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MARIPOSA

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Time for subscription renewals –

This is the last issue of Volume XIV (July 2002 through April 2003), and it's time to renew your subscription to *Mariposa*. There is no change in the cost, which remains –

\$10.00 – Domestic

\$13.00 – Foreign

My plans for Volume XV call for the last issue (in April 2004) to be a comprehensive index to all fifteen volumes. It will list all “Species of the Issue,” trip reports, contributed articles, summaries of other published materials, letters to the editor, etc., by topic and by author, and will probably be eight pages long. This current issue is also “special” – being eight pages rather than six, and devoted primarily to a brief – and incomplete – synopsis of Tom Patterson’s PhD dissertation on his DNA studies of the genus *Calochortus*. I am asking readers to let me know their preferences regarding the possibility of offering a more complete summary of the thesis, at the time they send in their renewals; please see the box below –

- (1) What you have already presented is sufficient (at least for the time being).
- (2) No – I want to know more. Please give us a fuller summary (which would require at least twenty pages of text, tables, and figures – and totally dominate most of the next volume of *Mariposa*).
- (3) No – I want to know more – but not at the expense of displacing “Species of the Issue” and the other usual features in the newsletter. Please offer a fuller summary separately (at an estimated extra charge for printing and mailing of about \$5 for domestic and US\$8 via air mail for overseas readers).

A Possible New *Calochortus* ?

Member Ed Rustvold reports a possible new species, in the Greenhorn Mountains east of Bakersfield, Kern county, CA. It has quite large mariposa-type flowers. The petal exteriors are creamy white, flushed yellow on the lower third-to-half. The petal interiors are yellow on the lower half-to-two-thirds. The gland is a straight line or nearly so, with short yellow “hairs” or trichomes; longer yellow hairs are scattered elsewhere on the petals; and there is a “blotch” above the gland. (*C. superbis* of course also has such a “blotch”. The yellow coloration hints of *C. luteus*. Flower size suggests that it may be a tetraploid. It is noteworthy that some rather bizarre forms of *C. superbis* can be found within 50 miles to the north. So this plant may be a tetraploid form of either an existing species or of a hybrid – since *C. luteus* and *C. superbis* frequently hybridize with each other – rather than a new species.) At present only a single site is known, of about 350 blooming-size plants, growing in poor soils on a southwest-facing, thinly grassed slope at about 2000 feet of altitude. The population was found by Wayne Roderick and Joe Dahl from Tilden Botanical Park (east of San Francisco Bay). Specimens have been provided to the Jepson Herbarium at UC-Berkeley and to several botanical gardens; and its chromosome count and other details are being investigated. Frank Callahan (among others) is traveling to see it this spring. I hope to have pictures of it for the next issue of *Mariposa*.

DNA Studies of *Calochortus*

Member Brad Carter was able to obtain Tom Patterson's thesis on *Calochortus* through the Library at UC-Davis, via Inter-Library Loan, and kindly provided both me and Frank Callahan with a copy. The formal reference is – Thomas B. Patterson, *Phylogeny, Biogeography, and Evolutionary Trends in the Core Liliales and Calochortus (Calochortaceae): Insights from DNA Sequenced Data*. PhD Thesis, University of Wisconsin-Madison, Department of Botany, May 1999.

The thesis is in three chapters – plus tables and figures – and is more than 140 pages long. There is no way I can condense it fully into a single issue of *Mariposa*. The material here is a very brief synopsis of his major findings, after first explaining some of the methodology behind his work – but many of his points have been given “short shrift”. Of necessity, it includes some technical terms, which are defined when first introduced and appear in boldface at that point, to help the reader find the meaning again if needed. The definitions are from *The Facts on File Dictionary of Botany* (Market House Books Ltd., 1984). I am asking readers to let me know their preferences regarding a more complete summary when they send me their renewals.

Background – Cladistics, the “Core Liliales,” etc.

Patterson's work used **cladistics**, an approach to **taxonomy** or the classification of plants in which the relationships among them are depicted by a branching **cladogram** or “tree” representing how the individual plants relate to each other, i.e., the likelihood they have a common ancestor. Traditional taxonomy usually relied on plant **morphology** – external form and structure. Nowadays cladograms are often based on DNA evidence, using “markers” or segments of DNA that are known to evolve rapidly, to try to trace shared ancestry. The use of this method to represent plant **phylogeny** (or evolutionary history) has increased rapidly with the development of new techniques for the laboratory amplification of specific segments of DNA, and the availability of highly sophisticated computer programs for analyzing the data. These programs use the principle of **parsimony**, seeking the shortest or most parsimonious “tree” that fits the data.

Cladistics differs from more traditional methods of phylogenetic analysis in another important respect: it specifies that the only valid natural groups are those that contain all the descendants of a common ancestor; such groups are called “**monophyletic**”. Groups are **paraphyletic** if they do not contain all the descendants of a common ancestor; in traditional schemes of plant classification, the dicots (see next paragraph) are a paraphyletic group because their ancestors also gave rise to the more advanced monocots. **Polyphyletic** groups include taxa derived from two or more ancestral lines which were combined in the past because of similar appearance – but similar appearance may have resulted from “**concerted convergence**” – a concept which asserts that distantly related (or even unrelated) plants evolve and develop characteristics favoring their survival – and a similar appearance – in response to the requirements of a new or changed environment, rather than to descent from a common ancestor. “Concerted convergence” concludes that just because two species LOOK similar does NOT necessarily mean they are closely related. In addition, plants may exhibit “**phylogenetic niche conservatism**” – while a taxon may change in appearance as it shifts to a new habitat, its closest relatives may not, because they remain in the original habitat. **Introgression** – the incorporation of genes from one species into another related species, as a result of hybridization followed by backcrossing of the hybrids with one of the parent plants – is thought to have been another source of confusion for a classical taxonomy based on morphology alone. Introgression is believed to have been a major factor in the evolution of many plants.

A few more definitions may be useful. The **monocots** are all those plants whose **cotyledon** or first leaf from seed is a single leaf; as opposed to the **dicots** all of whom have two “seed leaves.” Among the monocots, the “**Core Liliales**” are presently defined as the LILIACEAE, the CALOCHORTACEAE (see below), and part of the UVULARIACEAE. On DNA evidence, the “Core Liliales” form a monophyletic group, as long as they include

only the directly related portion of the UVULARIACEAE. The “Core Liliales” are all herbaceous **geophytes** (plants with buds situated below ground) and are distributed throughout Asia and North America, in Mediterranean-type, arctic-alpine, and forest-understory habitats.

Patterson's Thesis

Chapter 1 – Patterson examined two separate segments of nuclear DNA from 33 species within 23 genera, to ascertain the phylogenetic relationships among the “Core Liliales.” While not absolutely identical, the cladograms produced by both of these DNA sequences supported each other strongly, so he combined the results. The combined cladogram indicated that the genus *Calochortus* should be considered a separate family – the CALOCHORTACEAE – rather than a member of the LILIACEAE. Despite morphological similarities, the LILIACEAE and the CALOCHORTACEAE – both of which were monophyletic – did not emerge as each other's closest relatives. The closest or “**sister**” genus to the *Calochortus* was *Tricyrtis* – a genus of 10 to 15 species with the common name “Toad Lily”, found from the Himalayas to Taiwan and Japan (according to *Hortus Third*, Macmillan, 1976). This conclusion, though based on the DNA evidence, was supported by the existence of four distinct morphological similarities between the two –

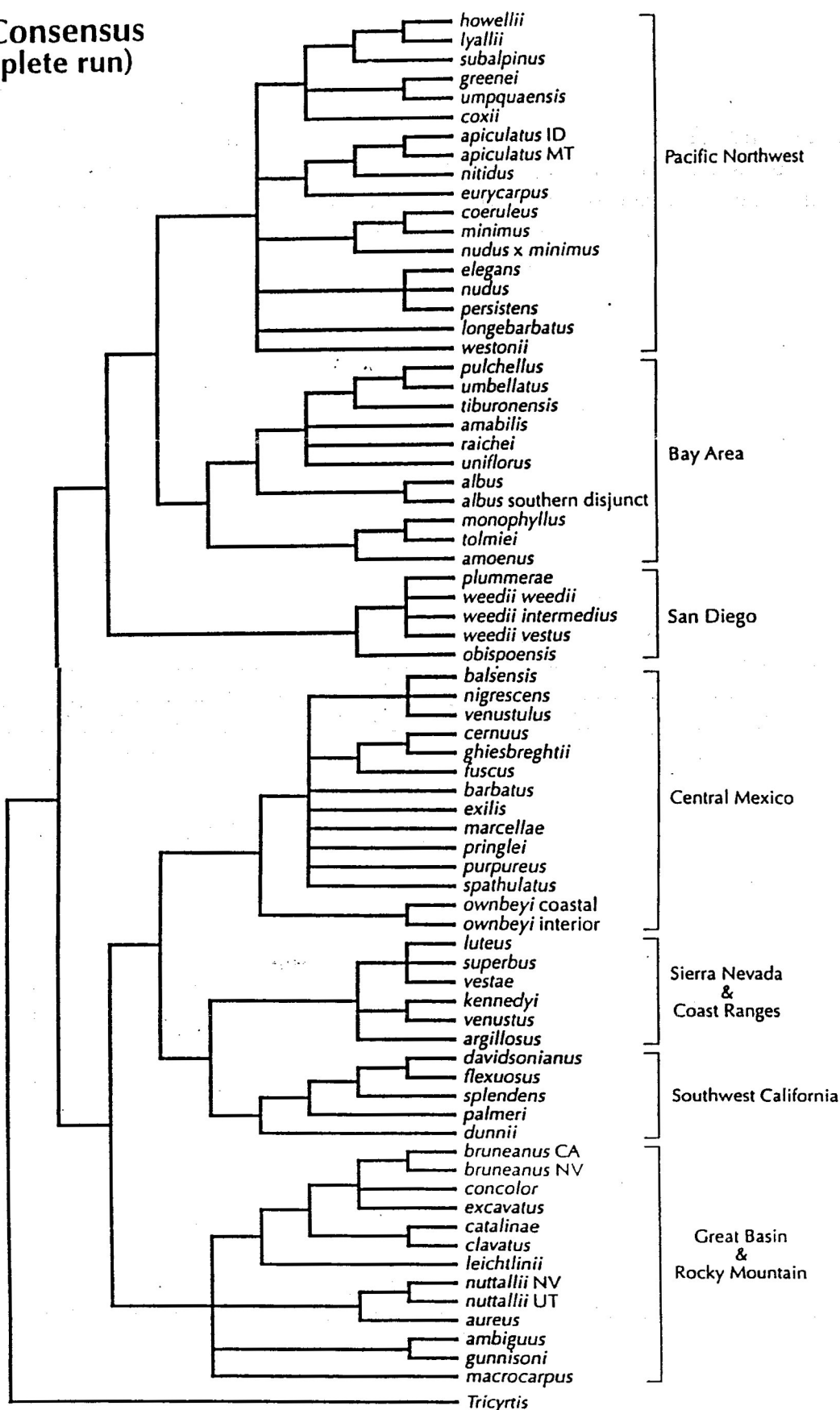
- (1) a **septicidal** capsule which splits longitudinally along lines between ovary cells; as opposed to a **loculocidal** capsule which splits longitudinally along lines midway within each ovary cell (the latter is the type of capsule found in all nine members of the LILIACEAE).
- (2) a **pseudo-staminal column** (in which the anther-supporting filaments rising up and around the ovary are in contact with each other but not fused, as they would be in a “true” staminal column)
- (3) **saccate nectaries** (nectaries or sugar-secreting glands in the shape of a sack or pouch)
- (4) **heavy tepal pubescence** (the **trichomes** or “hairs” on the petal surfaces)

Patterson associated each of these characteristics, together with the development of a bulb as an underground storage organ, with a movement out of closed (shady) habitats, to open habitats with high light availability, but characterized by a short time available for plants to remain photosynthetically active (for example, in Mediterranean climates, arctic and alpine zones, or deciduous forests where spring tends to be brief). The data suggested to him that the LILIACEAE and the CALOCHORTACEAE each arose independently with the transition from closed to open habitats – evolving bulbs, showy flowers, capsules enclosing multiple seeds (as opposed to berries), and narrow leaves with veins running parallel to the central axis. The morphological similarities between them arose from “concerted convergence.” Other members of the “Core Liliales” kept their “more primitive” character states – rhizomes, inconspicuous flowers, berries, and broad leaves with **reticulate** (branching or net-like) leaf veins – because they remained in closed, shadier habitats.

Finally, the phylogenetic cladogram from this DNA evidence indicated that the “Core Liliales” originated in North America, with a minimum of seven intercontinental dispersal events thereafter. Specifically, the family LILIACEAE appeared to have arisen after dispersal to Eurasia and then “returned” to colonize North America at least four separate times– in *Lilium*, *Fritillaria*, *Erythronium*, and *Lloydia*. Further, the data implied that the common ancestor to the *Calochortus* and the *Tricyrtis* was initially North American, and that *Tricyrtis* arose in conjunction with a movement to and separate colonization of Eurasia from that of the LILIACEAE.

Chapter 2 – Patterson stated he recognized 67 known species of *Calochortus*, but 70 (plus vars.) were listed in his thesis [see end note]. Materials from 74 taxa – species, varieties, and special forms or populations, plus one hybrid – of *Calochortus* were studied, using three rapidly evolving segments of DNA from **chloroplasts** (non-nuclear green “organelles” or structures within plant cells that contain the pigment molecules essential for photosynthesis). Initial results were incomplete because of computer memory limitations, although seven major **clades** or monophyletic groups within the genus could be identified. The material was then reduced to 28 taxa (two to five species per clade, depending on clade size) and the analysis repeated. The results

Strict Consensus (incomplete run)



confirmed the existence of seven major clades, each showing strong **geographic cohesion**, meaning that the members of each clade tended to occur in close geographic proximity to each other. He proposed that this pattern of seven geographically cohesive clades resulted from two attributes within the genus: (1) poor seed dispersal capacity (*Calochortus* seeds are relatively heavy and lack scattering devices such as “wings” or “umbrellas” or “stick-to-it’s”); and (2) distribution in a mountainous landscape that could synergistically reinforce the isolating effects of poor seed dispersal. The seven clades were as follows –

- (1) a Pacific Northwest clade (centered on Oregon, Washington, and Idaho)
- (2) a Bay Area clade (with most species distributed near San Francisco Bay)
- (3) a San Diego clade (with most species in or near San Diego county and adjacent Baja California)
- (4) a Coast Range-Sierra Nevada clade (with species showing parallel lines of distribution in the mountain ranges bordering California’s Central Valley)
- (5) a Southwestern California clade (centered on the southern California coast, with *C. flexuosus* and some populations of *C. kennedyi* occurring further east);
- (6) a Great Basin-Rocky Mountain clade
- (7) a Central Mexico clade

[The “tree” reproduced opposite is from Figure 2 in Patterson’s Chapter 2 – but bear in mind that it presents the results obtained from the first, incomplete run, to enable readers to see the relative placement of as many species as possible. So the results themselves are “incomplete” and may well distort some relationships.]

Patterson observed that there was only partial agreement between these seven clades and Ownbey’s three Sections, and considerable differences from most of Ownbey’s subsections. For instance, the DNA data supported Section CALOCHORTUS as a monophyletic group found within clades (1) and (2) above; but Section CYCLOBOTHRHA appeared to be polyphyletic: subsection WEEDIANI of Section CYCLOBOTHRHA, constituting the San Diego clade, was “sister” to Section CALOCHORTUS; while the members of the Mexican clade – the balance of Ownbey’s Section CYCLOBOTHRHA – were embedded within the paraphyletic Section MARIPOSA, and thus were “sister” to those portions of Section MARIPOSA included in clades (4) and (5). Clade (6) constituted the remaining members of Ownbey’s Section MARIPOSA [see end note].

The DNA data supported the idea that a lack of tolerance of serpentine soils was the “basal condition” in the *Calochortus*, but that serpentine tolerance arose multiple separate times within the genus. Serpentine tolerance was concentrated in two clades occurring in areas with many exposed serpentine outcrops – the Pacific Northwest and the Bay Area – but also in *C. obispoensis* (in the San Diego clade), *C. vestae* (in the Coast Range-Sierra Nevada clade), and *C. clavatus* (in the Great Basin-Rocky Mountain clade).

The data suggested that each of the four principle flower forms or **syndromes** within *Calochortus* (catsear, fairy lantern or globe lily, star tulip, mariposa) had arisen independently two or more times within the genus, presumably in response to shifts into new habitats, as well as other possible factors which favored one flower form over another (such as available pollinators). Parallel floral forms appeared to have evolved in widely separated regions that were otherwise similar in their elevation, topological complexity, amount of shade available, etc., Patterson wrote. In short, they appeared as a result of “concerted convergence”.

Species with mariposa-type flowers arose in the closely related Southwestern California, Coast Range-Sierra Nevada, and Great Basin-Rocky Mountain clades, as well as in the more distantly related Pacific Northwest clade [this last because of Patterson’s decision to use the term “mariposa” for the flower form of species such as *C. nitidus* and *C. greenei* – which Ownbey called “star tulips”]. Species with nodding, fairy lantern or globe lily flowers were concentrated in the Bay Area clade but also appeared in the distantly related Central Mexico clade, nearly 3,000 miles to the south. The catsear flower form was found in the two most northerly clades (Bay Area and Pacific Northwest) but also in the most southern (Central Mexico). [Traditionally, each floral type indeed has been associated with a particular habitat. Those with mariposa flowers appear mostly

in open settings such as dry grasslands and chaparral; while catsear species are found primarily in montane woodlands. Species with fairy lantern or globe lily flowers generally occur in closed-forest understories; and star tulips are usually found in open moist meadows or open rocky sites.]

The high degree of geographic cohesion for the seven main clades was probably the result of speciation generally being highly localized within the genus because of poor seed dispersal, Patterson suggested. With species unable to easily disperse to similar yet geographically distant habitats in other regions, they may have been forced to adapt to habitats in geographic proximity, even if those habitats presented environmental challenges. He noted that the overall distribution of *Calochortus* includes nine massive mountain ranges – the Cascades, Rockies, Siskiyous, Coast Ranges, Sierra Nevadas, and Transverse Ranges in the U.S.; and in Mexico, the Sierra Madre Oriental, the Sierra Madre Occidental, and the Eje Volcanico Transversal. A landscape of such extreme topological complexity could further promote local speciation by acting to isolate populations in small geographic areas – for example, within valleys, or on either sides of mountain ranges – and could synergistically enhance the isolating effects of poor seed dispersal, he wrote.

Nevertheless, Patterson considered several cases of apparent long-distance dispersal. For example, *C. albus* and *C. elegans* both have striking range disjunctions; and the Central Mexico clade as a whole is found far south of any other known *Calochortus* species, being confined to the central Mexican Plateau with no known intervening species between them and their northern relatives. In these cases, he wrote, there may have been plants or species “in between” that are now lost because of **vicariance** (the splitting of an original species or group into several isolated species or groups by past geological events or climatic changes, with the isolated plants developing and evolving independently). Or intermediaries may exist but simply have not yet been discovered (this was particularly possible in the case of the Mexican group, he suggested).

Chapter 3 – Patterson here focused on Ownbey’s Section CALOCHORTUS within the genus *Calochortus*, using yet another type of nuclear DNA to examine a total of 27 taxa. The analysis included three samples of *C. albus* (a “coastal” plant from Santa Clara county, a “var. *rubellus*” from San Luis Obispo county, and a “southern California” variant from Los Angeles county), two samples of *C. apiculatus* (one from Bonner county, Idaho, and one from Glacier National Park in Montana), as well as a sample of *C. nudus* X *minimus* – a commonly found hybrid – from Siskiyou county, CA. *C. persistens* was not included, because despite repeated attempts, its DNA resisted amplification and failed to produce enough material for testing. After the initial analysis, second samples were tested for *C. tiburonensis* and *C. umbellatus* – about which more below. The results were “back-checked” against those from Chapter 2 (which used segments of chloroplast DNA). Strong conflicts appeared within the Chapter 3 data for *C. greenei*, *C. minimus*, and *C. westoni*, so these three species were removed from the analysis. Lesser incongruencies appeared between the Chapter 3 results and Chapter 2 results for other species, but Patterson deemed them insufficient to be of concern.

The Chapter 3 phylogeny showed a clear split between the Bay Area clade and the Pacific Northwest clade (as had the Chapter 2 phylogeny). For most species in Ownbey’s Section CALOCHORTUS, their “sister” species had neighboring, overlapping, or otherwise nearby geographic distributions, with little evidence of episodes of long-distance dispersal. *C. uniflorus* and *C. tolmiei* were used as one illustration of this: they emerged as “sister” species on the cladogram – and had virtually identical distributions in the Coast Ranges, Siskiyou-Klamaths, and (southern) Cascades. This supported Patterson’s two conclusions from Chapter 2 – that the effects of limited seed dispersal and a mountainous topography produced highly localized speciation.

The data also suggested that the **catsear floral syndrome** (spreading flowers densely covered with trichomes or “hairs” on the inner petal surfaces) and montane woodland habitats were the basal conditions within the Section. If we accept Patterson’s use of the term “mariposa” to describe species with large, brightly colored,

tulip-like flowers, such as *C. greenei* and *C. nitidus*, then the three other broad-scale floral syndromes (mariposa, fairy lantern or globe lily, and star tulip) evolved as species in the Section moved out into new habitats. Star tulip species were derived three times, in conjunction with a shift to open, generally moist meadow habitats. Fairy lantern types apparently arose twice from the catsear species, in conjunction with transitions from montane woodland to closed understory habitats.

The Chapter 3 phylogeny based on DNA evidence strongly disagreed with Ownbey's classical construct of subsections within Section CALOCHORTUS. Species in his subsections ELEGANTI and NUDI appeared in both clades. All species in subsection NITIDI were in the Pacific Northwest clade but did not form a monophyletic group within that clade. The species in subsection PULCHELLI were all in the Bay Area clade, but whether they formed a monophyletic group was uncertain because the data on the position of *C. tolmiei*-*C. uniflorus* was weak, Patterson wrote. One possible explanation offered for these differences was Ownbey's reliance on broad-scale floral morphology to subdivide the Section. But as noted above, the DNA data indicated that the different floral syndromes evolved separately and independently multiple times. Earlier work with other genera had suggested that a combination of shifts in habitat and in pollinators might be the driving force behind such evolutionary changes in flower form as those observed within Section CALOCHORTUS. The strong selection pressures acting on these floral syndromes might have generated increased **homoplasy** (similar characteristics and appearance arising from "concerted convergence" rather than development from a common ancestor) – which would challenge the validity of using similar morphology as a guide.

Patterson discussed four potential sources of error in his analysis, all arising from "molecular evolution" obstacles. "Pseudogenes" may occur in some portions of DNA, but were believed not to be a problem here because of the methods he chose. "Divergence" as a result of introgressive hybridization or ancient introgression was eliminated because the results that such occurrences usually produce did not surface here. "Bidirectional concerted evolution" which would produce an apparent "homogenization" of some results was eliminated because both the Chapter 2 and the Chapter 3 phylogenies identified a central basal split forming the two main clades in Section CALOCHORTUS (Pacific Northwest and Bay Area). "Chimeric" or recombinant versions of the kind of DNA used in Chapter 3 can occur when strands of DNA within a hybrid physically cross, and the chromosomes exchange genes as a result; Patterson theorized it was possible that such chimerics were responsible for the conflicts found in the data for *C. greenei*, *C. westoni*, and *C. minimus* which led to their exclusion from the analysis.

The pairing of *C. tiburonensis* and *C. umbellatus* as "sister" species despite their striking morphological differences was highly unexpected – so much so that second samples of each were obtained and the new material tested – with no change in the results. *C. tiburonensis* was of particular interest because of its unique characteristics, which seem to combine elements of Sections CALOCHORTUS and CYCLOBOTHRAS. However, the DNA data clearly placed *C. tiburonensis* in Section CALOCHORTUS, rather than in Section CYCLOBOTHRAS [as I had suggested in *Mariposa*, Vol XIV, No. 3]. *C. umbellatus*, its "sister" or closest relative, possesses a membranous bulb coat and a three-winged capsule. So why, Patterson asked, does *C. tiburonensis* have a fibrous-reticulate bulb coat and a capsule that is angled rather than winged (both characteristics of Section CYCLOBOTHRAS subsection WEEDIANI)? He considered such extreme morphological differences between "sister" species extraordinary, because it suggested rapid and extreme morphological evolution. One possible explanation considered was that *C. tiburonensis* simply evolved these characteristics independently – but other *Calochortus* species not having these traits occur in similar habitats and close geographic proximity to *C. tiburonensis*, which made this less likely. Another "more feasible" possibility was that *C. tiburonensis* had captured a Section CALOCHORTUS chloroplast via introgression with a neighboring species (presumably its "sister" and closest neighbor, *C. umbellatus*), he theorized. But both the Chapter 2 and Chapter 3 phylogenies put *C. tiburonensis* in the Bay Area clade – which Patterson said decreased the likelihood that the placement

of *C. tiburonensis* as a “sister” to *C. umbellatus* was the result of chloroplast capture. Yet another possible answer was that more than one kind of DNA had been introgressed simultaneously into *C. tiburonensis* from *C. umbellatus* (or vice versa), he wrote. Patterson concluded that the extreme morphological differences between the two might indicate that such a phenomenon had indeed occurred. Nonetheless, further investigation was clearly necessary to fully understand the relationship between the two species, he held.

Furthermore, Patterson noted, it was also possible that introgression is responsible for the apparently tight correlation between phylogeny and geography observed in Section CALOCHORTUS – but the consistency of that geographic cohesion argued against introgression being a complete explanation. Of greater interest to him were the few cases of long-distance dispersal or disjunction which do occur in the Section (*C. elegans* and *C. albus*). He theorized that perhaps those species migrated, with intervening species or populations later becoming extinct. Long-distance dispersal also might have been mediated by Native Americans, since they frequently used *Calochortus* bulbs as a food source. This might be especially probable for *C. elegans*, with populations on either side of the drought-prone intermountain region of eastern Oregon and western Idaho.

Comment – We (Frank and I) would add that *C. tiburonensis* and *C. umbellatus* (in their present forms) bloom about three months apart, which might make introgression a challenge to accomplish. And Patterson ignored another potential source of error – that strict adherence to the principal of parsimony in and of itself might conceivably falsify the actual relationships among the plants. As another point, one of the attractions of Ownbey’s classification scheme is that it is internally consistent with regard to chromosome numbers (see *Mariposa*, Vol. XIV, No. 3). But Patterson’s seven clades are sometimes inconsistent. For example, the initial Chapter 2 data put *C. kennedyi* (2N=16) in the Sierra Nevada-Coast Range clade – with *C. argillosus*, *luteus*, *superbus*, *venustus* (its “sister” species), and *vestae* – all 2N=14. And *C. catalinae* (2N=14) emerged in the Great Basin-Rocky Mountain clade, as “sister” to *C. clavatus* (2N=16); other members of the Great Basin-Rocky Mountain clade had chromosome numbers of 2N=14 or 16 or 18. “Sister” species with different chromosome numbers is especially troubling, since they presumably would be unable to hybridize – which would seem to remove introgression as a factor in their evolution. Patterson did not speculate about how different chromosome numbers might arise within a monophyletic group, let alone between “sister” species, or what the impact might be. In our view, DNA analysis of current species is unquestionably a useful tool for looking at plant relationships – but it ignores millions of years of evolution, with species arising and some disappearing (as has *C. monanthus*), creating gaps among the “branches” that can distort the “tree”. It needs to be supplemented with other data such as chromosome counts and biochemical analysis for a fuller picture.

End Note – The species for which Patterson examined various DNA segments and how they sorted into his clades is as follows –

- (1) Pacific Northwest clade – *C. apiculatus* (2 locations), *coeruleus*, *coxii*, *elegans*, *eurycarpus*, *greenei*, *howellii*, *longebarbatus*, *lyallii*, *minimus*, *nitidus*, *nudus*, *persistens*, *subalpinus*, *umpquaensis*, *westoni*
 - (2) Bay Area clade – *C. albus* “Sierra form” – “var. *rubellus*” – “Southern California disjunct”, *amabilis*, *amoenus*, *monophyllus*, *pulchellus*, *raichei*, *tiburonensis*, *tolmiei*, *umbellatus*, *uniflorus*
 - (3) San Diego clade – *C. obispoensis*, *plummerae*, *weedii* var. *intermedius* – var. *vestus* – var. *weedii*
 - (4) Sierra Nevada-Coast Range clade – *C. argillosus*, *kennedyi*, *luteus*, *superbus*, *venustus*, *vestae*
 - (5) Southwestern California clade – *C. davidsonianus*, *dunnii*, *flexuosus*, *palmeri*, *splendens*
 - (6) Great Basin-Rocky Mountain clade – *C. ambiguus*, *aureus*, *bruneauensis* (2 locations), *catalinae*, *clavatus*, *concolor*, *excavatus*, *gunnisoni*, *leichtlinii*, *macrocarpus*, *nuttallii* (2 locations)
 - (7) Central Mexico clade – *C. balsensis*, *barbatus* (2 locations), *cernuus*, *exilis*, *fuscus*, *ghiesbreghtii*, *hartwegi*, *marcellae*, *nigrescens*, *ownbeyi* (2 locations), *pringlei*, *purpureus*, *spatulatus*, *venustulus*
- Not examined – *C. foliosus*, *indecorus*, *invenustus*, *monanthus*, *panamintensis* – plus a number of widely recognized varieties and disparate forms. Taxon not mentioned in the thesis – *C. syntrophus*.