Mariposa

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C. luteus

The leaf turns ...

A reminder that this is my last issue as editor of ***Mariposa***. From this point, all correspondence about the newsletter, including back issues, should be addressed to –

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For those readers who want to stay in touch with me personally, my address is 13373 Plaza del Rio Blvd., Apt. # 5524, Peoria, AZ 85381 USA, and my phone number is AC 623 – 875-3950. I do not yet have an e-mail address (though I am hoping to have one soon).

My apologies for this issue's lateness – the process of packing, moving, unpacking, and getting settled took longer than I had anticipated Also, readers may notice that the masthead is a bit different – my 15-year-old computer "expired" during the move and I had to get a new one which does not have quite the same type faces available. This too contributed to the lateness of this issue.

Let me take this opportunity to thank many of you for the kind comments you have sent me over the years, as well as for the extra money some have sent to help defray the costs of printing color photographs. It has been a source of great pleasure to do this newsletter, and I've thought a lot about what to do with my last issue. Hugh MacDonald spent his final three issues considering some problems in the genus *Calochortus* (as well as reporting on some of his and Karen Stokkink's travels) and featuring pictures of some of the color forms of *C. venustus*. I've decided to follow his lead – sharing some of Jim's pictures of the wonderful color forms from Stump Springs, for the pleasure of those who have not been there, as well as considering something that has always interested me – the widely variant forms this species presents in a more or less consistent regional pattern.

In so doing I will be providing a brief summary of a master's thesis submitted to the Department of Biology at UC San Francisco in 1993 by Randy K. Zebell ["A Systematic Reevaluation of Three Species of *Calochortus* (LILIACEÆ) – *C. venustus, C. simulans, and C. argillosus*"]. Zebell's research, which was conducted under the supervision of Professor Peggy Fiedler, studied the different colors found in *C. venustus* in considerable detail. In addition, he firmly established that Hoover's *C. argillosus* and *C. simulans* were valid separate taxons, settling the many years of dispute about them. *C. argillosus* in particular has been

regularly misidentified as *C. venustus* in the Bay Area. For example, it has appeared on the plant list for Edgewood Park in San Mateo county for many years as *C. venustus*, but the latter species in fact does not grow there, while *C. argillosus* is fairly common in and around the park.

The different forms of *C. venustus* –

The most common form of *C. venustus* – petals of creamy white marked in shades of red – is often called the "South Coast" or the "two-spot" form, but both of these terms are actually misnomers. True, it is the dominant form in the South Coast ranges, from the valleys north of Mount Hamilton to Ventura and Los Angeles counties (although it has become more rare in the more heavily populated portions of southern California). But this form can also be found in the Sierras. To give just two examples, there is a sizeable and very vigorous population east of Jackson, along Highway 88 (so vigorous that one might suspect tetraploidy). However, many of the flowers there lack the "second spot" which most (but not all) of the flowers in the South Coast ranges have. There is also a population in the Merced River canyon along Highway 49, north of the river, where many of the flowers do have the second spot. This population is less vigorous in appearance than those found east of Jackson – a fact that might be accounted for by a dryer climate.

The accompanying photos show *C. venustus* at its most glorious – the myriad of brilliant colors which seem to reach their peak near Stump Springs, in the northeastern corner of Fresno county at an altitude of about 6000 feet, and further east and higher still around Huntington Lake. These beautiful plants continue to the northwest at least to the ridges east of Columbia; and to the southwest toward Shaver Lake, then descend toward Pine Flat Lake. However, the brilliancy of the colors tends to soften into rich pastels as you lose altitude. There is then a gap of some 100 air miles or so to the area around Fort Tejon, along that portion of I-5 known as "the Grapevine," where once again one sees the rich pastels and rarely the more brilliant colors. (Reportedly, there used to be many more of the brilliant colors, but over-vigorous collection has reduced their numbers there.) In between Fort Tejon and Fresno county, *C. venustus* is considerably less common than *C. superbus*, although they can be found east and south of Bakersfield in the Tehachapis, where they most often resemble the "two-spot" form but with the upper margins of the petals blushed pink.

Then south and west of Fort Tejon, on the eastern and northern slopes of Mount Piños at about 6000 feet, is found the special form that takes its common name from its location. The "Mount Piños" form is very consistent in appearance, the petals a rich red on the interior but nearly white on the exterior, and all petal markings – including the gland – a creamy white-to-pink. Most of the other forms of *C. venustus* have glands of golden-yellow to golden-brown. Another form of *C. venustus* can be found on the mountain – especially a little west and a little higher than the "Mount Piños" form – and these most closely resemble the creamy-white-tinged-pink populations east and south of Bakersfield, except that they tend to be more vigorous – perhaps as a result of higher rainfall.

Finally, Jim and I found an large population of mariposas near the western end of the Antelope Valley, a few miles east of I-5. Their glands were a little inconsistent – many fairly square, but some more rectangular than square, and some rather irregular in shape. Most of them were blushed, some quite extensively so, but in shades of lavender, from pale to rich, rather than pinks or reds. They were growing in wide open and rather flat ground with a few thin grasses – not the sort of habitat *C. venustus* usually prefers. The year we found them, which had been a high-rainfall year for the Antelope Valley, there were hundreds and hundreds of them, but the following year (which had been much dryer in that area) there were very few. We thought they might be some ancient *C. venustus* hybrid that had somehow found a niche it liked and thrived there. But we could only speculate about how they might have arisen.

Calochortus venustus color forms –

– more photos on page 5

What draws this array of forms together as a single species is their sharing of a "± square" gland (the shape of the gland was what Ownbey considered the most important delineator in his taxonomic organization of the genus). Yet Jim and I always wondered just how closely related the different forms were. It intrigued us that the very colorful forms often display a sort of "echo" of the "two-spot" form. In some cases (as can be seen in some of the pictures here) there is an area in the central-upper part of the petal – and it is sometimes a large area – in a color not quite the same as the dominant petal color. This "echo of the two-spot effect" made it easier for us to accept that they might be variants of a single species, that there is more evidence than just the shape of the gland to tie them together.

I had imagined that Tom Patterson's analysis of *Calochortus* DNA might help clarify things, but his research did not offer much enlightenment. In all but a few cases his work apparently was based on a single sample for each species. The origin of the sample of *C. venustus* was given simply as "Kern county." Kern county is very large and includes populations of both the "two-spot" form and the territorial extension of the very colorful form at Fort Tejon, as well as possibly even a small stand of the "Mt. Piños" form. Without further information about the sample of *C. venustus* he used, we don't know which was the form he subjected to DNA analysis. Since I was unable to elicit a reply from either Patterson or his thesis supervisor, I could not get further clarification. (I am aware that much of the DNA research being done these days is based on analysis of single samples, but in general, I believe this practice detracts from the value of such research efforts and from the reliability – not to mention the replicability – of the results.)

Zebell's thesis –

Zebell took a much different approach, collecting many samples of buds, petals, and seed, from three locations for *C. argillosus* (Point Sal, Morro Bay, and west of Morgan Hill); three locations for *C. simulans* (all in interior San Luis Obispo county); and 17 locations for *C. venustus* (five in the Sierras, three in the Transverse ranges – including two at Mt. Piños – and nine in the South Coast ranges). Collections were made during the late spring and summer of both 1991 and 1992.

He germinated the seed and processed the resulting root tips in order to examine the chromosomes of each species. He established chromosome counts of N=7 for all three, placing them firmly in Ownbey's subsection VENUSTI. He found that all three occasionally had extra chromosome fragments, but was not able to confirm any chromosomal similarities or differences in greater detail. He developed systems for measuring petal shape and size, gland shape, gland position, and position of petal markings, using 13 separate dimensions to categorize 468 individual petals (consisting of 65 *C. argillosus* petals from 3 locations, 72 *C. simulans* from 3 locations, and 341 *C. venustus* from 13 locations). He also classified the dominant color of the petal surfaces (both adaxial or inside, and abaxial or outside) of 1,570 flowers, using a "Munsell Book of Color – 80 Hue" [Anonymous, undated, Macbeth Division of Kollmorgen Corp., Baltimore], a system that establishes numeric values for **hue** (basic shade or color), **value** (the lightness or darkness of a color), and **chroma** (the intensity of a color). In addition he classified each sampled population of *C. venustus* according to the frequency of specific dominant petal colors and to the incidence (or lack) of a second spot. Finally, he subjected the data thus obtained to multivariate analysis (a method of establishing statistical significance when there are multiple variables to consider).

Zebell concluded that *C. simulans* differed significantly from the other two by petal shape (less clawed); by the position of the ± square gland (lower on the petal); and by the darkness and position of the red petal markings (never above the lowest third of the petal). (The test of "significance" in all cases was a probability of 0.01 or less that the results were random rather than consistent.) *C. argillosus* could be distinguished by its

More color forms of *C. venustus* –

– All photos by Jim Robinett

gland shape (± rectangular – lying cross-wise on the petals); the existence of a green stripe on the exterior of the petal, running from behind the gland down to the petal base; and the occurrence of pale yellow, green, and lavender markings on the interior of the petal, and lavender on the outside, in hues which are not found in the other two species. He also concluded that the coastal and inland forms of *C. argillosus* and the various color forms of *C. venustus* were insufficiently distinctive to justify their being formally named "vars."

The occurrence of a second spot in *C. venustus* varied from population to population, being least frequent in Santa Barbara county and in the more northern Sierra locations. Flowers with dominantly cream-colored petals were found in all locations, even the most highly colored populations of the southern Sierras. Each population examined had a dominant petal color that occurred significantly more often than any other. Zebell noted with interest that the proportions of second-spot and/or colored forms in a specific population differed between the two collection years (both of which were relatively dry) and speculated that, particularly in times of drought, individual bulbs probably did not bloom every year. (Those of us who have grown *Calochortus* would add that this may also occur under controlled conditions, when plenty of water is provided during the growing season.)

Finally, Zebell discussed how the color variations in *C. venustus* might have arisen. He cited studies of other genera which suggest that specific color variants become established because they are more successful at attracting pollinators; and noted that the mariposas in general display characteristics frequently found in plants pollinated by bees (stems sturdy enough to bear the weight of a bee, and wide open bowl-shaped flowers). Other research has shown that different bees from a single hive can be attracted to different colors – for example, blue or yellow. But Zebell also commented that he never saw bees pollinating mariposas during his field work, but only small black beetles (and that was our experience also). He concluded that the attraction of pollinators was not at play here. Instead, he speculated, the wide range of colors might be caused by "transposons" – which are segments of chromosomes known to often change their positions during cell reproduction. Again, studies of other plants have demonstrated that transposon shifts can be associated with changes in flower color. The variances in color could become established simply because the pollinators were indifferent to such changes, he conjectured.

Comments –

I was impressed by the thoroughness of Zebell's research, by the ingenuity of his color analysis and the methods he developed for assessing petal shape and markings. His work struck me as astonishingly comprehensive for a master's thesis. I could only wish he might extend his efforts to the rest of the VENUSTI as a PhD project, adding DNA analysis of multiple samples to his other efforts.

I would be particularly pleased to see a study focusing not only on multiple samples of the different forms of *C. venustus*, *C. argillosus*, and *C. simulans*, but also on the other mariposas growing nearby – *C. superbus* (there are extensive populations in the southern Sierras and Greenhorns), *C. leichtlinii* (which also grows along Stump Springs), and *C. invenustus* (which also occurs on Mt. Piños), in an effort to pin down how recently (or remotely) these species might have been related. Ideally, such an effort would select from among the more "traditional" analytic tools, such as chromosome comparisons, petal shapes, glands, color analysis, flavenoid (color) compounds, cross-fertilization efforts, etc., as well as DNA analysis, to offer the fullest possible examination of their relationships. We may never be able to trace completely the origins of these different forms and species, at least not with current technology. Nevertheless, I believe such an effort would be worth pursuing, in the hope that it would at least suggest some answers. Certainly, until someone tries, we can only speculate about their relationships.