Aerial view of the Santa Rosa Plateau showing three vernal pools on the Mesa de Colorado. Populations of the rare Santa Rosa Basalt Brodiaea (*Brodiaea santarosae*) are found almost entirely on outcrops of Santa Rosa Basalt that date back ten million years. All photographs by W.P. Armstrong.

THE SANTA ROSA BASALT BRODIAEA: A NEW SPECIES "HIDDEN IN PLAIN SIGHT"

by Wayne P. Armstrong, Tom Chester, and Kay Madore

THE FASCINATING HISTORY OF THE SANTA ROSA BASALT BRODIAEA

Before roughly ten million years ago, the landscape of Southern California was as flat as eastern Kansas is today, a land of low rolling hills. There were no mountains, no frequent earthquakes, no San Andreas Fault, and fewer habitats for plant species, resulting in much less diversity. Furthermore, due to the absence of great mountain chains like the Sierra Nevada and Peninsular Ranges, Southern California received summer rainfall.

Then, about ten million years ago, an oceanic spreading center was subducted under the North American continental crust here. This began the process of mountain building in Southern California, including formation of the San Andreas Fault, migration of the Baja California peninsula away from mainland Mexico, the loss of our summer rainfall, and the diversification of species for which California is famous.

In a dying gasp, one of the segments of the oceanic spreading center repeatedly covered what is now southern Orange County, northwestern San Diego County, and southwestern Riverside County with lava (Kennedy, 1977). This flood basalt, called the Santa Rosa Basalt, completely covered the nearly flat landscape, killing all the plants formerly present, and providing a fresh surface that eventually became ready for colonization by pioneer plants.

However, basalt soils, like those derived from serpentine and gabbro, are not well tolerated by most plant species. These soils are deficient in some nutrients required for plant growth such as calcium and potassium, and they contain large amounts of minerals such as magnesium and iron that are toxic to many plant species. This is a strong stimulus for the evolution of new species that can thrive on such soils. Some plant genera, such as *Brodiaea*, have genes that make them more adept than others in being able to evolve species that can tolerate difficult soils. Two species in northern California, *B. pallida* and *B. stellaris*, have adapted to serpentine soils.

The authors recently discovered a new *Brodiaea* species that similarly adapted to the Southern California basalt. We named it *Brodiaea santarosae*, the Santa Rosa Basalt Brodiaea (Chester, Armstrong, and Madore, 2007a). Amazingly, this species had been seen by numerous botanists in the last half-century, yet it had gone unrecognized because it is superficially similar to two other *Brodiaea* species, *B. filifolia* and *B. orcuttii*. Even more surprising is that the confinement of this species to basalt soils only became apparent after we determined that it was taxonomically distinct from all other *Brodiaea* species and were writing our paper.

In addition to the probable origin of *Brodiaea santarosae* discussed above, this species has a number of other fascinating stories connected to it. We discuss two of them below. First, how this species was "hidden in plain sight" until its masquerade was uncovered. Second, how it was finally determined that this species was a basalt endemic, and how that led to the discovery of an ancient valley that was filled with basalt and has been recently uncovered by erosion.

A SPECIES "HIDDEN IN PLAIN SIGHT"

Brodiaea santarosae was first collected at the Santa Rosa Plateau in 1960, with the specimen determined as *B. orcuttii* by none other than Theodore F. Niehaus, who would 11 years later write what still remains as the definitive monograph on the genus *Brodiaea*. In 1985, another specimen of *B. santarosae* was determined as *B. filifolia*. In 1992, another specimen of *B. santarosae* was determined as a possible hybrid between *B. filifolia* and *B. orcuttii*. In all, we found a total of nine collections of *B. santarosae*, from six different botanists, determined as one of these three possibilities.

The confusion here stems from a remarkable variation in the staminodes of *B. santarosae*. Staminodes are flower parts that appear somewhat similar to stamens, hence the name, but do not contain pollen. They are often crucial in distinguishing species, such as some orchids and penstemons, in many plant families. *Brodiaea* staminodes range from thread-like to petal-like. From 10-50% of the flowers of *B. santarosae* have no staminodes at all, as do all flowers of *B. orcuttii*. The other 50-90% of the flowers of *B. santarosae* have thread-like or tapered staminodes, a property also shared by *B. filifolia*. It was not surprising that botanists mistook *B. santarosae* as one of these two other species; both the authors had also done so in the past when we had seen individual specimens.

Steve Boyd, Timothy Ross, Orlando Mistretta, and Dave Bramlet were the first to realize that this population of plants was distinct from previously known species. In their 1995 *Flora of the San Mateo Canyon Wilderness Area*, they reported that most of the plants found there appeared to be specimens intermediate between *B. filifolia* and *B. orcuttii*, and reported them as hybrids, or a hybrid swarm, between those two species.

In late May 2006 at Clay Hill, a small hill just to the west of the Mesa de Burro in the Santa Rosa Plateau, Kay Madore found a *Brodiaea* population that looked different to her. When Kay showed this population to Wayne and Tom, our jaws dropped wide open. We had never seen a *Brodiaea* population like this in the four years we had been studying *Brodiaea* species in Southern California. We were like kids in a candy store, going from one flower to the next in a delighted trance. We were shocked by the variability in the staminodes, and kept calling to each other, "Look at the staminodes of this flower!"

We quickly realized that these had to be members of the same population reported by Boyd et al. from San Mateo Canyon, and could hardly wait to begin studying samples at home. By coincidence, Tom had

Santa Rosa Basalt Brodiaea (*Brodiaea santarosae*) on Miller Mountain.

gathered samples of *B. filifolia* elsewhere at the Santa Rosa Plateau earlier that day, in order to begin trying to understand why those seemingly-pure plants of *B. filifolia* were so different from the descriptions of *B. filifolia* and hybrids from San Mateo Canyon. To study *Brodiaea* species in detail, fresh flowers are required since the staminodes and other important small flower parts are often lost to study when the flowers are pressed. Those parts are usually obscured by the petals and often destroyed by attempts to remove the petals in fragile, dried specimens.

The first step of the analysis was to split open the flowers and tediously measure 14 characteristics, most to the nearest 0.1 mm using a microscope, from each of 26 flowers, a total of 364 eye-straining measurements. We also gathered the range for each of those characteristics reported by Niehaus (1971) in his monograph for *B. filifolia* and *B. orcuttii*. We then took the measured characteristics two at a time and plotted them against each other, along with the Niehaus range for each.

The plots stunned us, since they contradicted our expectation from the field and from the San Mateo Canyon report that these were hybrids between *B. filifolia* and *B. orcuttii*. Kay's plants seemed to be a new species very different from *B. filifolia*, *B. orcuttii*, or a hybrid between those species. (See sidebar, "How is a Plant Species Defined?") In particular, despite our seeing plants in the field that we thought were *B. orcuttii*, no member of this population came close to *B. orcuttii* for many of the measurements.

By comparison, the specimens of *B. filifolia* gathered elsewhere on that same day were nearly perfect fits to the Niehaus range for that species, without any resemblance to *B. santarosae* except for the shape of the staminodes.

Thus *B. santarosae* was finally unmasked. We, like previous botanists, had been misled by the variation in the staminodes and had failed to see characteristics that in hindsight stood out like a sore thumb. For example, the style of *B. santarosae* is much longer than any other Southern California species of *Brodiaea*; on average, it is twice the length of the style in *B. filifolia* and 40% longer than the style in *B. orcuttii*.

However, a lot more work was necessary before we could be confident that *B. santarosae* was a new species. We needed to gather and analyze much more data on many different populations to make sure we weren't being misled by any number of different possibilities. For example, it was possible that *B. santarosae* and *B. filifolia* separated out well only here at Clay Hill, and they were indeed intermixed elsewhere as part of a hybrid swarm. Also, the true range of characteristics for both *B. filifolia* and *B. orcuttii* could be larger than reported by Niehaus.

With the help of Steve Boyd in telling us where he had found populations of plants similar to ones at San Mateo Canyon, as well as Avenaloca Mesa locations from Zach Principe, we quickly collected and measured specimens from all other known populations of *B. santarosae*. We also used the Consortium of California Herbaria online database to find locations of both *B. filifolia* and *B. orcuttii*, and we measured

Foreground: Flat grassland with Santa Rosa Basalt boulders on Avenaloca Mesa. Background: Elsinore Peak (with antennae). Ten million years ago, the entire area shown in the picture was nearly flat and covered by basalt. Today, erosion has left basalt remnants in this picture only in the foreground and on Elsinore Peak. This picture shows nearly the full north-south current extent of both the Santa Rosa Basalt and Santa Rosa Basalt Brodiaea (*Brodiaea santarosae*), about 11 miles, with both existing only in the same small remnant patches.

specimens from many known locations of both species. We also had the good fortune to find two specimens that turned out to be true F1 hybrids of *B. filifolia* and *B. orcuttii* at the vernal pools in San Marcos, the only location where those two species coexist (Armstrong, 2007). We also measured samples of *B. terrestris* ssp. *kernensis*, since it is the only other *Brodiaea* that occurs in the range of these three species. This work created a database of fresh specimens of all *Brodiaea* taxa found in this area that could be objectively analyzed to determine how separate these species were, as well as any possible relationships between those species.

We visited the three major Southern California herbaria, located at the San Diego Natural History Museum, Rancho Santa Ana Botanic Garden, and the University of California at Riverside, and measured as many characteristics as were possible on their specimens determined as *B. filifolia*, *B. orcuttii*, and *B. filifolia* X *B. orcuttii*.

The final dataset from our fieldwork consisted of 16 characteristics measured on each of 132 flowers (a total of 2,112 measurements!), along with additional measurements on the entire flowering stems for these samples, and measurements from herbarium specimens. These flowers came from 14 different locations spanning a distance of 50 miles north-south and 33 miles east-west.

ANALYSIS OF THE DATASET GAVE UNEQUIVOCAL RESULTS

1. Four separate species existed, each virtually equally distant from the other species in our analysis plots. In particular, *B. santarosae* was no closer to *B. filifolia* or *B. orcuttii* than it was to *B. terrestris* ssp. *kernensis*.

2. The San Marcos hybrids of *B. filifolia* X *B. orcuttii* were almost exactly intermediate to the

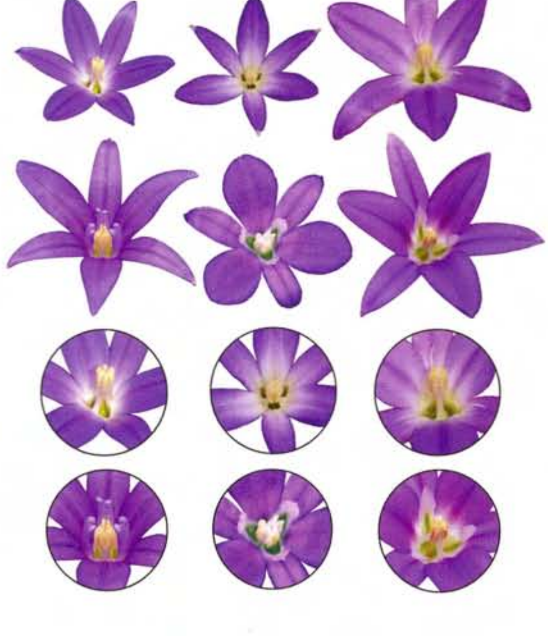
HOW IS A PLANT SPECIES DEFINED?

In botany, a *species* is a population of plants whose members have at least one, and usually many, recognizably distinct characteristics, along with a geographic range that is generally unique. Such a population consists of members that interbreed freely with each other, but not with other species, under natural conditions, and hence forms a closed gene pool. Species generally result when a population acquires some trait that prevents them from sharing genes with other closely related populations. Such changes are often due to geographic isolation, an ancient hybridization event, or a sudden mutation that results in different flowering times or acquiring different pollinators.

We have identified 11 characteristics of *B. santarosae* that distinguish it from the two other species with which it has been confused, *B. filifolia* and *B. orcuttii*. *B. santarosae* has a very distinctive range that corresponds to the current locations of the Santa Rosa Basalt. *B. santarosae* is completely geographically isolated from populations of *B. orcuttii*, and only a few populations of *B. filifolia* come within the range of *B. santarosae*. *B. santarosae* is isolated from *B. terrestris* ssp. *kernensis* by a failure to form fertile hybrids; we found only one hybrid between those two species, and it produced no pollen.

A sterile hybrid *Brodiaea* found growing on the Santa Rosa Plateau. The parents are presumably *B. santarosae* and *B. terrestris* ssp. *kernensis* which have different chromosome numbers.

BELOW LEFT: Upper: The six *Brodiaea* species of Southern California at roughly their correct relative sizes. Clockwise from upper left: *B. orcuttii*, *B. filifolia*, *B. santarosae*, *B. elegans* ssp. *elegans*, *B. kinkiensis*, and *B. terrestris* ssp. *kernensis*. Lower (in circles): Magnified view of the staminodes for these six species. Staminodes are modified sterile stamens that appear just inward from the petals, and are useful in separating many *Brodiaea* species. • BELOW RIGHT: Santa Rosa Basalt Brodiaea (*Brodiaea santarosae*). Note the long stamens and long, thread-like staminodes.



two parent species, precisely as expected of F1 hybrids in wild plants, and were just as distant from *B. santarosae* as were its parent species.

3. All populations of each of the four species were consistent with each other, with no evidence of geographic variation.

Details of the characteristics of these four species, and the analysis, are given in our *Madroño* paper and online (Chester et al., 2007a, b). Here are two brief examples of the uniqueness of *B. santarosae*:

1. The average value for the length of each of seven flower parts (flower tube, flower lobes, filament, anther, style, ovary, and staminode) varies significantly between the species. Each species has a characteristic signature in how many of its parts are significantly smaller or larger than those of at least one other species (see Table 1). In particular, *B. santarosae* has six parts that are significantly larger than at least one of the other species; i.e., all but its staminodes are larger than at least one other species. This demonstrates clearly how distant it is from the two species with which it was previously confused.

TABLE 1. COMPARISON OF LENGTHS FOR SEVEN FLOWER PARTS

	B. filifolia	*B. orcuttii*	*B. terrestris* ssp. *kernensis*	*B. santarosae*
# parts smaller	6	6	3	0
# parts larger	0	1	4	6
# parts not smaller or larger	1	0	0	1

2. The leaves, flowering stem, and the stalks connecting the individual flowers to that stem are significantly longer for *B. santarosae* than for any of the other three species. The common name of *B. filifolia* is thread-leaved brodiaea for its small very narrow leaves of typical length 30 cm (12 inches) with widths of one to two mm. The leaves of *B. santarosae* are so large that they can easily be mistaken for those of Mariposa lilies (*Calochortus*), with lengths of 60 cm (24 inches) and widths of up to six mm.

The flowering stem for *B. santarosae* can be up to four times longer than the stems of *B. filifolia* and *B. orcuttii*, and is also longer than stems of the *B. filifolia* X *B. orcuttii* hybrid. The upper right photograph on page 26 shows plants of *B. santarosae* and *B. terrestris* ssp. *kernensis* grown in identical conditions in pots containing soil derived from San Marcos Gabbro, which is chemically similar to basalt. The longest observed flowering stem of *B. santarosae* was 76 cm (30 inches). During a one week period in June 2007, the stem grew 18 cm. This is roughly one inch per day or one millimeter per hour!

If *B. santarosae* did not have such variable staminodes, it would have been recognized as a separate species long ago.

Tom Chester is standing on Clay Hill in the foreground, the type locality for *Brodiaea santarosae*, with the Mesa de Burro in the background. Basalt caps the mesa, Clay Hill, and also extends in a narrow finger from the left edge of the mesa down to the bottom of the road in the distance. Santa Rosa Basalt Brodiaea grows only in these basalt areas, and not in the seemingly identical surrounding areas.

B. SANTAROSAE LEADS TO GEOLOGIC DISCOVERIES

Plant species often grow differently on soils derived from different rock types. Sometimes the difference is so marked that aerial photographs can indicate geologic boundaries due to a change in vegetation. Some species are even confined to specific soils, especially the basalt-serpentine-gabbro soils that, as mentioned above, present challenges to plant colonization. For more information on this interesting subject, see Kruckeberg, 2006.

We are botanists, not geologists, and get most of our geologic knowledge from detailed geologic maps. We were very aware of the Santa

Rosa Basalt, which is clearly marked on geologic maps and could hardly be missed in the field since it forms the flat-topped mesas that define the Santa Rosa Plateau. We knew the rest of the Santa Rosa Plateau Ecological Reserve contained mostly two other rock formations: granodiorite plutonic rocks producing obvious exposed whitish boulders, and metasedimentary rocks that were easily weathered and hence produced few obvious exposures.

The first specimens we saw of *B. santarosae* were at Clay Hill, 0.3 miles west of, and 100 feet below, the nearest mapped basalt on the Mesa de Burro. That location is mapped as metasedimentary rock, and since there was no flat-topped basalt layer there and no obvious whitish boulders nearby, that seemed reasonable to us. Hence at the very beginning of our analysis, we had no inkling that this species was confined to basalt.

All subsequent specimens but one were found on Santa Rosa Basalt. The exception was at Elsinore Peak, which contains no flat-topped area, was not mentioned as being a location of Santa Rosa Basalt (Kennedy, 1977), nor was it mapped as basalt in Kennedy's map. Thus at the end of our field and herbarium work, we had found *B. santarosae* at six locations, four of which were on basalt, and two of which we thought were not.

One necessary detail for our paper was to give the rock type found at Elsinore Peak. By luck, instead of consulting Kennedy, 1977, we consulted the *Geological Map of California: Santa Ana Sheet*, 1966. We were shocked; it was mapped as basalt with the same geologic age as the Santa Rosa Basalt!

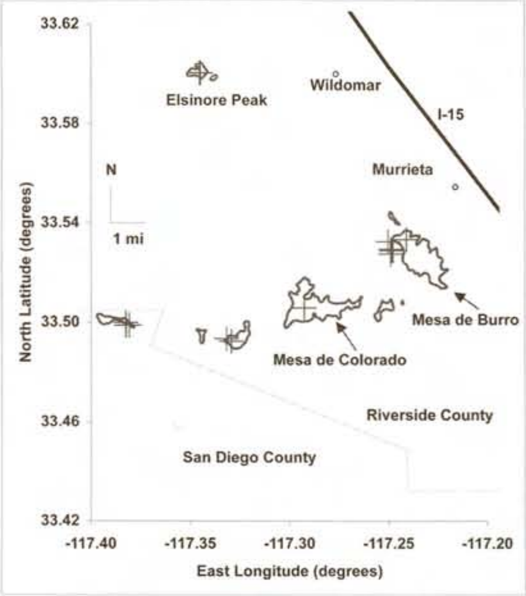
Suddenly it became clear to us that the soil at Clay Hill either might still be influenced by basalt—since the Santa Rosa Basalt had only recently geologically been stripped from that surface—or *B. santarosae* had simply persisted there for a short geologic time after the basalt vanished. This meant that *B. santarosae* was actually a basalt endemic, or nearly so.

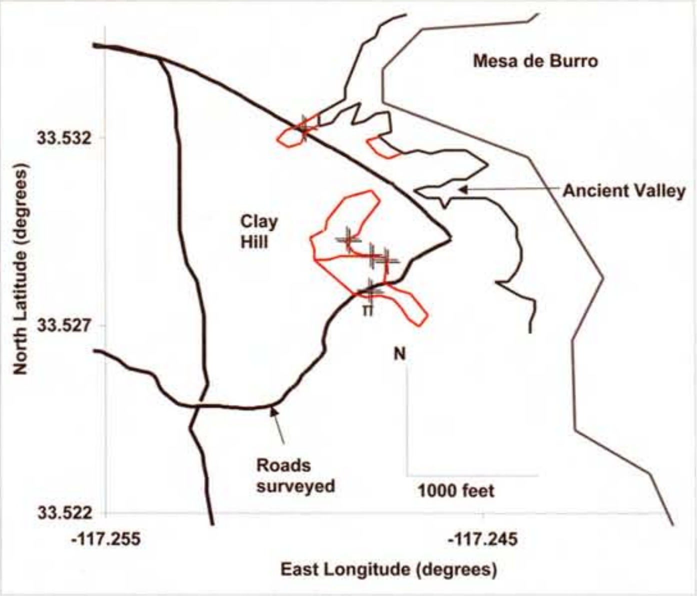
We revised the draft of the paper to make the important claim that *B. santarosae occurs only on or very close to the Santa Rosa Basalt*, and thought we had properly addressed that issue.

Fortunately, one of the *Madroño* reviewers of the scientific paper asked us if we had done any chemical soil analysis to understand why one population grew on non-basalt soil. As a result, we revisited Clay Hill and for the fourth time were dumbfounded by this species: there was unmapped basalt at Clay Hill! This meant that every vouchered population was found on basalt soils, and *B. santarosae* was a true basalt endemic. We revised our paper accordingly and it was published in October 2007.

Little did we know that *B. santarosae* had two more surprises for us. The surprises came when we returned to the type locality of Clay Hill in November 2007 to map the extent of the basalt in that area. Not surprisingly, our mapping revealed just how faithful *B. santarosae* is to the basalt. There are 1.72 miles of road surrounding Clay Hill that were completely surveyed both for *B. santarosae* and for basalt. In our 2006 plant survey, made without any suspicion that *B. santarosae* was confined to basalt, we found two locations of *B. santarosae*, at mile 0.26 and mile 0.73. In our 2007 basalt survey, we found basalt only at precisely the *B. santarosae* loca-

Remaining areas of Santa Rosa Basalt (black lines) and areas of Santiago Peak Volcanics (red lines), along with locations of *Brodiaea santarosae* (crosses). LEFT: Area map. RIGHT: Detail map of Clay Hill area.





ABOVE: *Brodiaea santarosae* (left) compared with the San Marcos *B. filifolia* X *B. orcuttii* F1 hybrid. The hybrid flower is about 40% smaller, and its internal parts have distinctly different relative sizes. • RIGHT: Comparison of *Brodiaea santarosae* (left) with *B. terrestris* ssp. *kernensis*. Both plants were grown in San Marcos Gabbro soil. The *B. santarosae* plant was 76 cm tall, the tallest species of *Brodiaea* in Southern California.

tions. Yet to the eye, there is no obvious difference at all between the habitat on and off the basalt.

The first surprise came when we looked at Mesa de Burro from Clay Hill and suddenly realized we were seeing an ancient valley from 10 million years ago that was still preserved in its west face. This ancient valley had not been noticed before because it is very broad and shallow, about 2,000 feet wide at its top

POSSIBLE FUTURE OF *B. SANTAROSAE*

CNPS is proposing to place *Brodiaea santarosae* on List 1B.3; rare, threatened, or endangered, but without current significant human threats to the population. However, the greatest threat to this species may be the natural loss of its habitat.

B. santarosae is primarily associated with the Santa Rosa Basalt. At least 97% of the basalt has been eroded in the 8-11 million years since it formed, with most of that erosion probably coming in the last three million years in which the Santa Ana Mountains were uplifted.

It will take much less than another 30,000 to 300,000 years (3% of the previous erosion interval, using two different estimates of the erosion interval) to erode the remaining basalt since the basalt has now been broken up into small areas and is now being eroded on all sides. Thus *B. santarosae* is doomed to go extinct in the wild in the near geologic future (about 100,000 years or so) unless it can adapt to non-basaltic soils, or unless viable populations are found to be present on basalt soil not derived from the Santa Rosa Basalt.

With the recent discovery that *B. santarosae* can at least persist for some time on the basalt of the Santiago Peak Volcanics, there is hope of finding such populations in the San Mateo Canyon area, where there are extensive exposures of that formation. We plan future surveys there in order to untangle the previous confusion with *B. filifolia*, and to examine the geologic formations on which *B. santarosae* grows.

and only 100 feet deep. Our basalt mapping revealed about 500 horizontal feet of the lowermost part of that valley was still covered with the first lava flows to fill that area, but which had not been noted before since the lava was heavily eroded. We also found traces of lava flows that covered a portion of the sides of that valley another 1,200 feet downstream. For more information, see Chester et al., 2007c.

The second surprise came when we were showing the rocks at Clay Hill to a geologist, Norrie Robbins. Due to her insistence on splitting open the rocks to see a fresh surface, we discovered that the basalt at Clay Hill itself was actually from the approximately 150 million year old Santiago Peak Volcanics! This simultaneously mortified us, that we had misidentified the rock formation, and delighted us, that this meant there was the possibility that *B. santarosae* could outlast the Santa Rosa Basalt. (See sidebar, "Possible Future of *B. santarosae*.")

Who would have thought that a plant could lead to finding previously unknown areas of basalt, as well as a previously unrecognized preserved ancient valley?

REFERENCES

Armstrong, W.P. 2007. *Brodiaea* Species in San Marcos. Accessed at http://waynesword.palomar.edu/vernal1d.htm

Chester, T., W.P. Armstrong, and K. Madore. 2007a. *Brodiaea santarosae* (Themidaceae), A New Rare Species From the Santa Rosa Plateau Area of the Santa Ana Mountains of Southern California. *Madroño* 54(2): 187-198.

Chester, T., W.P. Armstrong, and K. Madore. 2007b. *Brodiaea santarosae* —The Santa Rosa Basalt Brodiaea. Accessed at http://tchester.org/plants/analysis/brodiaea/santarosae.html

Chester, T., W.P. Armstrong, and K. Madore. 2007c. Ten Million Year Old Drainage at the Santa Rosa Plateau Reconstructed by Analysis. Accessed at http://tchester.org/srp/geologyancient_drainages_by_reconstruction.html

California Division of Mines and Geology. 1966. *Geological Map of California: Santa Ana Sheet*. California Division of Mines and Geology, Sacramento, CA.

Kennedy, M.P. 1977. *Recency and Character of Faulting Along the Elsinore Fault Zone in Southern Riverside County, California*. California Division of Mines and Geology Special Report 131.

Kruckeberg, A.R. 2006. *Introduction to California Soils and Plants*. University of California Press, Berkeley, CA.

Niehaus, T.F. 1971. A Biosystematic Study of the Genus *Brodiaea* (Amaryllidaceae). *University of California Publications in Botany* 60: 1-67.

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