

Morphological Variation in *Mimulus* section *Diplacus* (Scrophulariaceae)

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INTRODUCTION

Mimulus section *Diplacus* is a group of perennial shrubs found from northern Baja California to southern Oregon. The taxa are ecologically and morphologically diverse, and inhabit many different communities and elevations from sea level to 2300 meters. The taxonomy of this section has a long history of debate, resulting in a variety of treatments that name different species and subspecies. Since the first species description by Curtis (1796), there have been numerous changes and additions to this group, including its split into a separate genus, *Diplacus*. Recent treatments also have little consistency between them. McMin (1951) retained this group as a separate genus, *Diplacus*, and recognized fourteen species. Munz (1973) included the group in *Mimulus*, and recognized seven species, four subspecies, and one variety. The latest treatment by Thompson (1993), in *The Jepson Manual*, placed all but one of these into a single species because of intergrading and hybridization, implying that no easily distinguishable differences can be made between the taxa.

Intertaxon hybridization is an important cause of these differing treatments. Hybrid populations appear to occur frequently when there is overlap between taxa and may obscure taxonomic boundaries.

This project has four goals:

- Identify and characterize previously named species and subspecies, using existing keys and descriptions.
- Sample locations throughout the geographic range of this section, including areas of overlapping taxa.
- Determine the extent of hybridization or intermediacy in natural populations and its impact on the taxonomy of this group.
- Delineate boundaries between the taxa by use of quantitative measurements of floral and foliar features.

MATERIALS AND METHODS

During the flowering season of 1999 and 2000, 953 plants were sampled from 155 locations chosen to represent the geographic range of all named taxa. Measurements were made of the uppermost mature flower with digital calipers. Three flowers per plant were measured during the 1999 season to address within-plant variation, and one flower per plant was measured during the 2000 season. Vouchers of populations will be deposited at Rancho Santa Ana Botanic Garden (RSA) and pressed specimens of each plant sampled are located at California State Polytechnic University, Pomona (CSPU).

Plant identification was based primarily on the keys of Munz (1973), with additional reference to McMin (1951) and specimens at RSA. Eleven named taxa were distinguished: *M. aridus*, *M. aurantiacus*, *M. aurantiacus* ssp. *australis*, *M. aurantiacus* ssp. *lompoensis*, *M. bifidus*, *M. bifidus* ssp. *fasciculatus*, *M. clevelandii*, *M. flemingii*, *M. longiflorus*, *M. longiflorus* ssp. *calycinus*, *M. puniceus*. Plants that did not easily fit into one of these taxa are likely of hybrid origin and were treated separately.

Principal components analysis (PCA) and discriminant function analysis were performed using the SAS statistical package (SAS Institute, Inc. 1996). Mapping was carried out with ArcView 3.2 (ESRI Corp., 1999).

RESULTS

Principal components analysis

The first three principal components (PCs) account for 85.8% of the total variance of the data (59.6, 16.2, and 9.7% respectively for PC1, PC2, and PC3). PC1 has the highest loadings for all of the corolla features, especially BLLN, UCOS, and THRO and high negative loadings for filament lengths. PC2 has the highest loadings for corolla tube length, calyx measurements, and style length and high negative loadings for numerous corolla features. PC3 has the highest loadings for filament lengths and style length.

The scatter diagram of the first two components distinguish four major groups:

- *M. aridus*
- *M. clevelandii*
- Taxa with large corolla features (*M. bifidus*, *M. longiflorus*, *M. longiflorus* ssp. *calycinus*)
- Taxa with small corolla features (*M. puniceus*, *M. aurantiacus*, and *M. flemingii*).

The data space between the last two groups contains the two subspecies of *M. aurantiacus* (ssp. *australis* and ssp. *lompoensis*) and *M. bifidus* ssp. *fasciculatus*, as well as numerous populations that could not be assigned to a given taxon and are assumed from their intermediate morphology to be of hybrid origin. Most taxa separated on the basis of corolla features, but PC2 separates *M. aridus* and *M. longiflorus* ssp. *calycinus* because of their large calyx and style lengths.

Discriminant analysis

The first three canonical variables (CVs) account for 90.9% of the variance of the data (64.1, 22.6, and 6.9% respectively). Corolla tube length accounts for most of the variation in CV1 separating the same small and large flowered groups as in the PCA. Corolla tube length was also high on CV2, as well as the corolla features WLCL and THRO, and calyx height. Characters loading highest on CV3 were both calyx features and style length. The scatter plot of the first two canonical variables is similar to that of the PCA except for the position of *M. aridus* which is placed high on both CV1 and CV2 because of its long corolla tube length.

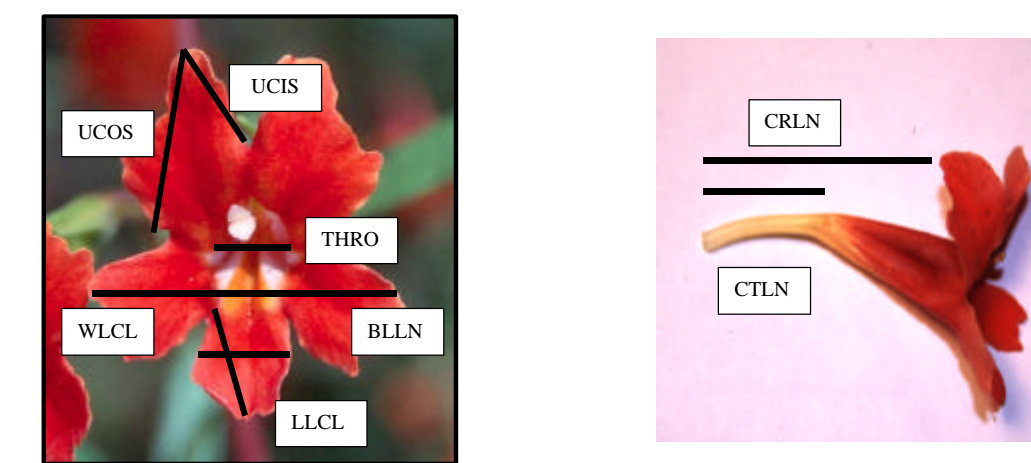
DISCUSSION

Qualitative features not used in the analyses can further distinguish these taxa.

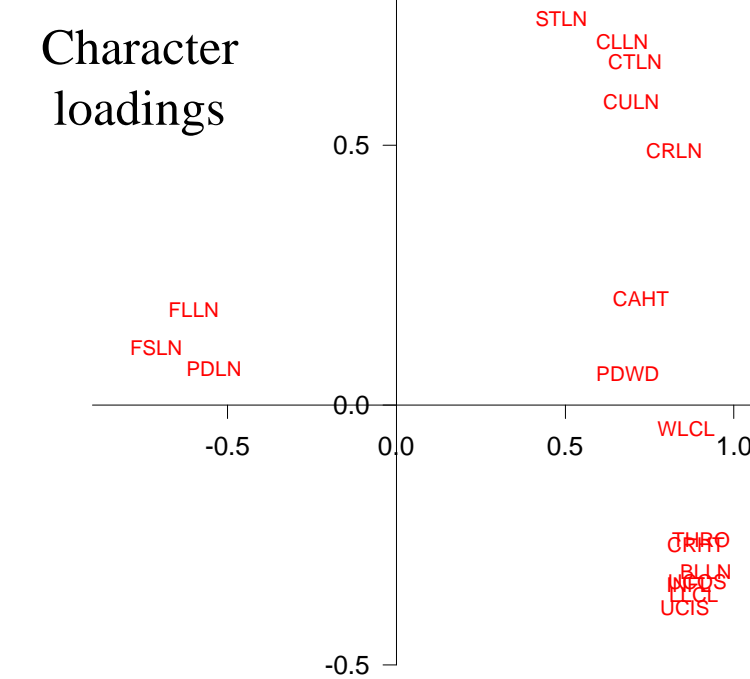
- Flower color separates the red *M. puniceus* and the orange *M. aurantiacus*, as well as the lemon-yellow flowers of *M. longiflorus* ssp. *calycinus* from the salmon *M. longiflorus*.
- Both *M. bifidus* and *M. bifidus* ssp. *fasciculatus* are separated from other taxa because of distinctive notching of the upper corolla lobes.

Through most of the geographical range of these species, the taxa are allopatric and are clearly distinguishable. Two taxa, *M. aurantiacus* ssp. *lompoensis* and ssp. *australis*, appear intermediate between the large-flowered taxa and small-flowered taxa, and may be of hybrid origin. And where taxa overlap, hybrid populations exist that cannot be placed into a single taxon. These populations are often characterized by a wide range of corolla colors within and between plants and have floral features intermediate to their putative parents. Hybrid populations are repeatedly found along road cuts, and human disturbance may contribute to their frequency. There are two main regions of hybridization:

San Diego county: Species overlap is greatest in San Diego county, especially between populations of *M. puniceus* and *M. aurantiacus* ssp. *australis*. Hybrid populations have intermediate floral features between these species and flower color varies within and between plants from near white to orange to dark red. Ssp. *australis* itself is more similar to *M. longiflorus* than *M. aurantiacus*, and the analyses place it between the former and *M. puniceus*.



| Code | Character |
|------|---|
| CRNL | Corolla length |
| BLLN | Length across bottom lobes |
| UCOS | Apex of upper corolla lobe to inner sinus |
| INFL | Apex of upper corolla lobe to outer sinus |
| WLCL | Width of lower center lobe |
| LLCL | Length of lower center lobe |
| THRO | Opening of throat |
| CRHT | Corolla height |
| CTLN | Corolla tube length |
| STLN | Style length |
| FLN | Length of long filament |
| FSLN | Length of short filament |
| CULN | Calyx length to upper lobe |
| CLLN | Calyx length to lower sinus |
| CAHT | Calyx height |
| PDLN | Pedicle length |
| PDWD | Pedicle width |
| LFLN | Leaf length |
| LFWD | Leaf width |
| STWD | Stem width below measured flower |

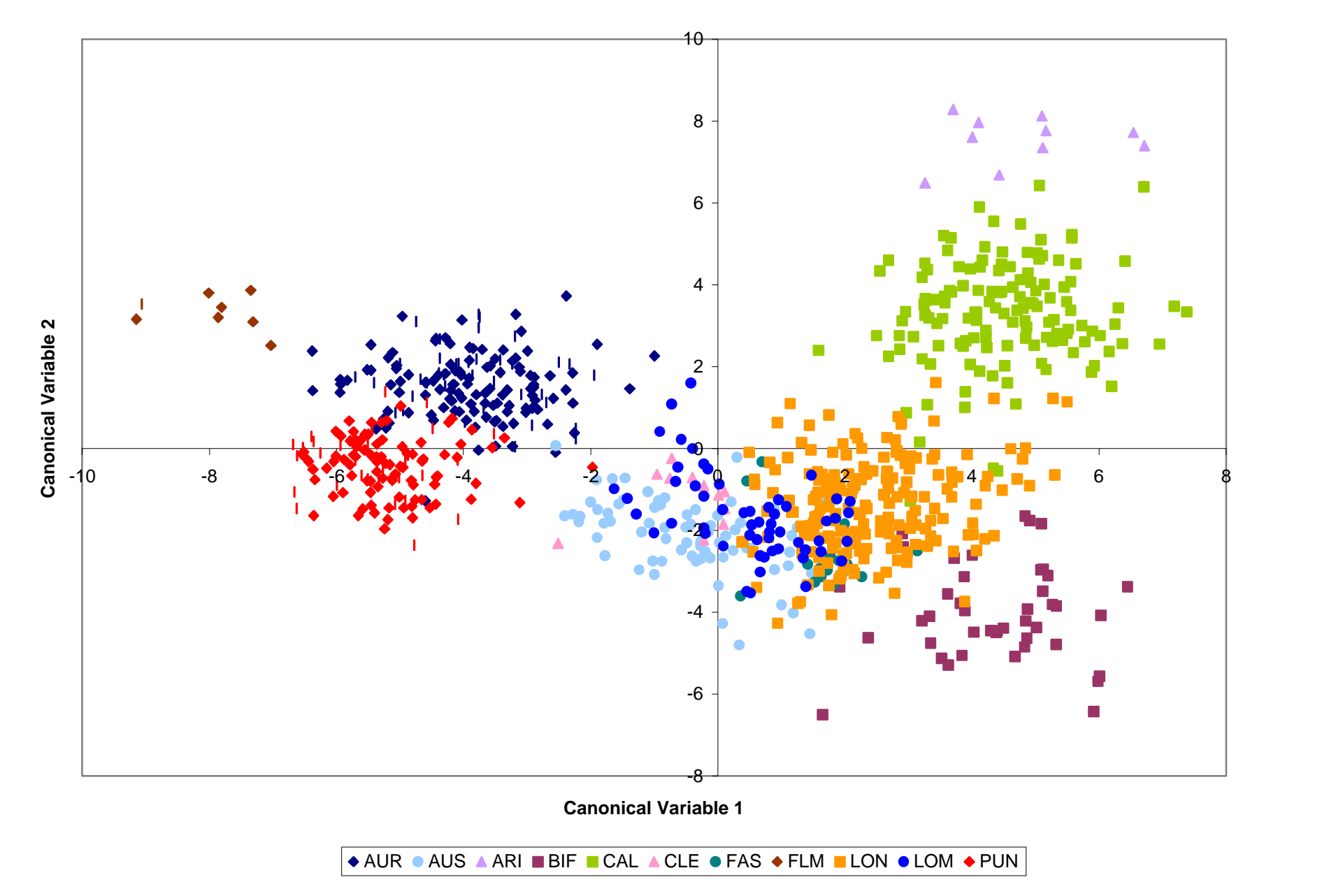
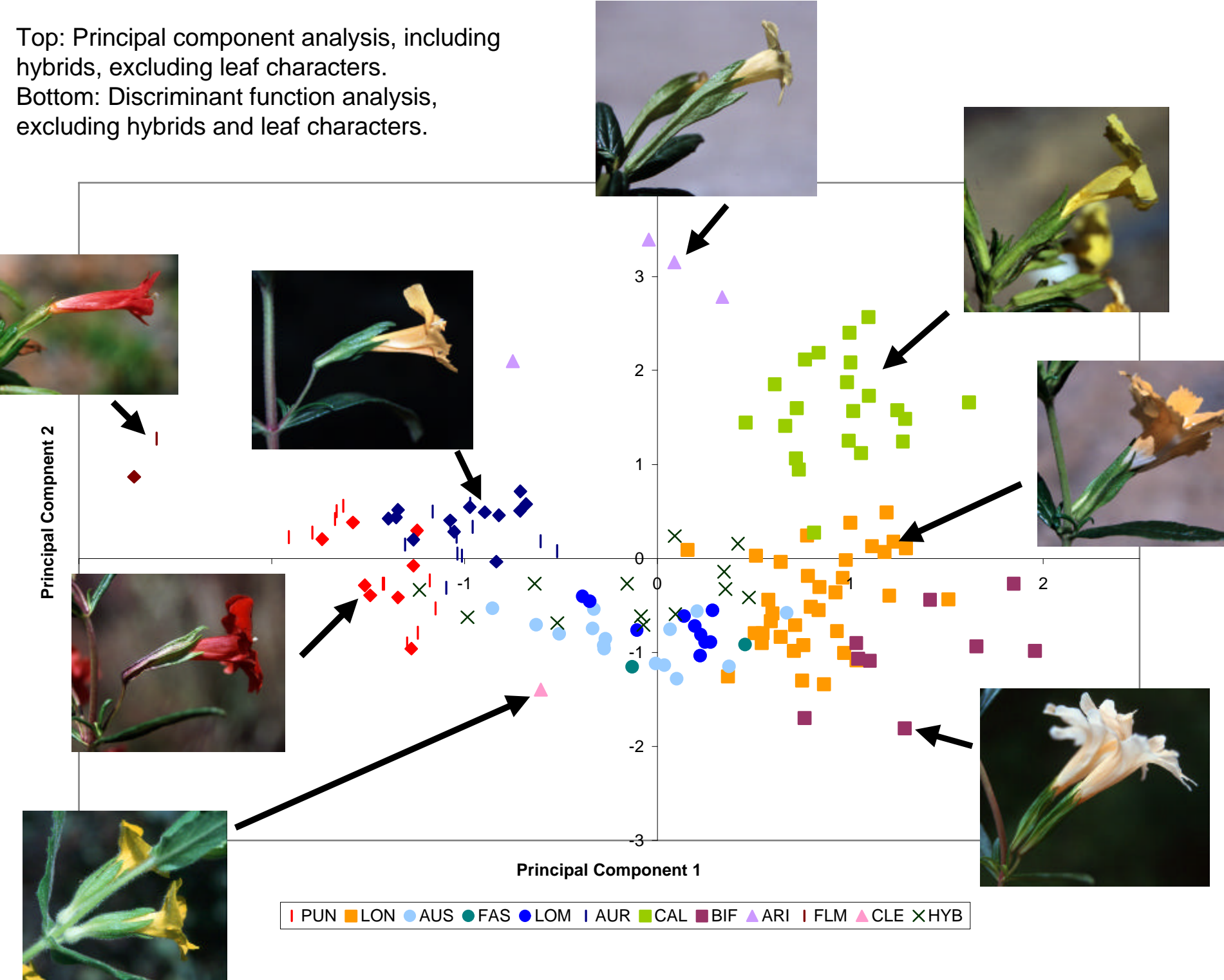
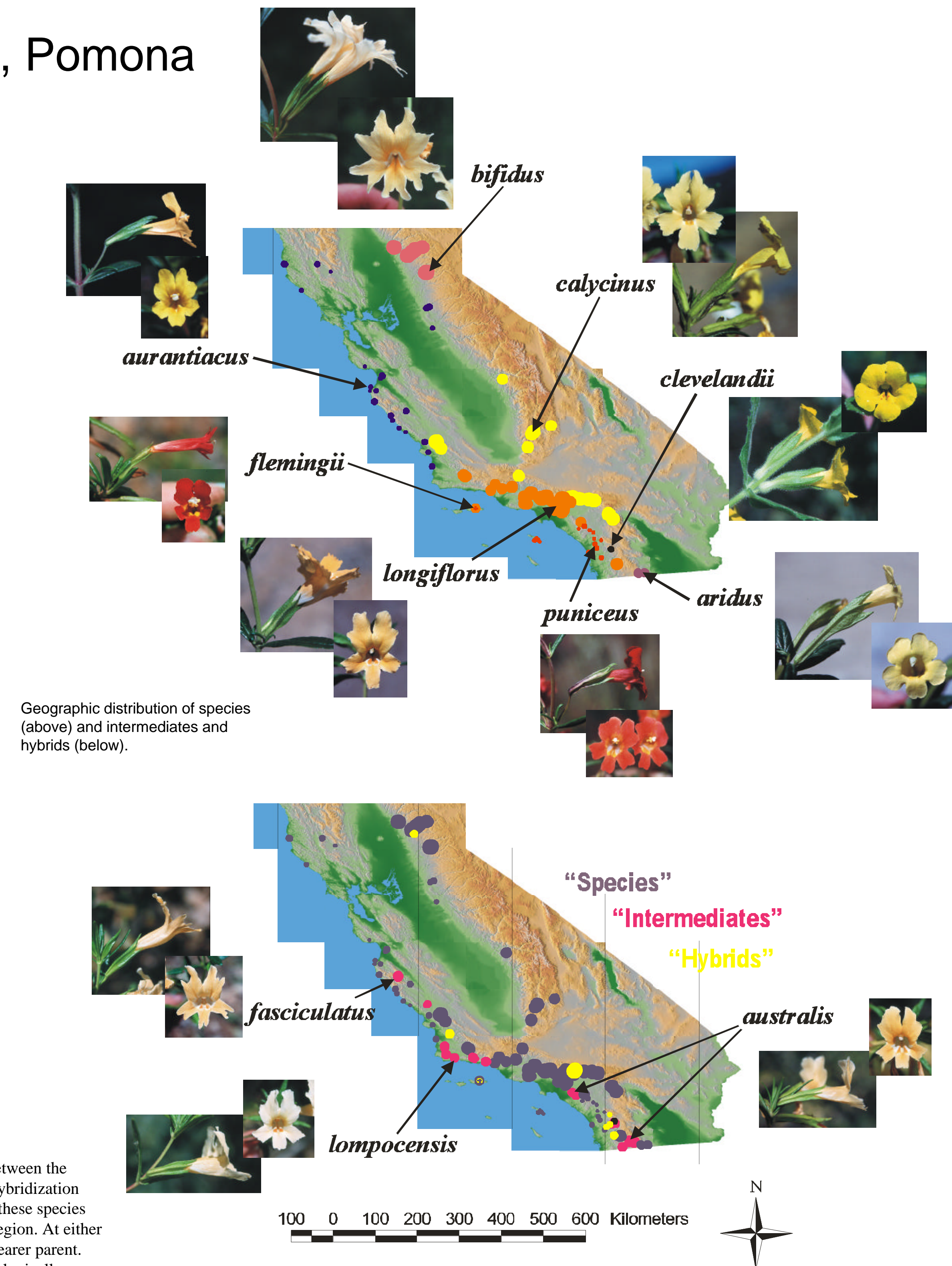


Santa Barbara county: *M. aurantiacus* ssp. *lompoensis*, falling between the ranges of *M. aurantiacus* and *M. longiflorus*, is likely the result of hybridization between these species, and has intermediate floral features between these species on PC1. This taxon has formed stable populations throughout this region. At either end of its distribution, populations may more closely resemble the nearer parent. Considering that both *M. aurantiacus* and *M. longiflorus* are morphologically consistent across broad regions, *M. lompoensis* is perhaps best interpreted as a zone of introgression.

Acknowledgment and recognition of species boundaries will be important to the conservation of rare taxa in this group. The latest treatment of this group by Thompson (1993) lumps all but one of the taxa into a single species, *M. aurantiacus*. Most of these taxa are endemic to California and occupy distinct habitats. This includes *M. aridus*, which differs ecologically from other taxa and has a very limited distribution in San Diego county and northern Baja California (Reiser 1994) and *M. flemingii* (listed as rare by the California Native Plant Society; Skinner 1994), which is restricted to the Channel Islands, where ecosystems have been heavily damaged by feral animals. A misunderstanding of the diversity in the group has evidently also resulted in the southernmost population of *M. longiflorus*, a freeway-side planting well out of its natural range.

CONCLUSION

There are distinct morphological differences between named taxa in *Mimulus* section *Diplacus* which can easily be distinguished in the field. Both principal components analysis and discriminant analysis separate *M. aridus*, *M. clevelandii*, and two groups of small and large flowered taxa. Within each group, qualitative features and geographic range further distinguish the taxa. Hybridization in areas of taxon overlap in southern California does obscure species boundaries; however, throughout most of the range of the taxa, hybridization is limited and taxa are clearly defined.



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