity. Flowering May–June.

All measurements above are for fresh, not pressed, specimens, collected in the relatively dry year of 2006. Measurements might be somewhat greater in a wetter year. The flower parts in dried specimens shrink by roughly 10%. The ranges in the measurements above are exactly the ranges of our measured values; it is expected that the true population range is somewhat greater.

Type: USA, California, Riverside Co., Santa Ana Mountains, Santa Rosa Plateau region: Clay Hill, 0.55 km south-southwest of the northernmost high point of the Mesa de Burro; 33.52927° N, 117.24857° W [NAD27]; 580 m elevation; 15 June 2006, *T. Chester, W. Armstrong, K. Madore 927* (holotype UCR; isotypes RSA, SD).

Paratypes: All from USA, California, Santa Ana Mountains. Riverside Co. specimens: Elsinore Peak, 0.3 km southwest of the Peak, 33.60049 decimal degrees N, 117.34514 degrees W [NAD27], 1045 m elevation, 10 June 2006, *T. Chester, W. Armstrong 918 (UCR),* 15 May 1992, *S. Boyd 7385 (RSA, UCR)*; Mesa de Burro, 23 June 1983, *R. Gustafson and G. Wallace 2716 (RSA),* 25 May 1977, *C. Davidson 5639 (RSA),* 0.4 km west of the north end, 17 May 1988, *S. J. Myers s.n. (UCR)*; Mesa de Colorado, 18 May 1985, *R. Thorne et al. 60644 (RSA)*, 27 May 1960, *E. Lathrop 5221 (RSA)*, Via Volcano Road just north of Avocado Mesa Road, *T. Chester, W. Armstrong 921 (UCR)*; Avenaloca Mesa, west side, northwest of intersection of Corona Cala Camino and Avocado Mesa Roads,
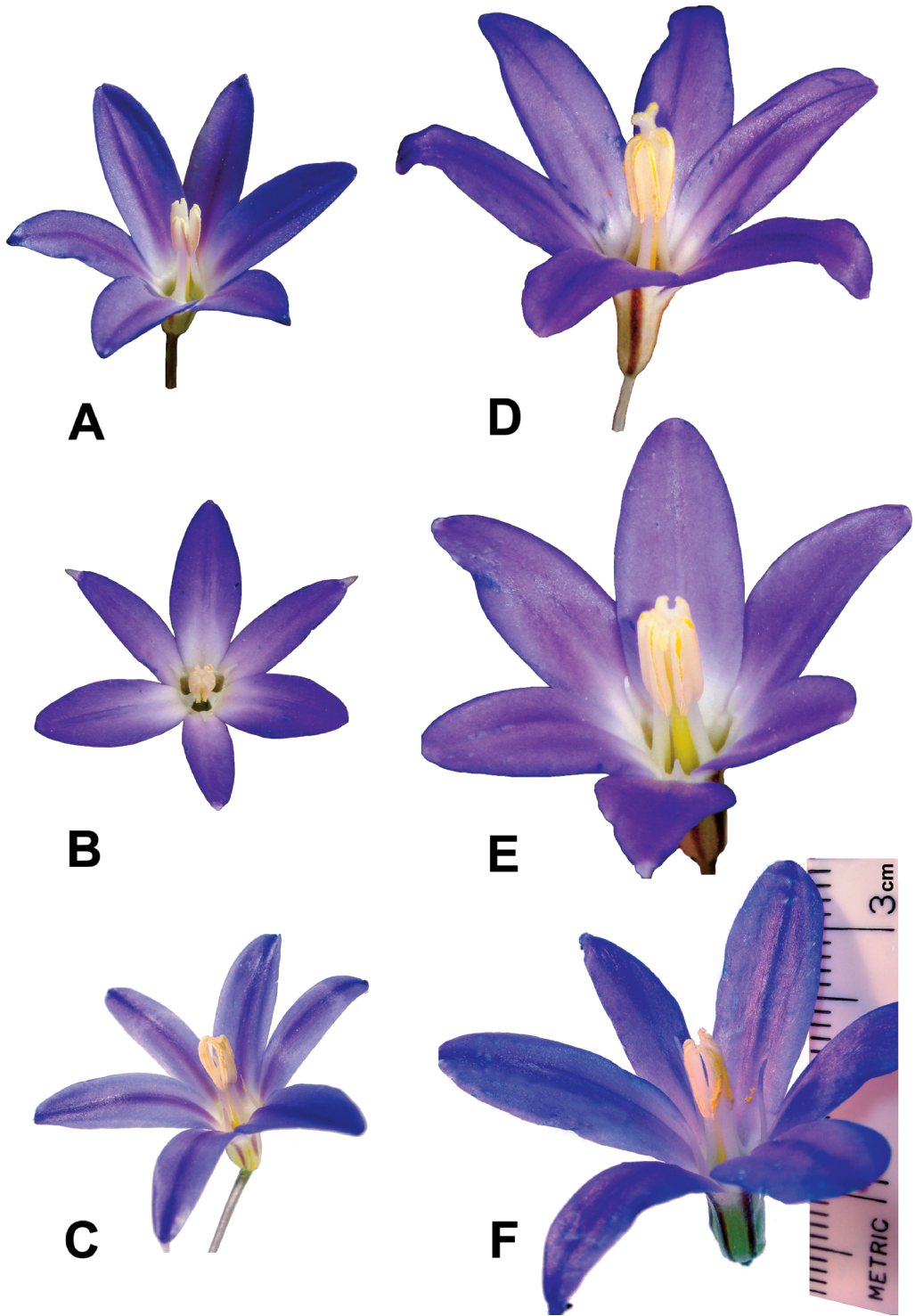
FIG. 1. Comparison of flowers of *B. santarosae* with *B. orcuttii*, *B. filifolia* and *B. filifolia X B. orcuttii*. (A) *B. orcuttii* (B) *B. filifolia* (C) *B. filifolia X B. orcuttii*. (D–F) *B. santarosae*. The flowers shown in D and E are from the same corm. All flowers are to the scale shown in F, and are shown in the same proportion to each other as for the median-size flower for each taxon.

33.49379° N, 117.33178° W [NAD27], 720 m elevation, 22 June 2006, *T. Chester, W. Armstrong 934 (UCR)*. San Diego County: south flank of Miller Mountain, about upper portion of Miller Canyon, ~730 m, 6 May 1992, *S. Boyd et al. 7289, 7304B* (RSA), *7304A (SD)*.

Epithet etymology, pronunciation, and common name. The epithet is for the Santa Rosa Basalt closely associated with this species. The suggested pronunciation is *san-tuh rose' ee* (U.S.), or *san-tuh rose' eye* (European). The suggested common name is *Santa Rosa Basalt Brodiaea*.

Distribution

Brodiaea santarosae is found only in a unique location in southern California, an area of low topographic relief that was flooded by the Santa Rosa Basalt 8–11 million years ago. Its range mostly, but not entirely, separates the populations of *B. filifolia* and *B. orcuttii*.

Fig. 2A shows the geographic range of these three species, along with the estimated minimum original extent of the basalt. Populations of *B. orcuttii* are found entirely to the south and southeast of the basalt. Populations of *B. filifolia* are found mostly to the north and west of the basalt, with just a few occurrences to the south, and only one population within the basalt area. That population, at the Mesa de Colorado, occurs at the biggest vernal pool, in heavily-leached dark vernal pool soils unlike the reddish basalt-derived soil elsewhere on the basalt; it is not accompanied there by *B. santarosae*.

The Santa Rosa Basalt has been dated as 8–11 million years old (Hull and Nicholson 1992; Hawkins 1970; D. Krummenacher, cited in Kennedy 1977). It formerly covered an area of at least 500 km^2 (Kennedy 1977), from Elsinore Peak on the north, to the Murrieta Hogbacks and Oak Mountain on the east, to somewhere south of the Mesa de Colorado on the south, and to the area of Miller Mountain on the west. This is a minimum extent, estimated simply by taking the surviving patches of basalt and assuming basalt originally was continuous between them. Erosion has removed at least 97% of the original basalt area; the basalt now covers only disjunct areas of about 15 km^2 (within a region of approximately 40 km^2) plus a few very small patches such as the two patches at Elsinore Peak 11 km distant.

We include the "Basalt of Elsinore Peak", dated only as "Miocene" (Morton et al. 1999), as part of the Santa Rosa Basalt. Because these basalts most likely derived from the same or very similar source, and are from the same time period, they are highly likely to be substantially the same, and are treated as such here.
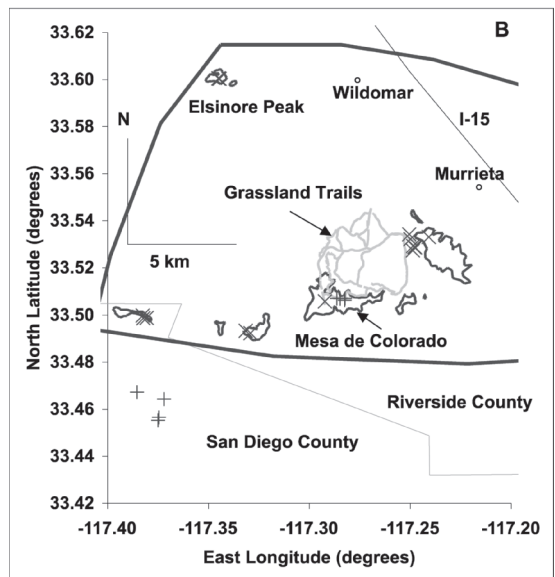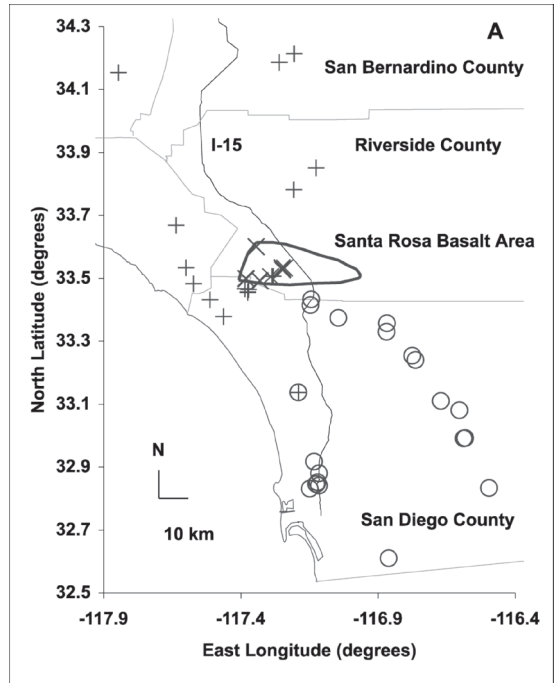

Fig. 2. Geographic distribution of *B. filifolia* (+), *B. santarosae* (X), and *B. orcuttii* (O) in southern California, USA from vouchers, both ours and ones at RSA, SD and UCR verified by the authors. The minimum original extent of the Santa Rosa Basalt is outlined using the present position of the Basalt. A. Map showing all populations. B. Expanded-scale map showing remaining areas covered by Santa Rosa Basalt (black outline areas) and trails of the Santa Rosa Plateau Ecological Reserve in grassland (light gray).

Fig. 2B shows the largest remaining areas of the basalt, along with all vouchered locations of *B. santarosae* and *B. filifolia* in that area. Voucher locations of most *B. santarosae* specimens are not precise; locations such as *Mesa de Burro* have been arbitrarily placed on the Mesa. Most of the extant basalt is on the mesas of the Santa Rosa Plateau, not all of which have yet been surveyed for these species. All Santa Rosa Basalt areas surveyed to date contain *B. santarosae*.

Perhaps the most remarkable feature of *B. santarosae* is that every population we surveyed grows in soils derived from the Santa Rosa Basalt. Every surveyed population except one, and all vouchers we determined as *B. santarosae*, were from soils underlain by the Santa Rosa Basalt as mapped in Kennedy (1977). The exception was the population immediately west of the Mesa de Burro. Although the basement rock there is mapped as metasedimentary, the soil had abundant basalt rocks within it and on its surface, remaining from the geologically-recent past when the Santa Rosa Basalt was still intact here. Thus this soil is derived, at least in part, from the basalt.

This distribution thus shows tremendous fidelity to the basalt areas, since both the populations and the major remaining basalt areas (not including the unsurveyed Oak Mountain) span a distance of 15 km by 15 km, yet both *B. santarosae* and the basalt only cover almost the identical ~7% (15 km²/225 km²) of that area.

This coincidence is not due to habitat considerations; there are extensive grasslands inhabited by *B. terrestris* Kellogg subsp. *kernensis* (Hoover) T. Niehaus outside the basalt areas. No other populations of *B. santarosae*, *B. filifolia*, or *B. orcuttii* have been documented even though those grasslands have been intensely studied. The first and third author surveyed the grassland trails of the Santa Rosa Plateau Ecological Reserve shown in Fig. 2B in 2001–2006; Lathrop and Thorne (1985) surveyed most of the area shown in Fig. 2B south of Murrieta; Boyd et al. (1995) surveyed the rest of the area shown in Fig. 2B; and there have been numerous surveys for residential development.

Thus, it is likely that there are no other populations of *B. santarosae* other than those shown, except for more populations in the basalt areas themselves. In particular, Redonda Mesa and Mesa de la Punta may contain additional populations. In addition, there are a few locations that have small remnants of the Santa Rosa Basalt, not shown on the map, such as the Murrieta Hogbacks and Oak Mountain. These areas should be searched for *B. santarosae*. It is also possible that small populations of *B. santarosae* might occur in drainages from basalt areas, carried there by runoff.

KEY TO THE SPECIES OF *BRODIAEA* IN SOUTHERN CALIFORNIA

This key is an artificial key to separate all species of *Brodiaea* in mainland southern California. In this key and subsequently in this paper, the properties of the staminode refer only to its free portion and do not include the lower continuation of the staminode that is fused to the outer perianth.

1   Staminodes 0 in all flowers . . . . *B. orcuttii*
1'   Staminodes present in 90–100% of flowers . . . (2)
2   Staminodes oblong to rectangular in outline, tapered only near tip if at all . . . . (3)
2'   Staminodes filiform or uniformly tapered from base to tip . . . . (4)
3   Staminodes generally erect, edges flat to inrolled, sometimes hooded, generally purple. . . . . *B. terrestris* ssp. *kernensis*
3'   Staminodes recurved, edges flat, not hooded, pointed at tip, generally white; Mission Trails Regional Park . . *B. elegans* Hoover subsp. *elegans*
4   Filaments 0–1.5 mm; staminodes 1.0–4.5 mm long, reflexed against perianth . . . . *B. filifolia*
4'   Filaments 2–8 mm; staminodes 0.0–7.0 mm long, recurved to erect. . . . . (5)
5   Perianth length 19–24 mm; style 8.0–9.5 mm; ovary 4.0–5.0 mm; anther 5.0–5.5 mm; San Marcos . . . .*B. filifolia* × *B. orcuttii*
5'   Perianth length 24–36 mm; style 10.5–17.0 mm; ovary 3.5–8.2 mm; anther 5.4–8.9 mm; Elsinore Peak to Miller Mountain . . . .*B. santarosae*

Because only three specimens of *B. filifolia* × *B. orcuttii* are known, the range of measurements for it in the above key will require slight extensions as more specimens are found. However, the principal component analysis presented below indicates that those extensions will be much smaller than the differences from *B. santarosae*.

PHENETIC ANALYSIS OF *BRODIAEA SANTAROSAE* AND OTHER *BRODIAEA* SPECIES IN SOUTHERN CALIFORNIA

Data and Analysis Methods

We surveyed, photographed, and sampled populations from the following areas, mapped in Fig. 2A, specifically for this analysis, on 1, 4, 5, 10, 13, and 22 June 2006. The species determination for each specimen was made later from the analysis in this paper. Numbers in parentheses are collection numbers of Chester et al. *B. filifolia*: Santa Rosa Plateau Ecological Reserve (SRPER): Vernal Pool Trail near Main Pool (909); San Marcos (912); San Mateo Canyon Wilderness: Mud Canyon 1 (920, 933), Mud Canyon 2 (924). *B. filifolia* × *B. orcuttii*: San Marcos (917, 936). *B. orcuttii*: Miramar (915); Cuyamaca Lake (916); Tierra Santa (935). *B. santarosae*: SRPER: Clay Hill Area (910–911,

925–930), Via Volcano Road (921); Elsinore Peak (918); Avenaloca Mesa (934). *B. terrestris* subsp. *kernensis*: Elsinore Peak (919); SRPER: Via Volcano Road (922).

Mud Canyon is the informal name used for the drainage in the San Mateo Canyon Wilderness Area near Devil Canyon that contains Mud Springs. Mud Canyon 1 is a drainage from a fairly large upstream meadow area. Mud Canyon 2 is a small grassy area a few hundred feet south of Mud Canyon 1.

In each area, we photographed the full range of variation seen in the flowers, and we selected 5–10 inflorescences or flowers to measure in detail. The samples were selected mostly geographically, from the edges of each area and from the center, in order to avoid having multiple samples from the same clonal population. (*Brodiaeas* often reproduce by corms, and hence the population in a small area is often clonal.) Samples were also taken of extreme members of the population if the geographic sampling did not encompass all the variation seen in the population. The one exception to the above sampling was on the 18 June 2006 visit to San Mateo Mud Canyon 1, where we intentionally sampled only the largest flowers from the *B. filifolia* population in an attempt to discover any population intermediate to *B. santarosae*. (Later analysis showed no intermediates were found.)

For comparison purposes, especially to study any possible hybridization, we also used data collected in 2005 from the SRPER for fresh samples of *B. terrestris* subsp. *kernensis*.

Fourteen independent characteristics were measured for each fresh flower before pressing, in addition to the scape and bract length for each inflorescence. In addition, all herbarium samples of "*B. filifolia*", "*B. orcuttii*", and "*B. filifolia* × *B. orcuttii*" from RSA and SD were examined and measured for all quantities visible on each specimen, and re-determined.

These characteristics were then analyzed directly and with principal components analysis.

Principal Components Analysis. The measurements of seven floral parameters (perianth lobe, perianth tube, filament, anther, ovary, style, and staminode) were analyzed for principal components, with the results separated by geographic populations in Fig. 3.

We removed the mean from each floral parameter and then computed the principal components in two ways, once dividing each parameter by its standard deviation and once without such division. Since the resulting plots were essentially identical except for scale ($r^2 = 0.95$ for PCA1 and 0.96 for PCA2), we present here the version without such scaling which allows the coefficients to be more easily interpreted. The scale factors that will closely
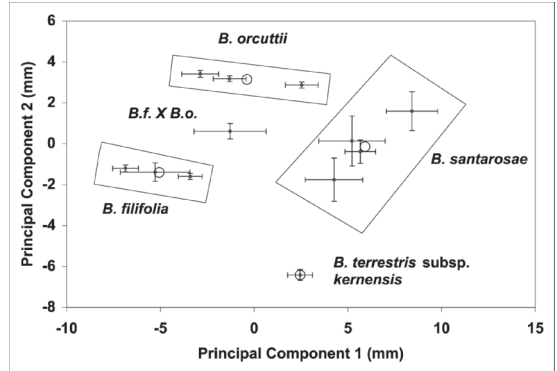

FIG. 3. Principal Components Analysis of floral parameters not scaled by standard deviation. The mean values with their one-standard deviation error bars are shown for the eleven geographically-distinct populations given in Table 1. Rectangles delineate individual taxa with more than one population; circles denote the mean for each taxon. To convert to PCA values from floral parameters scaled by standard deviation, multiply PCA1 by 0.389 mm^{-1} and PCA2 by 0.425 mm^{-1}.

give the other version are given in the caption for Fig. 3.

Results of Analysis of Characteristics of the *Brodiaea* Species

The coefficients of the first two principal components (PC1 and PC2) are given in Table 1, along with the variation in PC2 contributed by each variable. These two components accounted for 89% of the total variance in the data.

Principal Component 1 is a length parameter, essentially a scale factor times the perianth length plus the portion of the length of the floral parts that is correlated to the perianth length. Principal Component 2 is essentially a scale factor times the lengths of the filament plus the style minus the perianth tube minus the perianth lobe minus the staminode, where the staminode contributes roughly twice the variation of the other parameters. The variable staminodes of *B. santarosae* account for most of the spread in values of PC2 for that taxon. Table 1 also shows the variation in PC2 contributed by each parameter.

TABLE 1. COEFFICIENTS FOR PRINCIPAL COMPONENTS PC1 AND PC2, AND VARIATION IN PC2, BY PARAMETER.

Parameter	PC1	PC2	PC2 Variation (mm)
Tube	0.19	−0.36	−3.28
Lobe	0.70	−0.16	−3.46
Filament	0.36	0.46	3.73
Anther	0.18	0.02	0.11
Ovary	0.21	−0.15	−1.00
Style	0.51	0.22	2.94
Staminode	0.09	−0.76	−6.64

The error bars in Fig. 3 were computed by dividing the population standard deviation for each species by $(n-1)^{1/2}$, where n is the number of individuals in each population. Note that some populations, such as *B. filifolia* and *B. filifolia* × *B. orcuttii* from San Marcos, are represented by only three specimens, which accounts for some of the larger error bars.

Fig. 3 shows four distinct taxa that are nearly equally distant from each other, the three distinct clusters denoted by labeled rectangles and the point corresponding to *B. terrestris* subsp. *kernensis*. The *B. filifolia* × *B. orcuttii* specimens plot almost exactly intermediately between the parent species, as expected for F1 hybrids. Since these specimens are found only in the single location where the parent species occur together, the evidence for their hybrid origin is strong.

The separation of the taxa in Fig. 3 demonstrates that *B. santarosae* is a taxon as distinct as any of the other three taxa, with characteristics not intermediate to any of those three taxa. In particular, these specimens are not direct hybrids of *B. filifolia* and *B. orcuttii*, nor are they part of any hybrid swarm between those species. Our discovery of clear hybrids between *B. filifolia* and *B. orcuttii*, from the only location where the populations overlap, confirms these conclusions.

The clusters denoted by the labeled rectangles in Fig. 3 are robustly defined. Note in particular the very small error bars on the PC2 values for all taxa except *B. santarosae;* within each of those clusters, all populations show extremely good concordance for PC2 in Fig. 3, reflecting the uniform staminodes of each taxon. The populations of *B. santarosae* also show good concordance, with each having significant spreads in the values of PC2, reflecting the staminode variability of that species being consistent between populations.

For both PC1 and PC2, the mean of each population is consistent with the corresponding species mean (Fig. 3), except for the *B. orcuttii* population with the highest value of PC1. That population (San Marcos) is 3.3 standard deviations away from the species mean value. Since PC1 is essentially the perianth length, this simply means that the San Marcos flowers in our sample were significantly larger than the other two populations from Miramar and Cuyamaca Lake.

Although the San Marcos specimens possessed somewhat-larger flowers, they are otherwise consistent with the other two *B. orcuttii* populations in all respects. In particular, they have the distinctive properties of *B. orcuttii* described below, including the complete absence of staminodes. Herbarium specimens show a much smaller separation of San Marcos flowers from the other two populations in other years, indicating that the apparent difference in our samples was either sampling variation or perhaps related to the unusual rainfall pattern in 2006. For additional detail, see Chester et al. (2007).

Comparison of Individual Characteristics of *Brodiaea* Species in Southern California

Measured ranges for each parameter for each species are given in Table 2, along with the number of samples measured. We did not include *B. elegans* or *B. kinkiensis* in the analysis here since they do not come into the geographic range of any southern California *Brodiaea* except for *B. terrestris* subsp. *kernensis*, and we therefore didn't sample them for this analysis. (For this analysis, we treat southern California specimens determined as *B. jolonensis* Eastw. as *B. terrestris* subsp. *kernensis*. They have numerous differences from specimens of *B. jolonensis* from the type locality of Jolon, CA, and are nearly identical to specimens of *B. terrestris* subsp. *kernensis*.) The sampling of *B. terrestris* subsp. *kernensis* was not extensive enough to give the full range for its parameters, especially from other locations.

Brodiaea santarosae showed the following substantial differences from *B. filifolia* and *B. orcuttii*:

(1)   It had larger flowers and larger floral parts. The median *B. santarosae* flower was 40% larger than the median *B. filifolia* and *B. orcuttii* flower. Only a small percentage of *B. filifolia* and *B. orcuttii* flowers were larger than the *smallest B. santarosae* flower.

(2)   The anther, ovary and style lengths of *B. santarosae* were all markedly longer than those for *B. filifolia* and *B. orcuttii*. There was almost no overlap at all for anther lengths, and only a small overlap for the other lengths.

(3)   The inflorescence bract and pedicel lengths for *B. santarosae* were typically much longer than those of *B. filifolia* and *B. orcuttii*. Two-thirds of the bract lengths for *B. filifolia* and *B. orcuttii* were shorter than 6 mm; none of the bracts of *B. santarosae* were that short. All pedicels of *B. filifolia* and *B. orcuttii* were shorter than 75 mm, but over one third of the pedicels of *B. santarosae* were longer than 75 mm.

(4)   The peduncle lengths for *B. santarosae* were also much longer than those of *B. filifolia* and *B. orcuttii*. However, this may simply be a consequence of the habitat difference. *B. santarosae* grows in areas with abundant tall non-native grasses, whereas the other two species grow in areas without as much such cover.

In the rest of this section, we compare all four species and give those properties in which one or more species significantly differed at close to or

TABLE 2. MEASURED CHARACTERISTICS, IN mm. Min = minimum, Med = median, and Max = maximum. Values in bold type indicate an extension to the parameter range in Keator (1993). The actual range of values for *B. terrestris* subsp. *kernensis* is larger than reported here, since we only used a single sample of plants from the Santa Rosa Plateau to compare with the other species.

Characteristic	*B. filifolia*				*B. orcuttii*				*B. santarosae*				*B. terrestris* subsp. *kernensis*			
	#	Min	Med	Max	#	Min	Med	Max	#	Min	Med	Max	#	Min	Med	Max
Peduncle	23	**45.0**	**158.0**	275.0	30	**13.0**	107.0	**325.0**	12	88.0	257.5	360.0	14	65.0	162.0	**330.0**
Bracts	23	5.0	6.0	8.0	32	3.5	6.0	8.0	14	6.5	8.5	11.0	14	8.0	9.5	15.0
Pedicel	38	13.0	30.0	**59.0**	43	**5.0**	38.0	**60.0**	30	18.0	56.0	107.0	15	25.0	39.0	**71.0**
Perianth tube	38	**4.5**	6.7	**9.0**	43	4.0	**6.0**	**10.0**	30	6.0	8.3	11.3	15	**8.2**	**10.0**	**13.2**
Perianth lobes	38	7.2	12.9	**20.0**	43	**11.4**	15.2	**22.0**	30	15.4	19.5	29.5	15	**14.9**	19.0	**21.8**
Perianth	38	**13.2**	19.5	**28.0**	43	17.0	21.0	**32.0**	30	24.0	28.1	36.5	15	**23.5**	30.0	**35.0**
Filament	38	0.0	**0.4**	**1.5**	43	**3.9**	5.2	**7.9**	30	2.4	5.8	8.2	15	1.2	3.0	4.0
Anther	38	**2.8**	4.5	6.0	43	4.0	5.2	**6.6**	30	5.4	6.8	8.9	15	**4.3**	5.1	**6.8**
Ovary	38	**2.9**	4.5	**7.2**	42	**2.7**	5.0	**7.1**	30	3.5	7.0	8.2	15	**6.5**	**7.6**	**9.2**
Style + stigma	37	**4.5**	6.3	**9.1**	42	**5.8**	9.0	**15.1**	30	10.5	13.0	17.0	15	7.0	8.0	**10.0**
Width anther axis	29	0.1	0.5	1.0	40	0.2	0.5	1.0	25	0.3	0.8	1.1	15	0.2	0.9	1.0
Width of anther sac	29	0.2	0.5	0.8	40	0.2	0.5	0.8	25	0.2	0.6	0.9	15	0.5	0.8	0.9
Perianth base width	21	1.9	2.3	3.1	42	2.1	2.7	3.2	24	2.0	2.9	3.9	7	2.0	2.5	2.8
Upper pedicel width	21	1.0	1.0	1.2	43	1.0	1.2	1.5	24	1.1	1.4	1.9	7	1.3	1.6	2.0
Staminodes (free portion)	38	**1.0**	2.5	**4.2**	43	0.0	0.0	0.0	30	0.0	3.3	7.0	13	4.8	7.5	8.8
Staminodes (including fused portion)	21	2.4	3.5	5.0	42	1.0	2.0	4.0	30	1.5	5.1	8.5	15	8.0	10.0	11.7
Distance from top of anthers to top of style (anthers above style positive)	31	−2.0	1.0	2.6	42	−1.8	2.0	5.2	26	−1.4	1.0	3.0	3	−0.2	1.0	2.2

exceeding the 95% confidence level (with a difference more than two standard deviations). Plots, histograms, and additional information are given in Chester et al. (2007).

Habitat. The habitats of the four species are distinct. *B. filifolia* and *B. orcuttii* are confined to the wettest areas such as flat streambeds, benches along streambeds, and vernal pool areas. *B. terrestris* subsp. *kernensis* and *B. santarosae* are less moisture-dependent. *B. terrestris* subsp. *kernensis* grows in many habitats, but generally does not occur in the wettest areas preferred by *B. filifolia* and *B. orcuttii*. It grows in drier drainages and along trails and roads in flattish areas.

Brodiaea santarosae grows in many habitats as well, including next to vernal pools, but can grow in drier locations than even *B. terrestris* subsp. *kernensis*. Surprisingly, *B. santarosae* even grows in disturbed areas such as Waterline Road next to the Mesa de Burro. That area was completely dug up to install a water main, and *B. santarosae* grows abundantly in the disturbed soil on top of the water pipe, as well as in roadside berms.

There is only one known occurrence of *B. filifolia* within the range of *B. santarosae*, on the Mesa de Colorado immediately surrounding the largest vernal pool. The area in which it grows was part of that pool for ~75 years, when the outlet of the pool was dammed to raise the level of the pool. The soil in that area is heavily leached, and does not have the red color of the surrounding basalt-derived soil. *B. santarosae* is not found on that vernal pool soil, only in the red basalt soil elsewhere on the Mesa de Colorado.

Of course, the most remarkable difference in habitat is the restriction of *B. santarosae* to basalt soil in areas on or near the Santa Rosa Basalt.

Peduncle and bract lengths. Histograms of these two parameters (Fig. 4) each showed two distinct patterns: *B. filifolia* and *B. orcuttii* had similar histograms that peak at shorter values, and *B. santarosae* and *B. terrestris* subsp. *kernensis* had similar histograms that peak at longer values. For example, 60% of the peduncles for *B. filifolia* and *B. orcuttii* were less than 150 mm, but only 27% of the peduncles for the other two species were that short. Even more dramatically, 65% of the bract lengths for *B. filifolia* and *B. orcuttii* were less than 6 mm, but none of the bract lengths for the other two species were that short.

Although it is possible that the peduncle length further distinguishes *B. santarosae* from *B. filifolia* and *B. orcuttii*, we suspect the peduncle length is subject to environmental modification by the height of the immediately-neighboring plants, which in turn derives from the different habitats of these species. Peduncles are shorter where there are few neighboring plants, and longer where the plant is surrounded by tall annual non-native grasses. Both *B. filifolia* and *B.*
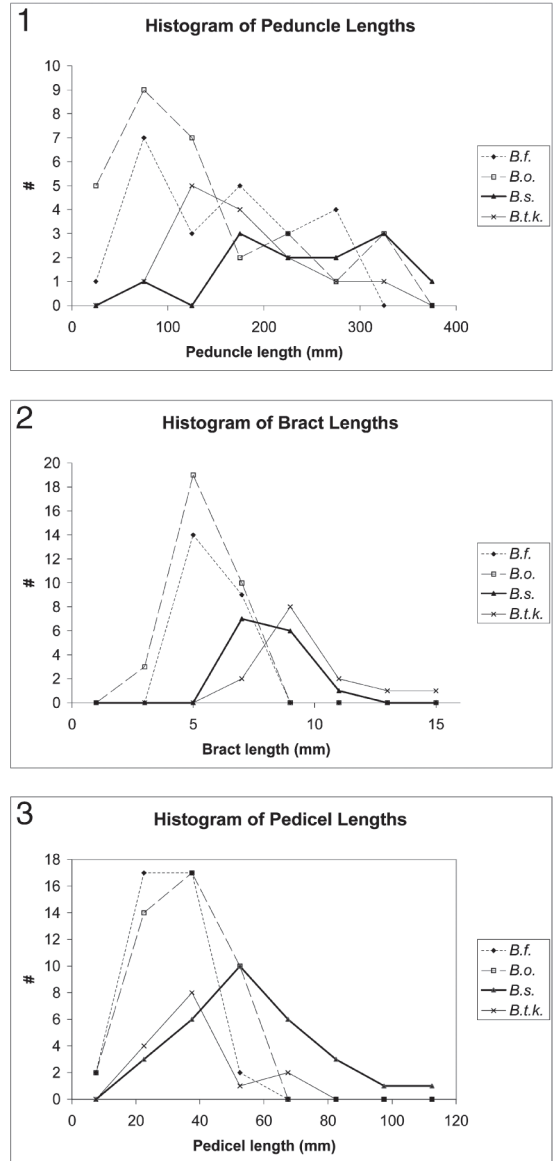

FIG. 4. Histograms of peduncle, bract and pedicel lengths for *B. filifolia* (*B.f.*), *B. orcuttii* (*B.o.*), *B. santarosae* (*B.s.*), and *B. terrestris* ssp. *kernensis* (*B.t.k.*).

orcuttii are found in habitats that largely exclude non-native annual grasses, whereas *B. terrestris* subsp. *kernensis* and especially *B. santarosae* are found in drier habitats that favor those grasses. Supporting our suspicion, the range of peduncles is essentially the same for every species even though the histograms are different, implying that each species grows its peduncle long enough for its flowers to be out in the open.

The difference in bracts is more fundamental since the range for bract lengths is very different among the species; there seems to be a firm upper

TABLE 3. SCALING OF FLORAL CHARACTERISTICS WITH PERIANTH LENGTH: SLOPE AND STANDARD DEVIATION. Slope values in bold type indicate characteristics significantly larger than for the other species; values in italics indicate significantly-smaller characteristics.

Characteristic	B. filifolia	B. orcuttii	B. santarosae	B. terrestris subsp. kernensis
Perianth tube	**0.20** ± 0.04	**0.31** ± 0.05	*0.05* ± 0.07	0.28 ± 0.07
Perianth lobes	0.80 ± 0.04	0.69 ± 0.05	0.95 ± 0.07	0.72 ± 0.07
Filament	*0.09* ± 0.02	**0.19** ± 0.03	**0.26** ± 0.09	0.11 ± 0.06
Anther	0.13 ± 0.03	0.13 ± 0.02	0.17 ± 0.04	0.16 ± 0.03
Ovary	0.19 ± 0.04	0.19 ± 0.03	−0.01 ± 0.06	0.14 ± 0.07
Style + stigma	0.31 ± 0.05	0.41 ± 0.05	0.37 ± 0.06	*0.17* ± 0.04
Staminodes (free portion)	0.04 ± 0.03	0.00 ± 0.00	−0.19 ± 0.14	0.16 ± 0.07

limit for the bract length of *B. filifolia* and *B. orcuttii*.

Pedicel lengths. As for the peduncle and bract lengths, *B. filifolia* and *B. orcuttii* had a similar pattern with histograms that peak at shorter values (Fig. 4). However, *B. terrestris* subsp. *kernensis* had a histogram shifted only slightly to larger values, whereas *B. santarosae* had a histogram shifted dramatically to larger values. For example, all pedicels of *B. filifolia* and *B. orcuttii* were less than 60 mm, but 37% of the pedicels of *B. santarosae*, and 13% of the pedicels of *B. terrestris* subsp. *kernensis*, were greater than 60 mm.

Floral parameter lengths. Analysis of seven floral parameters, plotted against perianth length and analyzed with linear regression, revealed that every floral parameter for every species scaled with the perianth length with two exceptions. First, the staminodes for every species except *B. terrestris* subsp. *kernensis* did not scale with perianth length. The staminodes for *B. terrestris* subsp. *kernensis* scaled with perianth length much the same as every other non-corolla floral parameter, which had slopes of 0.11 to 0.17. (This slope value means that for every 10 mm enlargement of the corolla, the other part lengthens by 1.1 to 1.7 mm on average.) All of the other species had fitted slopes consistent with zero within two standard deviations. (The slope was of course exactly zero for *B. orcuttii* since its staminode length is always zero.) The fitted slope of the staminode length for *B. santarosae* was actually negative with perianth length; i.e., there was a tendency for the maximum staminode length to *decrease* with increasing perianth length. However, the slope value was only 1.4 times its standard deviation, consistent with zero.

Second, the perianth tube and ovary length for *B. santarosae* did not scale with perianth length. It is tempting to say that these values have simply reached their maximum values for the large flowers of this species, but both characteristics had a significant positive slope for *B. terrestris* subsp. *kernensis*, which had equally large flowers. These two exceptional traits add to the suite of characters that make *B. santarosae* distinctive.

The scaling with perianth length for the other floral parameters, given in Table 3, was generally consistent between all species, with the following exceptions: the tube for *B. filifolia* grew more slowly with perianth length than did the tube for *B. orcuttii*, a difference of 1.7 standard deviations ($P = 0.09$ due to chance); the filament length for *B. filifolia* grew more slowly with perianth length than did the filament lengths for *B. orcuttii* and *B. santarosae*, differences of 2.9 standard deviations ($P = 0.004$) and 1.9 standard deviations ($P = 0.06$), respectively; and the style (including stigma) length for *B. terrestris* subsp. *kernensis* grew more slowly with perianth length than did the styles for the other species, differences of 2.1–3.9 standard deviations ($P = 0.04$–0.0001).

Table 4 gives the mean values and standard deviation of the mean for the floral characteristics. Significantly-larger mean values are in bold type; significantly-smaller values are in italics; the differences here range from 4.4-10 standard deviations ($P < 10^{-5}$). Six of the seven characteristics of *B. filifolia* and *B. orcuttii* were significantly-smaller than at least one of the other two species; in contrast, six of the seven characteristics of *B. santarosae* were significantly-larger than at least one of the other two species. Interestingly, *B. terrestris* subsp. *kernensis* had three significantly-smaller values and four significantly-larger values. In addition, the width of the anther axis tissue for *B. terrestris* subsp. *kernensis* was 0.5–0.9 mm and never became as narrow as the minimum value for each the other species of 0.2 mm.

CONCLUSIONS AND DISCUSSION

Brodiaea santarosae merits designation at the rank of species. The plants are taxonomically distinct in a number of significant features from all other *Brodiaea* species, and in fact are among the most distinctive *Brodiaea* species. The plants are not direct hybrids of *B. filifolia* and *B. orcuttii*, nor are they part of a hybrid swarm between those species. The plants form a homogeneous population with a well-defined geographic range. Further, as is often the case for many recently-recognized species, this species is

TABLE 4.   FLORAL CHARACTERISTICS MEAN AND STANDARD DEVIATION OF THE MEAN, IN mm. Values in bold type indicate characteristics significantly larger than for at least one other species; values in italics indicate significantly-smaller characteristics.

Characteristic	*B. filifolia*	*B. orcuttii*	*B. santarosae*	*B. terrestris* subsp. *kernensis*
Perianth tube	*6.7 ± 0.2*	*6.1 ± 0.2*	**8.3 ± 0.2**	**10.2 ± 0.3**
Perianth lobes	*13.5 ± 0.4*	*15.8 ± 0.4*	**20.0 ± 0.6**	**19.2 ± 0.7**
Filament	*0.5 ± 0.1*	**5.4 ± 0.1**	**5.6 ± 0.3**	*2.7 ± 0.2*
Anther	*4.6 ± 0.1*	5.3 ± 0.1	**6.8 ± 0.1**	5.4 ± 0.2
Ovary	*4.5 ± 0.1*	5.2 ± 0.2	**6.8 ± 0.2**	**7.6 ± 0.2**
Style + stigma	*6.6 ± 0.2*	9.4 ± 0.3	**13.1 ± 0.3**	*8.1 ± 0.2*
Staminodes (free portion)	2.6 ± 0.1	*0.0 ± 0.0*	3.3 ± 0.4	**7.5 ± 0.2**

closely associated with an unusual soil type, the unique area in southern California defined by the Santa Rosa Basalt. The discovery of this species supports the speculation in Kruckeberg (2006) that "*most new species will be in places … with kooky soils..in such remote places … as … out of the way places in southern California*".

Eleven separate characteristics distinguish *B. santarosae* from the two species with which it has previously been confused, *B. filifolia* and *B. orcuttii.* Five of those 11 characteristics also distinguish *B. santarosae* from *B. terrestris* subsp. *kernensis*: its staminode properties, anther and style lengths, and the lack of scaling with perianth length of the perianth tube and ovary. The other six characteristics are the lengths of the inflorescence bracts, pedicels, perianth tubes, perianth lobes, ovaries, and its habitat.

The association with the Santa Rosa Basalt makes *B. santarosae* an interesting species for further study. Raven and Axelrod (1995) speculate that genera with many species endemic to the California Floristic Province, such as *Brodiaea*, were in the area long before the climate transitioned to a Mediterranean one without summer rainfall at about five million years ago or so. Such taxa then gradually adapted to the lack of summer rainfall, and radiated to form new species as new habitats became available (Niehaus 1971).

The Basalt is accurately dated as 8–11 million years old (Kennedy 1977), and hence was present long before the climate changed. It is possible that *B. santarosae* originated before the climate change as well. DNA studies may be able to elucidate the evolutionary relationship between *B. santarosae* and its neighboring species with small geographic ranges, *B. filifolia* and *B. orcuttii.* Niehaus (1971) speculated that *B. filifolia* and *B. orcuttii* were young species from their diminished staminodes and their association with soils that have only appeared recently.

Brodiaea filifolia occurs primarily on "recent alluvial soil" and *B. orcuttii* occurs in the western part of its range on "old terrace soils which were previously submerged by the sea but recently became available" (Niehaus 1971). Both of these

soils appeared much later than the Basalt soil. Most alluvial soil on which *B. filifolia* is found is mapped as *Quaternary* (California Division of Mines and Geology 1962, 1966), although similar soil probably appeared earlier, perhaps two million years ago. The old terrace soils on which *B. orcuttii* is found are considered to have emerged only in the last one million years (Abbott 1999). However, Niehaus was apparently not aware of the populations of *B. orcuttii* in the Cuyamaca Mountains. Although that terrain has been present for a much longer time (Norris and Webb 1976), it isn't known whether *B. orcuttii* only recently spread to that terrain or originated there.

Future evolutionary studies of these three *Brodiaea* species may thus add new information to the evolution of the California flora. In contrast, the much-studied serpentine habitat, with its ~285 endemic taxa (Kruckeberg 2006) including *B. pallida* and *B. stellaris*, appeared after the shift to a Mediterranean climate. That habitat is less-accurately dated as having emerged in "*the late Pliocene and early Quaternary*" (Raven and Axelrod 1995), sometime more recently than about 5 million years ago.

The geographically-separate populations of *B. santarosae* may also allow DNA studies to give a minimum age of this species since those populations were last in full reproductive contact. An independent estimate of when those populations were isolated may also be possible from modeling the erosion of the Santa Rosa Basalt combined with estimates of the distance over which *Brodiaea* species can spread.

The association of *B. santarosae* with the Santa Rosa Basalt may imply that it is headed toward extinction in the near geologic future when the last trace of the basalt erodes away, unless it can adapt to non-basaltic soils. At least 97% of the Basalt has been eroded in the 8–11 million years since it formed. It will take much less than another 0.3 million years (3% of the previous erosion interval) to erode the remaining basalt, for the following two reasons. First, significant erosion of the basalt only began after the area was uplifted approximately 3.6 million

years ago (Gath et al. 2002). Second, the remnants are being eroded on all sides now, whereas most of the previous erosion was only along the edges of the formerly-intact basalt mass.

Conservation Status

Four of the known populations of *B. santarosae* are protected as part of the Santa Rosa Plateau Ecological Reserve and Cleveland National Forest. Another population, a large one on Avenaloca Mesa, is partially protected by the Nature Conservancy.

The discovery that the populations of *B. filifolia* in the San Mateo Canyon Wilderness Area and the Mesa de Colorado area are in fact pure *B. filifolia* adds two protected populations of *B. filifolia* to the list in U.S. Fish and Wildlife Service (2004). Formerly those populations were assumed to be hybrids and hence not as important as pure populations for the conservation of the species.

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