



APRIL, 1998

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I. Announcements RENEWAL NOTICE

Its dues time again, time to send in your \$8. (\$10. overseas) for next year's issues. After nine years as editor, I'm 'retiring' and turning over the newsletter to Jim Robinett and Georgie March. They have kindly consented to take over the newsletter. They are most qualified as they are both conversant with the botany of the family, pioneers in *Calochortus* horticulture and very experienced in observing the plants in the field. I thank everyone for their continued patronage of the newsletter and encourage them to continue their subscription. **Mail your dues to:**

Robinett, P.O.Box 1306, Sebastopol, Ca.95473

2. Habitat Cycles and *Calochortus* There are other cycles which *Calochortus* must endure beside burning (see last issue for a brief discussion of *Calochortus* and fires). The surrounding plant community goes through its own changes, such as reforestation, pioneer to climax changes, changes due to geologic action, etc. *Calochortus* spp. must adapt to these changes if they are to survive. One adaptive strategy is to move away if the canopy or geology changes significantly. Thus if the species is adapted to conifers, it may move on with these if they are replaced by climax species other than conifers. An alternative strategy is to stay in place and somehow adapt to the new conditions. *Calochortus minimus* can be found in both shade and sun; perhaps it simply stays put if the forest canopy is either cut down or grows back. What is amazing is how often *Calochortus* stands from long ago can still be found in the same location, perhaps reflecting the strategy of staying put and adapting to new local conditions.

II. Trips.

Since Hugh and I are leaving the newsletter in Jim and Georgie's capable hands, I thought I'd leave you by sharing our most memorably funny moment in Mexico.

We started out fairly early from the hotel, anxious to get to a stand of *C. barbatus* after our attempt to view *Tigridia* earlier had proved fruitless. We were passing through the state of Michoacan, taking in the lovely countryside, admiring the pristine town squares, and stopping once to buy some local handicrafts.

Finally we were at the site, which turned out to be on the side of route 40. We stopped our van and all got out. But before Hugh could join Tom in the hunt, nature called. Now, we had been pretty intelligent (we thought) in having brought with us a porta-potty. So, Hugh hauled it out of the back, and took it over a stone wall for some privacy. Tom went in search of the flowers, and I stayed by the car, as I hadn't been feeling well for a few days.

Well, unfortunately for Hugh, the porta-potty proved unstable. There was a Crack! Bang! from behind the stone wall, followed by a long silence, then a cry from Hugh for my help. As it turned out, the porta-potty had broken, sending Hugh plummeting into his own pile. He asked for one of the water jugs as well as a change of clothes. Again, unfortunately for him, I was distracted by the sudden appearance of the Angeles Verdes (Green Angels), a department of the Mexican Highway Patrol, that stops to aid travelers in trouble. I hurried over to them, thanked them for stopping, and explained we were a scientific expedition, looking for native flowers. (Meanwhile Hugh was swearing loudly for my help, not realizing I was engaged elsewhere.)

That was when I hear Tom's plaintive cry, "Hugh, where are they?", referring to the flowers. Now, granted they were in seed, but when I looked over in Tom's direction (about 30 feet away), I saw him standing right in the middle of the stand itself!

All's well that ends well. The Green Angels left, Hugh got cleaned up, and Tom had the flowers pointed out to him. To this day, we still laugh about that episode--and now you can, too!

III. Horticulture:

Germination Tests, 24th Installment: In-Ground Tests, Report on the outcome of trial growing tests conducted on *Calochortus*

Unamended clay soil was used for one plot, and amended for five others. Plot two was half clay, half sand; three was 1/2 redwood compost, 1/2 clay; four was 1/2 clay, 1/2 peat; five was 1/2 clay, 1/4 redwood compost, 1/4 sand; six was 1/2 clay, 1/4 sand, and 1/4 peat. Further, a duplicate six plots were set up using bulb fertilizer. Also, to test sandy soil, a flat was set up with 2/3 sand, 1/6 clay and 1/6 humus, both fertilized and unfertilized. The species tested were *Calochortus albus*, *C. albus v. rubellus*, *C. tolmiei*, *C. uniflorus*, *C. nitidus*, *C. venustus*, *C. luteus*, *C. clavatus* (Outer Coast Range form), *C. nuttallii*, *C. ambiguus*, and *C. obispoensis*. Each plot was sown with 20 seed of each of the above species.

The results were that species which grow in clay in the wild and which tolerate abundant rainfall did well, viz. *C. uniflorus* and *C. luteus*. The two desert species died off in the deluge of '95 as did most of the others. A few *C. albus*, *C. tolmiei*, *C. obispoensis*, and *C. venustus* survived in various plots but no trend was apparent. What was apparent was that the survivors in the fertilized plots did not do any better than those in the unfertilized plots, whether clay adapted or not. They grew as fast and seemed as healthy as those with fertilizer. Secondly, clay soil is not a good medium for species from dryer habitats. Both of the above desert spp. grow in clay soil in their native range, but receive considerably less rain. However, clay will work fine for species from wetter areas, e.g. *C. vestae*.

IV. The Horticultural History of *Calochortus*

[Third Installment of the article by Claude Barr, "Calochortus, Sensational Native American Tulips"]

"Alternate freezing and thawing during early growth is credited with being enemy number one of *Calochortus*. Granted that repeated freezing is injurious, the careful observations of years are (1) that frost injury...may be only an accessory act and...a clinging, smothering moisture does the dirty work after the freezing of a heavy, soggy, wet soil; meanwhile *Calochortus* bulbs are entirely immune in this same soil if on the dry side. (2) The semi-hardy ones really do not differ in their essential reaction, as I have had them resume growth after a sudden cold...when the soil warmed quickly and moisture was not excessive. And (3) that the bulbs perish in wet ground in an apparently identical manner without Jack Frost...

"with a knowing eye to a sloping surface and a subsoil that is fully capable of carrying downward and away any unbearable surplus of water...they grow in regions of low, irregular rainfall and active and desiccating winds. Further, the...soils which are acceptable to them...where a pick is required to extricate the bulbs contain little humus, and this leanness also aids drying.

"With these habitat characters in mind, the gardener will seek a moderately light medium such as will be readily warmed by the sun and avoid richness. A lean soil like the subsoil of an excavation...will return to relative dryness while rich soils are still reeking wet. Some fineness of texture at least in contact with the bulb seems their preference. Clay's...natural coldness...holds back growth when growth must be surging upwards. Clay, leafmold and humus increase moisture capacity...Avoid them, along with all that tends to defeat dryness. One must not fear to provide starvation rations, for an astonishingly little fat-of-the-land will nourish a mariposa's beauty.

"A medium of the desired qualities may be compounded of one-third very fine clean sand, one-third fine limestone chips and one-third lean loam. Alternates are coarser sand, any fine screened gravel, any convenient earth that has not been enriched. It may be necessary to employ a portion of the subsoil. If a heavy loam must be used the measure may be reduced by half to just enough to fill in...between any sand grains.

"In early planting, one species showed unmistakable dissatisfaction with drainage facilities or growing medium or both...*C. kennedyi*...I vowed to build a suitable desert for *C. kennedyi*. Well out in the open a place was selected, away from the close air and fitful reflected heat of walls and with practically a full day of sun. An excavation of 20" exposed an absorbent shale which...would take care of subdrainage. Twelve inches of coarse gravel were tamped in, an inch of fine gravel to support the soil layer, three inches of sand with just a slight admixture of loam. At this depth, four inches, the

bulbs were placed, covered with the same soil, and the balance of the hole filled in with almost pure sand... *C. kennedyi* [bloomed well]

"...A similar planting was made another year, with the difference of a little more and 'better' soil. The result?...The *C. kennedyi* lives but has never flowered. And the leaf growth is narrower, more channeled, lacking...well-being...the gravel layer ...is not intended to remain a reservoir; an outlet must be assured. Thus...capillary moisture is cut off from below...The gravel may be shallower if the escape is good. Some coarser gravel may be added to the recommended sand-limestone chip-lean loam mix, up to the level of the base of the bulbs, augmenting drainage...For most species a 4" rooting layer is preferred as many kinds are stronger growing.

V. Landscape Uses of *Calochortis*

Calochortus in containers can be used as an attractive specimen planting for any outdoor area. The container can be placed on a deck or patio or brought indoors while the plant is in bloom. Containers can be filled entirely with *Calochortus* or mixed with other natives. One can even plant different species with similar growing requirements but different bloom times in the same container and watch them bloom in succession. Similarly one could combine different species in one container for different combinations of form and color.

In the ground, *Calochortus* can add accent to a bed of natives or form an attractive planting by themselves. The smaller species are excellent in rock gardens, while the larger are suitable for borders. *Calochortus* can be used as accents or specimen plants in gardens with other Mediterranean plants that require dry summers. A more specialized planting of this type would consist simply of Mediterranean-climate bulbs, e.g. those from Greece or S. Africa along with natives. *Calochortus* spp. could also be included in a planting of California bulbs alone or in gardens with plants from specialized habitats, such as all desert species.

Unlike many plants, *Calochortus* tolerate, and in some cases prefer, poor soils such as "serpentine." They can be used to make a showy seasonal planting in what otherwise would be a barren area. Many grow on slopes in the wild and can be used to beautify a previously unremarkable hillside. Woodland species can add color to shady areas.

VI. Botany: Part III Preliminary Findings

[Part Three of the article on *Calochortus* phylogeny by Tom Patterson, PhD candidate in Botany at University of Wisconsin]

As was discussed in Parts I and II, my work involves generating a DNA based phylogeny (i.e., family tree) for *Calochortus* and its near relatives. A phylogeny makes it possible to understand how the various species and groups of species are related to one another, and to learn more about their evolution and biogeography. In this concluding segment, I will report on the results generated thus far in this ongoing study. It is important to note, and emphasize, that the results are *not complete* and changes could occur with the addition of more data and further analysis.

One of the major goals of my work entails finding out where *Calochortus* fits in with the rest of the monocots. Historically, *Calochortus* was believed to be a member of the Lily family (*Liliaceae*) and closely related to another family, the *Uvulariaceae*, or, because it has many unique characteristics, in its own family. I sequenced a relatively slowly evolving gene in *Calochortus* as well as all potential relatives, to see if DNA analysis could help sort through these various hypotheses. The results are quite interesting and a bit surprising. *Calochortus* appears to be closely related to *Tricyrtis*, *Streptopus*, *Prosartes* and *Scoliopus*, with the Asian genus *Tricyrtis* being its sister group (i.e., its closest relative). While it has not previously been proposed that *Calochortus* and *Tricyrtis* are sister genera, they do happen to share several morphological traits that, *a fortiori*, add supporting evidence to the DNA results. For example, they both have septicidal [seed] capsules [which break open at a natural dividing line--ed.] (members of the *Liliaceae* have loculicidal [cell-like] capsules); some members of *Calochortus* (i.e., subsection Weediani, the California Cyclobothras) have un-fused "staminal columns" that are very similar to those found in *Tricyrtis*, and both genera tend to have hair on the insides of their petals. However, the results of this analysis also show that *Calochortus*

has many unique DNA mutations which are distinctive and which separate it from both *Tricyrtis* and all other genera. Because mutations take a long time to accumulate, this implies that *Calochortus* has been isolated (i.e., separated from *Tricyrtis*) for a long, long time. Such a high degree of genetic, and hence evolutionary, distinctiveness probably warrants placing *Calochortus* into its own family, the *Calochortaceae*.

Another major goal of my work is to establish how the various species within the genus are related to each other. To this end, I examined a more rapidly evolving segment or stretch of DNA, so that mutations which have accumulated between (closely related) species which have diverged relatively recently could be analyzed. Although the resulting phylogeny is not fully resolved, i.e. not all the species have unique placements in the family tree, there are nonetheless several broad conclusions that can be drawn. First, the DNA phylogeny is largely consistent with the traditionally recognized sections [first delineated by Prof. M. Ownbey-ed.], viz. *Calochortus*, *Mariposa* and *Cyclobothra*. This is good news because it implies that the way in which Ownbey (1940) divided the genus was natural and thus no major revisions will be necessary. There were, however, a few qualifications to this schema based on the DNA analysis. The most prominent is that some members of section *Mariposa* (e.g. *C. dunnii*, *C. splendens*, *C. superbus*, *C. argillosus*, etc.) are more closely related to the Mexican members of section *Cyclobothra* than they are to other members of section *Mariposa*. Further, the California *Cyclobothra*, i.e. subsection *Weediana*, are basal to section *Calochortus*, rather than closely related to the Mexican *Cyclobothra* (and may be basal to the entire family). Among other things, this suggests that the fibrous-reticulate bulb coat, a key characteristic identifying section *Cyclobothra* may have arisen, or been lost, more than once in the evolution of the *Calochortus* family as a whole.

Second, the DNA phylogeny shows a strong relationship to geography with species found in relatively close proximity tending to be each other's closest relatives. These fall into geographic groups. There appears to be a Pacific Northwest group (including *C. apiculatus*, *C. longebarbatus*, *C. persistens*, *C. lyallii*, etc.), a Bay Area/N. Sierra Nevada group (including most of the fairy lanterns, *C. tolmiei*, *C. umbellatus*, etc.), a group which grows primarily east of the Sierras (including *C. ambiguus*, *C. macrocarpus*, *C. excavatus*, *C. leichtlinii*, etc.), a group primarily from S. California (with *C. dunnii*, *C. venustus*, *C. vestae*, etc. and finally a Mexican group (including all the *Cyclobothra* but excluding the California *Cyclobothra*, the *Weediana*). Given the fact that the seeds of the *Calochortus* family are relatively heavy, wingless and, on the whole, lack the means for long distance dispersal, these results are probably not too surprising.

Finally, ecological shifts between forest understory, woodland and relatively open (i.e. meadow, grassland or chaparral) habitats have occurred numerous times in the genus [i.e. as the species of *Calochortus* have spread, they have re-adapted to similar habitats in new places far removed from the original-ed.]. These shifts generally coincide with shifts between the three major floral syndromes: fairy lanterns, cat's ears and mariposa types [i.e. the reemergence of these types or forms in similar but geographically remote habitats-ed.]. For example, species with pendant, more or less closed flowers (the fairy lanterns, broadly defined to include Mexican bells) are found in the N. California and the Mexican groups, generally in dark forest understories in each region. The large, tulip-like, mariposa forms are found in the Pacific Northwest, the Great Basin-Rocky Mt. and the S. California groups in open habitats, like meadows and grasslands. And the cat's ear type, with hairy petals, is found in species of mountain, open woodland forests in the Pacific Northwest, the N. California and the Mexican groups. Thus similar types have evolved in similar habitats which may be thousands of miles apart and which have no intervening habitats. That is, the woodlands of N. California and those of Mexico are not connected by intervening woodlands, but are discontinuous and separated by hundreds of square miles of desert, habitat unsuited to woodland species. Yet the fairy lantern type evolved in both N. California and central Mexico. This suggests that the shift to a new habitat is accomplished by the reemergence of, or parallel evolution of a form or type suited to that habitat. Further, it constitutes evidence suggestive of radiation patterns for the genus as a whole.

Although my research on *Calochortus* is still in progress and, hopefully, many more insights will emerge, this concludes the series on "Calochortus Phylogeny." A full discussion of these results will

be available soon as a PhD dissertation from the University of Wisconsin. [All photos by HP McDonald]

