

AN EVOLUTIONARY STUDY OF THE GENUS *MARINA* (FABACEAE): PHYLOGENOMIC  
SYSTEMATICS, OVERLOOKED BIODIVERSITY AND DROUGHT ADAPTATIONS OF THE  
FALSE PRAIRIE CLOVERS.

by

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## ABSTRACT

*Marina* (Fabaceae) is a primarily Mexican genus of seasonally dry tropical forests and arid deserts, including many rare and narrowly endemic species. Despite recent increases in *Marina* collections, five species are still known from a single locality and many species have very limited data on their distribution and biology. In a time of rapid land conversion and climate change, the urgency to document biodiversity is urgent. However, the species' circumscriptions and the intriguing evolutionary hypotheses introduced in the last monograph of *Marina*, almost fifty years ago, have not been revisited. Our goal is to use novel phylogenomic approaches and sequencing technologies to revise the taxonomy for this group, test hypotheses about species' ages and origins, and use *Marina* to understand questions on legumes' potential for adapting to highly seasonal environments.

After studying *Marina* in the field and across herbaria in USA and Mexico, we developed a densely sampled phylogeny using target capture methods to test taxonomic hypotheses at the species level and above. We used this phylogeny to date lineages, elucidate evolutionary history, and explore correlations between relatedness and nutrient cycling. We tested whether leaflet traits of *Marina* and related genera were explained by climate or by phylogeny and determined that precipitation is the best explanation for the variation we found of intrinsic water use efficiency across our samples. We generated morphological, ecological, and genetic support and completed the necessary descriptions for a monotypic genus sister to *Marina*, six undescribed species and one new combination within *Marina*. In conclusion, we have a revised taxonomy that will provide an up-to-date understanding to inform conservation decisions for the genus and a better understanding of how taxa may adapt facing drier, hotter conditions.

## INTRODUCTION

This investigation into *Marina* began on a three-month road trip from Berkeley down and up the Baja California Peninsula. I had previously ventured into a dozen states across Mexico, often in search of plants, but this was my first visit to Baja California and for me there was little on the agenda other than immersion and familiarization with the Baja California flora. There were other more concrete goals for the trip too: to assist in an interdisciplinary biosurvey of San Basilio near Loreto and to collect rock daisies for Isaac's (my now husband) dissertation research. I was primarily focused on photographing every new plant and diving into a previously well-used copy of Baja California Plant Field Guide (Rebman et al 2016), some printed floristic checklists, and Wiggins' flora (1980). I had been working as a California botanist for six years and felt comfortable with how things worked in California: the floristic provinces, the vegetation types, the plant families, road expectations, where to camp etc., but here, everything was new.

I had been contemplating returning to graduate school, after finishing a master's in floristics the previous year, to gain skills as a systematist and a deeper understanding of evolution. I hoped to be a valuable community member by contributing to our collective knowledge of life on earth, but wasn't yet sure what my role would be. If given a choice, I would study legumes because they were diverse and abundant in my favorite places and at the same time continued to surprise me (i.e. stepping out of a ski plane on the terminal moraine of a glacier in the Alaska Range to find the curling pods of *Astragalus nutzotinensis* popping up out of granite with nothing but ice in all directions). The legume diversity in Baja California seemed infinite and increased as we drove south. When we got to the location of the biosurvey, Jon Rebman gave us a crash course in the plants around us and introduced me to *Marina* as a legume

genus that would make for a challenging systematics PhD project for someone who wanted to dive into a taxonomic puzzle. I was intrigued.

The last month of the trip we targeted the narrowly endemic *Marina* species of Baja California Sur to better understand the described diversity, morphology, ecology, and associated taxa. This was smart because a pandemic was looming, and field work would be called off for the next year. During that initial introduction to *Marina*, I was amazed by the vast diversity that existed in small, but overlapping pockets, along this narrow strip of land. I began to contact potential advisors who all pointed me towards legume experts Marty Wojciechowski and Matt Lavin and I enrolled at Montana State in the fall of 2020.

My next season was restricted to the USA due to the pandemic. I visited the hottest and driest places that *Marina* lives, during one of the hottest and driest years on record. Everything was fried and the lack of spring flowers felt dystopic. *Marina* grew and bloomed regardless, which led me to develop questions about drought adaptations, legume biogeography and climate change. From there, the *Marina* project grew into an interdisciplinary evolutionary exploration.

### Phylogenomics

The first chapter applies novel target capture methods to illuminate the evolutionary history of *Marina*. Collectively, we are currently testing the limits of target capture approaches and this study successfully achieves shallow taxonomic scale resolution from historic herbarium specimens. The implications of this are that specimens previously thought to be unusable for DNA analysis, including rare, extinct, and impossible to collect populations, can easily and affordably be incorporated into phylogenomic studies, proving the importance of protecting these irreplaceable resources moving forward.

We tested hypotheses about *Marina* and related genera that were eloquently expressed by Rupert Barneby in the last monograph (1977). Barneby's thorough investigation provided a strong morphological dataset and a detailed understanding of the diversity known at the time. Since his monograph, specimens from remote places were accumulating as well as an entirely new toolkit to examine genetic variation.

We found that the two described sections of *Marina* were not monophyletic and instead the two major groups were geographically structured. One group has undergone most of its diversification since the formation of the Baja California Peninsula. We found support for hypotheses surrounding the evolution of the flora in seasonally dry tropical forest introduced by Pennington & Lavin (2016): species ages are generally old and species are geographically structured with high diversity and endemism in patches of seasonally dry tropical forest (Pennington & Lavin 2016). We also uncovered many undescribed species, some more morphologically cryptic than others.

### Taxonomy

This study contributes to an improved taxonomic understanding of *Marina*, which includes rare, narrowly endemic species, as well as an overlooked genus. We prioritized the taxonomic implications of our phylogenomic study and described multiple novel taxa in Chapters 2 and 3. Many of the new species have restricted geographic distributions and are vulnerable to climate change and threats caused by human impact. As the biodiversity crisis worsens worldwide, there has been a quiet decline in taxonomists as well due to a lack of positions funding taxonomy, a focus strictly on publication metrics and the increasing difficulty in obtaining permits for scientific collections (Löbl et al 2023). Experiencing this deficit in



scientists, specifically in the USA, willing or able to spend the time on taxonomy, even if their research illuminates the need for taxonomic revision or descriptions, means the gap between our understanding of biodiversity and our communication about biodiversity is widening.

### Legume Adaptations

Intrigued by *Marina*'s ability to thrive in the most extreme drought in recent memory, we began to think about what gave *Marina* this advantage. *Marina* exemplifies many known legumes traits in arid or drought-prone settings: high nitrogen leaflet content, drought deciduous leaflets, opportunistic blooming (McKey 1994) but did these traits allow for *Marina* to enter these prohibitive environments or were these traits adaptations to these conditions? We collected leaflet data from across the ranges *Marina* and related genera to better understand how these traits vary within and between species as well as across bioclimatic variables. We found high levels of variability for nitrogen content, intrinsic water use efficiency (iWUE), and specific leaf area (SLA) within and between taxa, with the best explanation for these traits (especially iWUE) being precipitation in the wettest season. In areas experiencing the wettest wet seasons, iWUE was lowest, resulting in incredibly dispensable leaflets that litter the plant. We introduce this leaflet type as one *Marina* generates readily in a seasonally dry tropical setting.

My hopes for graduate school were to add important gaps to our understanding of biodiversity, especially for organisms and regions that are facing immediate consequences due to land conversion and climate change. I hope the taxonomic findings presented here inform future conservation efforts, the methods provide support for the global fight to keep herbaria funded and employed, and the ideas discussed add to our understanding of legumes' evolutionary success.

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PHYLOGENOMICS OF *MARINA* RESOLVES SPECIES RELATIONSHIPS, ILLUMINATES  
OVERLOOKED BIODIVERSITY, AND PROVIDES INSIGHT INTO A RADIATION ON  
THE BAJA CALIFORNIA PENINSULA.

Abstract

*Marina* Liebm. is a genus of 45 minimum rank taxa in the legume family (Fabaceae) that includes many rare, overlooked, and geographically restricted species distributed primarily throughout Mexico. We examined Barneby's taxonomy in a phylogenomic context to address questions such as whether fruiting traits are useful for forming a higher-level taxonomy among *Marina* species. We present the first densely sampled phylogeny of the legume genus *Marina* derived from a target enrichment approach that yielded hundreds of phylogenetically informative low copy nuclear loci. Phylogenetic analyses of these data resolved relationships with strong clade support within and among species, which aided our goal of improving the species level taxonomy of *Marina* using well supported phylogenetic relationships among *Marina* species and populations. Our phylogenomic approach led to the discovery of previously undetected species of *Marina* and that some of the currently circumscribed species groups form monophyletic clades (ser. *Chrysorrhizae* marked by a compressed, harp-shaped pod and a gland-sprinkled banner) whereas others do not (sect. *Marina* marked by a nutlike pod). Many of Barneby's *Marina* taxa that are not supported by our results come from a radiation of 14 species almost entirely restricted to the Baja California peninsula each with an age estimate of mostly less than 2 Ma. Overall, phylogenetic evidence, field expeditions, and extensive museum studies all led to

a phylogenomic scale data analysis that clearly resolved relationships within and among *Marina* species and among higher level taxa of daleoid legumes.

### Significance

This study contributes to an improved taxonomic understanding of *Marina*, including rare taxa of conservation concern. Specimens collected during fieldwork will be deposited at multiple herbaria so that they are publicly available for future scientists and researchers. The lack of an understanding of the geography and ecology, especially of the rare *Marina* species, makes these specimens important for developing conservation efforts. DNA sequences are uploaded to GenBank and publicly available for future studies.

Many of the newly described *Marina* species are narrowly endemic, just as are many of the *Marina* species described in Barneby (1977). Most of the narrowly distributed species have long been poorly known ecologically and morphologically because they have been seldom collected. Fieldwork during this study has aided in the taxonomic circumscription and delimitation of *Marina* species, and therefore provided a framework for determining the conservation status of rare *Marina* species and varieties. Our phylogenomic analysis has facilitated the process of refining the delimitation of species and varieties and investigating the natural history, ecology, and morphology of rare *Marina* species. Verification of the many species of *Marina* with narrow geographic ranges is continually needed to update any required conservation efforts. The restricted geographic distributions of many *Marina* taxa, which form clades of closely related and recently evolved lineages, renders them vulnerable to climate change and human impact.

## Introduction

In the last comprehensive study of *Marina* Liebm., Barneby (1977) described thirteen of the 38 then-known *Marina* species, and each of them from less than five collections. Even with recent increases in botanical collections and despite the predilection of species of *Marina* to inhabit sites devoid of dense vegetation cover, which renders them often easy to detect, five *Marina* species are still known from only a single locality. In contrast, other species initially known from only a few specimens, especially those of Baja California Sur, are now well sampled from broader geographic ranges due to ongoing floristic work (Rebman et al 2016; León-de la Luz et al 2015; Vanderplank 2011). The tendency of *Marina* species to be narrowly distributed may be the reason we have detected so much overlooked population variation, which has resulted in our revision of species circumscriptions in *Marina*. Recent extensive collections of *Marina* specimens also have compelled us to revisit *Marina* using phylogenomic methods for a deeper understanding of species relationships and geographic range sizes.

Since Barneby's 1977 monograph, the landscape of Baja California Sur has changed dramatically by rapidly increasing tourism, development, and intensive livestock grazing. Yet, Barneby's hypotheses regarding the biogeography, ecology, and identity of species groups of *Marina*, in addition to species delimitations, remain untested. A better understanding of the identity of all the rare and narrowly endemic *Marina* species is critical to conservation efforts.

## Taxonomic History of *Marina*

The legume tribe Amorphaeae comprises the amorphoid and daleoid subclades, the latter of which was most recently monographed in 1977 by Rupert Barneby. Barneby's work includes *Marina* and closely related genera *Dalea* L. and *Psorothamnus* Rydb. (Barneby 1977) and since

his contribution *Psorodendron* Rydb. has been resurrected to contain some of the species within *Psorothamnus* (Piñeros et al 2023). Species of the amorphoid clade show a tendency to independently lose the ancestral papilionoid floral form via a reduction in petal number whereas species of the daleoid clade tend to have flowers with a classic papilionoid floral form (McMahon 2005). Among the daleoid Amorpheae, *Dalea* and *Marina* share the distinction of a flower with keel and wing petals perched on the staminal column (Barneby 1977; McMahon 2005).

*Marina* was described in 1849 by Liebmann in honor of La Malinche, Cortes' translator, based on *Marina gracilis* Liebm. (Liebmann 1849; Barneby 1977). Barneby (1977) expanded the genus *Marina* in his monograph of the "daleoid" legumes using cytological, geographical, and morphological evidence. Barneby circumscribed *Marina* as part of a comprehensive treatment of closely related genera, including the genera *Errazurizia* Philippi, *Psorothamnus*, *Marina*, and *Dalea*. Barneby (1977) distinguished *Marina* from its sister genus *Dalea* by the following characters: pedicellate flowers, ovary with a single ovule, both faces of the leaflet marked by fine sinuous lineoles, hairs that are stiff, short, not spiral, and unchanged when dry, calyx ribs that fade out before reaching the calyx tip, and 10 pairs of chromosomes. McMahon and Hufford (2004) resolved *Marina* species as a well-supported monophyletic genus within the tribe Amorpheae, although the *Marina* clade included *Dalea filiciformis* B.L. Rob. & Greenm., which is the focus of taxonomic study of Winitsky et al. (Chapter 2).

Of the genera treated by Barneby (1977), he was least satisfied with the taxonomic conclusions he reached regarding certain species of *Marina*. Barneby occasionally described such species with hesitation and admitted the need for more fieldwork to resolve any taxonomic

uncertainty. Currently, there are 40 described *Marina* species, two of which were added to the 38 treated in Barneby (1977) by Leon de la Luz (2002).

### *Marina* of Baja California Sur

One of *Marina*'s two centers of diversity falls within Baja California, Mexico, a biodiversity hotspot with floristic endemism estimated between 23-30% (Rebman et al 2012). Recent efforts to document Baja California's flora have resulted in discoveries of overlooked *Marina* taxa restricted to islands and sky islands (Leon-de la Luz 2002). Ten of the 15 *Marina* taxa currently known from Baja California are endemic to the peninsula (Rebman 2016). *Marina parryi* (Torr. & A. Gray) Barneby, *Marina orcuttii* (S. Watson) Barneby var. *orcuttii*, *Marina vetula* (Brang.) Barneby, *Marina chrysorrhiza* (A. Gray) Barneby and *Marina peninsularis* (Rose) are all taxa of Baja California whose distributions extend beyond the peninsula. *Marina parryi* occurs throughout the Sonoran Desert. *Marina orcuttii* var. *orcuttii* has populations in the Santa Rosa Mountains of California. *Marina vetula*, *Marina chrysorrhiza* and *Marina peninsularis* are all found across the Gulf of California in Sonora and northern Sinaloa, with one large disjunction to volcanic cones in Coahuila for *Marina vetula*. Even with an increase in collections throughout Baja California Sur (Rebman 2016, Leon-de la Luz et al 2008, Leon-de la luz et al 2015), the majority of *Marina* species in the Baja California Peninsula which belong to the taxonomic series *Chrysorrhizae*, remain rare and narrowly endemic, and include three island endemics. The seasonally dry tropical forests and woodlands of the Cape Region are particularly floristically diverse (Arriaga and Leon de La Luz 1989), a pattern reflected in *Marina*. The hyper-endemism and heterogeneous terrain of this region leads to questions surrounding a potential evolutionary radiation of *Marina* species within the Cape Region and whether

geographic, climatic, edaphic, or ecological factors are driving speciation in *Marina*. The diversity and ubiquity of *Marina* taxa in Baja California make it an ideal group in which to detail the correspondence of phylogeny with biogeography and ecology. This may aid in understanding ecological and geographical patterns of speciation in *Marina* and perhaps how those relate to plant diversity in this fascinating floristic region.

#### The Highly Seasonal Environment Inhabited by *Marina* Species.

Across Mexico, seasonally dry tropical forests and woodlands have been identified as cradles and museums of neo- and paleo-endemism, which is particularly true for legume species (Sosa et al 2018). The existence of diverse clades of species that are confined to seasonally dry topical woody environments suggests that constituent species of such clades are pre-adapted to droughty environments, which allows them to readily migrate among patches of seasonally dry tropical forests and woodlands (Pennington & Lavin, 2016). Because seasonally dry tropical woody environments experience irregular precipitation and extended drought periods, both within and among years (Pennington & Lavin, 2016), such an environment is often hostile to plant immigrants. Therefore, resident plant populations of such dry environments have the advantage over immigrants of being present and taking advantage of any erratic precipitation. This scenario can explain the narrow endemism of many taxa confined to seasonally dry woody environments, which have ages that range from recent to many millions of years old (e.g., Pennington and Lavin 2016).

The Cape Region of Baja California is an isolated pocket of seasonally dry tropical forests and woodlands, discontinuous from the expansive seasonally dry tropical woody environments of western Mexico, and surrounded by ocean and desert. We focus on Barneby's



(1977) series of *Marina* which has a high level of taxonomic diversity in the Cape to ask whether this region is a cradle of recently evolved species of *Marina*.

Within the Baja California peninsula, areas of endemism that have high diversity of *Marina* include the Cape Region, the east slope Sierra la Giganta including bay islands and the Magdalena plain (Riemann 2011, Ezcurra E. 2007). For example, these areas harbor 77% of the legume diversity (Garcillán 2003) found in Baja California, with 73% of legumes restricted to the southern half of the peninsula (Riemann 2011). Baja California has approximately 23 percent endemism, including 92 endemic legume taxa (Rebman 2011). This might be explained by limited migration among patches of seasonally dry tropical forests and woodlands. Within such a patch, as in the Cape Region of Baja California, islands and mountains often harbor high species richness and endemism due to reproductive isolation and available niches within topographically and edaphically heterogeneous terrain. *Marina* diversity is highest in the Cape Region where mean annual precipitation is relatively high and mean annual temperature low (Riemann 2007). Riemann (2007) explores this pattern across woody legumes, agreeing with the patterns we find for endemism and species richness in *Marina*, which differs from general floristic patterns of endemism in the peninsula that are considered to be highest in the central desert portion (Riemann 2011, Ezcurra 2007).

There are multiple hypotheses for the distinctness of the flora of the Cape Region. One idea is that the Cape Region drifted westward as a continental fragment and brought with it a representation of the Jalisco seasonally dry tropical woodlands (Gentry 1995), which are also rich in legume species. Another explanation for the percentage of legume endemism is the time the Cape Region spent as an island (Leon de la Luz 1989), leading to reproductive isolation from

more northern peninsular taxa. It is expected that under climate change that plant taxa endemic to the Cape Region of Baja California will retreat upwards into sky island habitats as the lowlands become hotter and drier (Roberts and Ezcurra, 2012). Such a possibility makes a study of Cape Region *Marina* species compelling for understanding of biodiversity in this region and prioritizing its conservation.

### Materials and Methods

In this study we present a densely sampled molecular phylogeny, which includes 171 accessions of *Marina* and closely related genera. This represents 38 of the 40 *Marina* species and all five previously recognized *Marina* varieties. We also present phylogenetic and morphological analyses that test Barneby's (1977) taxonomic hypotheses. Our phylogenetic results derive from DNA extracted from silica dried field collections and herbarium specimens, which were then enriched for targeted capture of hundreds of low-copy nuclear loci and analyzed using maximum likelihood, Bayesian inference, and pseudocoalescent approaches. Here, we combine decades of field research with novel phylogenomic methods to revisit in part the taxonomic uncertainties expressed by Barneby (1977).

### Fieldwork

*Marina* collection sites and exploration of potential habitats represented the entire span of the Baja California peninsula. Baja California fieldwork occurred during 2019 and 2022, Arizona and California fieldwork in 2020 and 2021, Sonora fieldwork in 2022, and Nuevo Leon in 2022. The Cape Region of Baja California tends to receive most of its precipitation between the months of September-November, so fieldwork targeting peninsular taxa took place from late

November to mid-January. Voucher specimens of *Marina* taxa collected during these field trips will be deposited at multiple herbaria including El Herbario del Centro de Investigaciones Biológicas del Noroeste (HCIB), Arizona State University (ASU), Montana State University (MONT), and San Diego Natural History Museum (SD).

Our initial phylogenomic analyses highlighted taxonomically interesting populations, which were then targeted for subsequent fieldwork and specimen collection. Field trips added ecological, geographical, and morphological data so that we could evaluate species concepts in a phylogenetic context. Fieldwork focused heavily on the peninsular section of *Marina*, which is centered around the Gulf of California. Fieldwork related to the mainland Mexican section of *Marina* was less intensive and systematic because this group will be the focus of a future phylogenomic and taxonomic study.

### Herbarium Studies

Many herbaria were visited prior to lab work to study morphological differences among taxa, choose representative accessions for phylogenetic analysis, and identify collections representing potentially undescribed taxa or accessions requiring further investigation. These included, where herbarium acronyms follow Thiers (2023), ARIZ, ASU, CAS, HCIB, MEXU, MO, MONT, NY, RSA, SD, UC/JEPS, UCLA and UCR. The herbaria ASU, MEXU and NY generously sent loans to MONT. Most valuable were the collections at SD because of the large quantity of *Marina* specimens and high quality of supplementary material, including field notes, photographs, and locality details.

### Taxon Sampling

Usable quantities of DNA was extracted from multiple accessions of all *Marina* taxa, excluding *Marina minor* Rose (Barneby) and *Marina gemmea* Barneby. *Marina gemmea* is known from a single collection with insufficient herbarium material to warrant sampling and *Marina minor* repeatedly yielded too low quantities of DNA extract to be included in the study. We also sampled accessions of other daleoid genera, including *Psorothamnus*, *Psorodendron*, and all subgenera of *Dalea*, except the monotypic subgenus *Asprolea*, which is represented by the rare Oaxacan *Dalea trifoliata*. *Amorpha californica* var. *napensis* was used as the outgroup to the daleoid ingroup.

A total of 171 accessions included samples taken from silica dried field collections and herbarium specimens (Table 1; Fig. 1). Dr. Rupert Barneby, Dr. Michelle McMahon, or Dr. Jon Rebman annotated these accessions. The first author confirmed their identifications and adapted them as needed to the taxonomic names used by Barneby (1977). When possible, these accessions came from type localities. These accessions also included specimens that did not fit morphologically to current *Marina* species circumscriptions, as well as populations representing large geographic range disjunctions.

### Phylogenomics Using Target Capture Methods at the Species Level:

High throughput sequencing has allowed for phylogenetics to reassess historically difficult polytomies, recent radiations, and relationships within and among species from DNA obtained historic and degraded specimens because of the vast increase of phylogenetically informative data (Baker et al 2021, Villaverde 2018). Most target capture investigations, especially those using the popular baitset designed to be informative across all of angiosperms,

Angiosperms353 (Daicel Arbor Biosciences, Ann Arbor MI), have aimed to resolve nodes in the tree of life (Baker et al 2021) that correspond to taxonomic ranks of order or family (Ogutcen et al 2021, Maurin et al 2021, Zuntini et al 2021). Recently, phylogenies inferred from target enrichment methods have supported revisions of evolutionary history even at the species and infra-species levels. At the genus and species level, target capture methods recently have been used to investigate the legume groups *Pterocarpus* (Schley et al 2022), *Dalbergia* (Cramer et al 2022), and *Guibourtia* (Tosso et al 2018). To achieve resolution at the species and infra-species levels, it is possible to include flanking regions caught by the target hybrids, called the “splash zone,” allowing for more variation than found in target regions alone (Baker et al 2021). Here, we use the target enrichment baitset, Angiosperms353, at the species level to resolve phylogenetic relationships within *Marina*.

We used curated collections and target capture approaches to generate the most densely sampled phylogenetic data set of *Marina* accessions. Analysis of these data has provided insights into species relationships and circumscriptions, which has permitted the detection of undescribed species and the identification of narrowly endemic taxa most in need of conservation. We also focus on the role of the Baja California Peninsula, especially the topographically and ecologically diverse Cape Region, in detecting recent evolutionary radiations in *Marina* that comprise diverse species complexes.

#### DNA Extraction, Library Preparation, and Sequencing

DNA was isolated from leaf material using Qiagen DNeasy Plant Mini Kits (Qiagen, Valencia, CA, USA). DNA extracts were prepared for target capture sequencing using the KAPA hyper-prep protocol. Qubit dsDNA BR (broad range) Assay Kit (Thermo Fisher Scientific,

Waltham, MA, USA) was used to quantify DNA fragments. DNA fragments were diluted and then sonicated using a QSonica at 40% amplitude, 15-15 pulse for 2:30 minutes. DNA isolates extracted from degraded herbarium specimens were already sufficiently fragmented and near the ideal range of 300-500 bp, therefore, these were not subjected to sonication. Double-sided size selection was performed, followed by end repair, A-tailing, and adapter ligation. Indexing PCR was performed using universal primers and a target concentration for products above 150 ng. Libraries were quantified using a Qubit dsDNA HS (high sensitivity) Assay Kit and libraries that were not sufficiently amplified were run again.

Pooled samples were enriched for hundreds of low-copy nuclear loci using the Angiosperms353 bait set (Johnson et al 2019), which was purchased from Arbor Biosciences (Ann Arbor, MI, USA). Following the MyBaits manual (<https://arborbiosci.com/mybaits-manual>), we used the standard protocol with an incubation time of 40 hours at 62 degrees C. Dual indexed libraries were pooled by total number of libraries and mass of libraries and suspended in a nuclease free buffer. They were then denatured, allowing for baits to hybridize with target regions, which are in turn bound to magnets and pulled from the general pool magnetically. The off-target regions were washed away, and the final product was amplified. Libraries were then pooled and sent to GeneWiz (South Plainfield, New Jersey) where whole genome shotgun sequencing of enriched multiplexed libraries was performed on a single lane of an Illumina HiSeq4000 2x150 bp sequencing.

#### Sequence Assembly and Phylogenetic Inference

Illumina adapters were trimmed, and initial reads were filtered for quality using Trimmomatic (Bolger et al 2014). Raw sequences were assembled using iterative reference

guided assembly was performed using the pipeline HybPiper (Johnson et al 2016). SPAdes v3.13.1 (Bankevich 2012) assembled sequences into contigs. Intronic and exonic regions were combined into supercontigs and these were used for the subsequent analyses, allowing for greater variability within closely related samples (Slimp et al 2021, Baker et al 2021). The `paralog.py` script in HybPiper was used to identify paralogs and the removal of paralogs was executed using a custom script based on the exclusion of any region in any sample that had more than one paralog assembled. The resulting supercontigs were trimmed using trimAL (Capella-Gutiérrez et al 2009) into aligned data matrices using MAFFT (Katoh 2013).

Phylogenies were inferred using two datasets: targeted exons solely and supercontigs, which included exons in addition to flanking intronic regions. The resulting phylogenies were then used to test monophyly of all formally described taxa as well as other evolutionary hypotheses above the species level. Trees were inferred using three approaches. The first was a maximum likelihood approach used RAxML (Stamatakis 2014) on XSEDE using the CIPRES Science Gateway portal (Miller et al., 2010) with a GTRCAT model of molecular substitution and 1000 rapid bootstrap replicates. Secondly, a Bayesian approach utilized ExaBayes (Aberer 2014) to infer trees and relevant parameters during one million generations of MCMC with a GTR+Gamma substitution model with four discrete rate categories applied to a concatenated data matrix. Results of the Bayesian analysis were inspected for convergence using Tracer (Rambaut et al., 2018) and after reaching stationarity summarized using a maximum clade credibility tree in the software program TreeAnnotator (Rambaut and Drummond, 2015). A pseudocoalescent approach employed Astral-III (Zhang 2019), which unlike the previous

methods, uses individual gene trees inferred with RAXML to then infer a species tree, while accounting for the effects of incomplete lineage sorting.

### Divergence Time Estimation

For divergence time estimation, in contrast to phylogenetic inference for taxonomic purposes, a species tree was inferred using only one accession that best represented each species. The one representative accession per species was chosen if it came from a locality in close geographic proximity to the type locality and in all regards fit the original species concept. A consensus tree was inferred using ASTRAL-III and divergence time estimation was performed using a relaxed molecular clock in RevBayes (Höhna et al., 2016) on a fixed topology, following the protocol described in [https://github.com/ilichtermarck/DTE\\_fixed\\_topology/blob/main/code/phylo-relaxed-clocked-with-fixed-topology\\_2.Rev](https://github.com/ilichtermarck/DTE_fixed_topology/blob/main/code/phylo-relaxed-clocked-with-fixed-topology_2.Rev).

Lavin et al. (2005) estimated the age of the Amorpheae stem clade (or the Dalbergioid crown clade) at  $55.3 \text{ Ma} \pm 0.5$  (node 34 in Lavin et al. 2005), the age of the daleoid stem clade (or the Amorpheae crown clade) at  $36.9 \text{ Ma} \pm 3.0$  (node 36), and the daleoid crown clade at  $24.7 \text{ Ma} \pm 2.7$  (node 37). Thus, the daleoids diversified into the amorphoid and daleoid subclades by the early Oligocene and each of these subclades began evolving extant diversity by the late Oligocene. Therefore, we set two density calibrations, one at the node representing the Amorpheae crown, using a normal distribution with a mean of 36.9 Ma and standard deviation of 3.0, and the other at the node representing the daleoid crown clade, with a mean of 24.7 Ma and a standard deviation of 2.7. Divergence times were estimated during two independent runs of



1 million iterations of MCMC in RevBayes and checked for convergence within and between runs in the program Tracer (Rambaut et al., 2018).

## Results

### Phylogenomics

Target capture sequencing using the Angiosperms353 bait set resulted in an aligned concatenated data matrix containing 608,187 base pairs for 174 accessions. Relationships between species were consistent across the supercontigs and exon datasets, but the supercontig dataset allowed for higher resolution at the population level due to the variation between intronic regions. Supercontig phylogenies were compared visually to assess discordance between the three methods of inference, ASTRAL-III, RAxML and ExaBayes. All methods produced trees with most nodes highly supported and mostly identical topologies. ExaBayes and ASTRAL-III resolved trees with higher support consistently across nodes. The ASTRAL-III phylogeny was used primarily to assess monophyly of clades and species because it accounted for incomplete lineage sorting and gene discordance.

Consistent with previous phylogenies, *Psorodendron* is fully supported in all methods as sister to other daleoid genera, with *Psorothamnus* as sister to the clade containing *Dalea* and *Marina* (Fig. 2). *Dalea* is fully supported as monophyletic by all tree building methods, except that *Dalea filiciformis* is sister to a monophyletic *Marina* (Fig. 2). *Marina* resolved into two principal clades and the different tree building approaches consistently identified the same members for each clade. One of these *Marina* clades includes species from the Baja California Peninsula, Sonora, Sinaloa, and the southwest USA (Fig. 3, clade A). The other *Marina* clade comprises species collectively distributed throughout mainland Mexico and absent on the Baja

California Peninsula (Fig. 3, clade B). Within the exclusively mainland clade (Fig. 3, clade B), which contains all taxa of Barneby's Section Carroa (Fig. 3, clade D), the widespread *Marina neglecta* is resolved as sister to the rest of the mainland clade (Fig. 3, clade I). The clade containing *Marina unifoliolata* (series *Unifoliolatae*) is then sister to the remaining members of the mainland clade (Fig. 3, clade F).

Conspecific accessions of *Marina* species were sometimes resolved as non-monophyletic. Within the Baja California clade, conspecific accessions of each of *Marina peninsularis*, *Marina maritima*, and *Marina divaricata* were non-monophyletic. *Marina peninsularis* accessions from Sonora are sister to a group including *Marina chrysorrhiza* and *Marina victoriae*. *Marina maritima* is paraphyletic within a clade containing some of the *Marina divaricata* accessions. *Marina divaricata* is highly polyphyletic within a clade that includes *Marina maritima*, *Marina capensis*, *Marina oculata*, *Marina catalinae*, and *Marina palmeri*. Both *Marina brevis* and *Marina victoriae*, which are known from only a few populations, are nested within *Marina evanescens* and *Marina chrysorrhiza*, respectively (Fig. 3, clade C). Within the mainland clade, conspecific accessions of *Marina greenmaniana* resolve as a grade (Fig. 3, clade F), those of *Marina diffusa* resolve into two geographically distinct clades (Fig. 3, clade H), and those of the widespread oak woodland species *Marina nutans* are polyphyletic (Fig. 3, clade H).

### Divergence Time Estimation

Two independent runs of MCMC converged on congruent divergence time estimates, and such runs were made multiple times such that all indications, including effective sample size (ESS)  $\geq 100$ , suggested MCMC sampling at likelihood stationarity. The overall net diversification rate, the number of species per million years, was estimated at 0.1062 [HPD 95%

0.0467, 0.1636]. Although we set the Amorpheae crown clade density calibration to have a mean of  $36.9 \pm 3.0$  Ma, our analysis estimated the split between *Amorpha* and the daleoid clade at 31.7 Ma [HPD 95% 29.0008, 35.9822] (Fig. 4, clade A). The daleoid crown clade density calibration was set at  $24.7 \pm 2.7$  Ma, but estimated at 26.7 Ma [HPD 95% 24.7004, 29.8362] (Fig. 4, clade B). The split between *Marina* and *Dalea* was estimated at 18.1 Ma [HPD 95% 13.7073, 21.8527] (Fig. 4, clade C) and the split between the mainland and Baja California clades, the *Marina* crown clade, was estimated at 12.2 Ma [HPD 95% 8.4358, 15.0487] (Fig. 4, clade D). The age distributions (Fig. 5) for the species representing the seven main *Marina* subclades (Fig. 3, clades C-I) revealed that species of *Chrysorrhizae*, comprising *Marina* species from the Baja California Peninsula, had a median age of less than 1.5 Ma (Fig. 5), but the age distribution *Chrysorrhizae* species was not significantly younger than the age distributions for the subclades *Orcuttii* (Fig. 3, clade D) and *Carroa* (Fig. 3, clade H; see Fig. 5). These age estimates derive from two density calibrations set for the Amorpheae and daleoid crown clades, mentioned above, and the attendant substitution rate estimate, which averaged over all branches  $8.0 \times 10^{-9}$  substitutions per site per year, falling within the range of reported rates with target capture data (Lichter Marck and Baldwin 2023, Muse 2000).

## Discussion

### Phylogenomic Analyses and Taxonomic Implications

Prior to this study, only seven *Marina* species had been included in a molecular phylogenetic analysis (McMahon 2005) and this was in the context of a comprehensive analysis of the tribe Amorpheae. Those seven *Marina* accessions were not resolved as monophyletic

because *Dalea filiciformis* was nested among the *Marina* accessions. Our analysis resolves with strong support a monophyletic *Marina* that is sister to *Dalea filiciformis* (Fig. 3). However, we focus on just *Marina* species and address the issues involving *Dalea filiciformis* separately (Winitsky et al. Chapter 2).

*Marina* species considerations. Impressively, many species described by Barneby from relatively few specimens each are here supported as monophyletic in our analysis. In contrast, seven *Marina* species from the Baja California peninsula, which were extensively collected and studied since Barneby (1977), are now known to harbor undescribed infraspecific diversity because they were not resolved as monophyletic. These five are *Marina chrysorrhiza*, *M. divaricata*, *M. evanescens*, *M. maritima*, and *M. peninsularis* (Fig. 3). Phylogenomic analyses combined with ecological, biogeographical, and phenotypic data strongly suggests overlooked species diversity harbored within these species, which is the focus of Winitsky et al. (Chapter 3). Outside the Baja California peninsula on the mainland of Mexico, species recognized by Barneby (1977) that were not resolved as monophyletic will be the subject of a future study. This includes *Marina diffusa*, *Marina greenmaniana* and *Marina nutans*. *Marina diffusa* is a species that requires additional investigation because it could potentially be split into a northern species centered in Sonora and a southern species centered in Jalisco (Fig. 3, H). Populations of *Marina diffusa* are not continuous and preliminary genetic and other evidence supports the recognition of at least two taxa, perhaps ranked at the species level. *Marina greenmaniana* forms a grade with an Oaxacan accession inferred as sister to Puebloan *Marina greenmaniana* and *Marina unifoliolata* together. Additional accessions of the glabrous variety of *Marina greenmaniana* var. *muelleri* and a focused morphological study of both *Marina unifoliolata* and *Marina*

*greenmaniana* will help inform taxonomic decisions for this group. A thorough morphological investigation of the widespread, showy *Marina nutans* is necessary to better distinguish morphological characters separating *Marina scopia*, *Marina grammadenia* and *Marina nutans*. Barneby (1977) was aware of undescribed geographic variation within *Marina nutans*, which is well represented by our phylogeny. The current morphological distinctions between these three species, which rely on a banner character for pressed specimens (*Marina scopia* versus *Marina nutans*) or fewer leaflets (*Marina grammadenia* versus *Marina nutans*), do not reliably separate them.

We realize that the criterion of monophyly of conspecific genetic samples is not necessary for delimiting plant species because many distinctive plant species are either too recently evolved, are polyploid, or have large effective population sizes such that conspecific samples would require many tens of million years to coalesce or reach complete lineage sorting (e.g., Fazekas et al. 2009; Naciri and Linder 2015). However, we commonly resolve conspecific samples of *Marina* as monophyletic and when we don't, we find that is then an indication of overlooked species. This common finding of monophyly of conspecific genetic samples likely reflects the antiquity of *Marina* subclades and species, as argued for various legume groups by Lavin and Pennington (2020), especially those that inhabit seasonally tropical forests and woodlands. Indeed, the species of *Marina* ser. *Chrysorrhiza* are some of the youngest in the genus, but they average an estimated age of about 1.5 Ma, whereas other *Marina* species range up to an estimated 10+ Ma (Fig. 5). We take these relatively old age estimates of *Marina* species to be neither biased young nor old given our estimated overall substitution rate at  $8.0 \times 10^{-9}$

substitutions per site per year, which is an expected rate for nuclear loci (Muse 2000, Wolfe et al 1997, Lichter Marck and Baldwin 2023).

Sections of *Marina*. Our phylogeny resolved two principal clades of *Marina* species (Fig. 3), but these do not correspond to Barneby's (1977) two sections of *Marina* (Fig. 6). Barneby's (1977) taxonomic split derives mainly from fruit characters. Barneby's *Marina* sect. *Marina* has compressed fruits with two crescent lines of glands, whereas Barneby's *Marina* sect. *Carroa* has nutlike fruits with no reliable gland pattern. Our phylogenetic results resolve Barneby's sect. *Carroa* as nested within his sect. *Marina* (Figs. 3, 6) and therefore suggest that a reorganization of the two Barneby sections is required so that higher level *Marina* taxa meet the criterion of monophyly. New taxonomic species groups of *Marina* will not reflect fruit characters but rather geography and other morphological traits. Here we propose the recognition of two principal taxonomic species groups of *Marina* that reflect evolutionary history. These are informally designated as the Baja California Marina clade and the mainland Marina clade (Fig. 3). McMahon and Hufford (2004) and McMahon (2005) resolved these two clades with a sampling of seven or fewer *Marina* species, but such limited sampling did not allow for the detection of the geographical distinction revealed by our analysis.

The Baja California Marina clade is found throughout Baja California, Baja California Sur, Sonora, northern Sinaloa, Arizona, New Mexico, and California. Species of this group have glands throughout the banner petal and are usually pubescent, if they are glabrous, the glandular banner will be the distinction. This section contains Barneby's (1977) series *Vetualae* and *Chrysorrhizae* and an additional undescribed series, referred to here as the Orcuttii group (Figs. 3, 6).

The mainland *Marina* clade is found throughout most Mexican states but lacking on the Baja California Peninsula (Figs. 3, 6). Plants of this clade are completely glabrous, or if pubescent, they will have a glandless banner. This section contains ser. *Unifoliolatae*, ser. *Crenulatae*, ser. *Marina* and likely the monotypic ser. *Gemmeae*, discussed below.

Taxonomic Series of *Marina*: We use phylogenetic, morphological, and geographic evidence to refine the membership of Barneby's (1977) series of *Marina* so that they conform to monophyletic groups, which our phylogenomic analysis revealed (Fig. 3) and that doesn't exactly conform with Barneby's classification of *Marina* species into taxonomic series (Fig. 6). Series *Chrysorrhizae* remains the same but now excludes *Marina procumbens* (DC.) Barneby, *Marina calycosa* (Gray) Barneby, and *Marina orcuttii* (Watson) Barneby (Fig. 6, A). This series is found throughout the Sonoran Desert of California, Arizona, New Mexico, Baja California, Sonora, and Sinaloa, but is most diverse in Baja California Sur. Series *Chrysorrhizae* includes many rare and narrowly endemic taxa in the Cape Region of Baja California. We informally recognize the *Orcuttii* group, which is segregated from ser. *Chrysorrhizae* to include *Marina calycosa* (Gray) Barneby and *Marina orcuttii* (Watson) Barneby (Fig. 3, D). Barneby (1977) recognized these two species as most closely related within his series *Chrysorrhizae*. These two differ from species retained in *Chrysorrhizae* by nodding flowers, shallowly buried root-crown, and appearing to have eglandular foliage. These two are also sky island species from southern California, southern Arizona, Baja California, and Baja California Sur. We suggest the informal name *Orcuttii* group to acknowledge the geographical distribution of *Marina orcuttii*, which includes mainly the Baja California peninsula, as well as southern California, perhaps the ancestral distribution of this group. The monotypic series *Vetulae* remains as Barneby described

it and includes only *Marina vetula* (Rydb.) Barneby (Fig. 4, E). *Marina vetula* is easily distinguished by having dense, pilose inflorescences and calyx teeth that are 2-3 times the length of the tube.

The type species of *Marina*, *M. gracilis* Liebm, was previously in its own series but is now also included in series *Unifoliolatae*, along with another addition of an undescribed Oaxacan species represented in the phylogeny by *Lavin 5173*, which is sister to *Marina melilotina* but morphologically unique (Fig. 3, F). *Marina procumbens* (DC.) Barneby, which Barneby included in series *Chrysorrhizae*, is found outside of the range of members of this series, distributed from Jalisco to Chiapas, and phylogenetically nested within the mainland *Marina* clade within ser. *Unifoliolatae* (Fig. 3, F).

Barneby's *Marina* sect. *Carroa* is nested within the mainland *Marina* clade (Figs. 3, 6) and better fits at the rank of a series. Our revised circumscription of sect. *Carroa* will retain all previous members of Barneby's *Marina* sect. *Carroa* (Fig. 6) with the addition of *M. dispansa* and *M. sarodes* (Fig. 3, H). Barneby's series *Crenulatae*, which included *M. crenulata*, *M. sarodes*, *M. dispansa* and *M. neglecta* is now supported as monotypic with only *Marina crenulata* (Fig. 3, G). A new series of *Marina* is revealed, which includes only *M. neglecta*, (Fig. 3, I).

Two species were not included in our phylogenomic analyses, *Marina minor* and *Marina gemmea*, as mentioned earlier. Barneby (1977) placed *Marina minor* in ser. *Chrysorrhizae* because it is similar in appearance to *M. alamosana* and *M. goldmanii*. These two species are also found in Sonora and share with *M. minor* such diagnostic traits as glandular petals, crescentic glands on the fruit, and a bicolored corolla. These shared traits suggest *Marina minor*



should group with species of ser. *Chrysorrhizae* once DNA sequence data becomes available. Barneby (1977) classified *Marina gemmea* in its own series *Gemmeae* based on a unique combination of traits including a compressed fruit with glands densely covering the entire surface of the pod. This is most distinctive because among the *Marina* species in general, a laterally compressed harp-shaped pod covaries with the presence of crescentic rows of glands on the pod. *Marina gemmea* is thus unique phenotypically and should remain in a unique taxonomic series until genetic data is forthcoming that reveals the actual relationships of this species.

#### Divergence Time Estimation

From the estimated ages of the *Marina* crown clade, at about 12 Ma (Fig. 4), and those of each *Marina* species, ranging mostly 1 to over 10 Ma (Fig. 5), we suggest that *Marina* has an antiquity in Mexico in seasonally dry tropical forests and woodlands and adjacent deserts, which is consistent with Pennington et al. (2009) and Pennington and Lavin (2016) who also find seasonally tropical woody environments harboring old and often narrowly endemic legume species. Signatures of antiquity include not just old age estimates but also coalescent conspecific genetic samples endemic to patches of seasonally dry tropical woody environments and sister taxa occurring in close geographic proximity (Pennington and Lavin 2016).

Amorpheae have been resident in North America for tens of millions of years (Lavin et al. 2005), allowing much time for speciation to occur within and among patches of seasonally dry tropical woody environments. Woody legumes and other species adapted to such environments tend to be dispersal limited, which is indicated by fragmented and island-like distributions of narrowly distributed species that are often endemic to patches of dry tropical woodlands (Pennington and Lavin 2009). This pattern is found among *Marina* species especially

in Baja California Sur. Localized isolation caused by highly seasonal environments in this area is likely reinforced by a high level of topographic variation at the tip of the peninsula (Riemann 2007), which is also isolated by surrounding by ocean and desert. Indeed, ranges sizes of individual *Marina* species are smaller in the Cape Region compared to range sizes in *Marina* species that have a more northern Baja California distribution, a pattern that is observed to some degree for all *Marina* (Fig. 7).

The Gulf of California has an estimated age of 5-10 Ma (Riemann 2007). The estimated ages of *Marina* species from Baja California are younger than this (the *Chrysorrhizae* clade in Fig. 5). The Gulf of California may have been a significant barrier to migration during the diversification of Baja California *Marina* species because the Cape Region *Marina* species are most closely related to each other or to other Baja California species, supporting that they speciated within the Cape Region, rather than by immigration. The sole exception involves *Marina capensis*, which recently evolved its sister species *M. palmeri*, which is confined to mainland Sonora, Mexico (Fig. 3). These specific results about the Cape Region *Marina* species do not support Gentry's (1995) hypothesis that the Cape Region flora evolved by vicariant continental rafting of the southern tip of Baja California from an original location in the region of Jalisco, Mexico, to its current location.

### Conclusions

We used a combination of historic herbarium specimens and recent field collections to infer a highly supported phylogeny for the genus *Marina* using a target capture approach with the bait set Angiosperms353. The successful application of this method to this group is related to the antiquity of *Marina* species, as well as the inclusion of variable intronic regions in addition to

the targeted regions. Our phylogenomic approach that included sampling nearly all species of *Marina*, in addition to many conspecific samples, revealed for the first time a higher level evolutionary split involving species mainly from the Baja California peninsula and those mainly from mainland Mexico. Our approach also allowed us to test taxonomic hypotheses of Barneby (1977) at the species, series and section ranks. Some of Barneby's taxonomy is supported by our phylogenetic evidence, including Barneby's suspicions that certain of the species he circumscribed could represent more than one species. Our dense conspecific sampling revealed a more accurate estimate of the levels of biodiversity in *Marina* and identified species that have narrow geographic distributions and varying conservation concerns. With a strongly supported taxonomy, we can prioritize *Marina* species most in need of conservation efforts that minimize extinction threats.

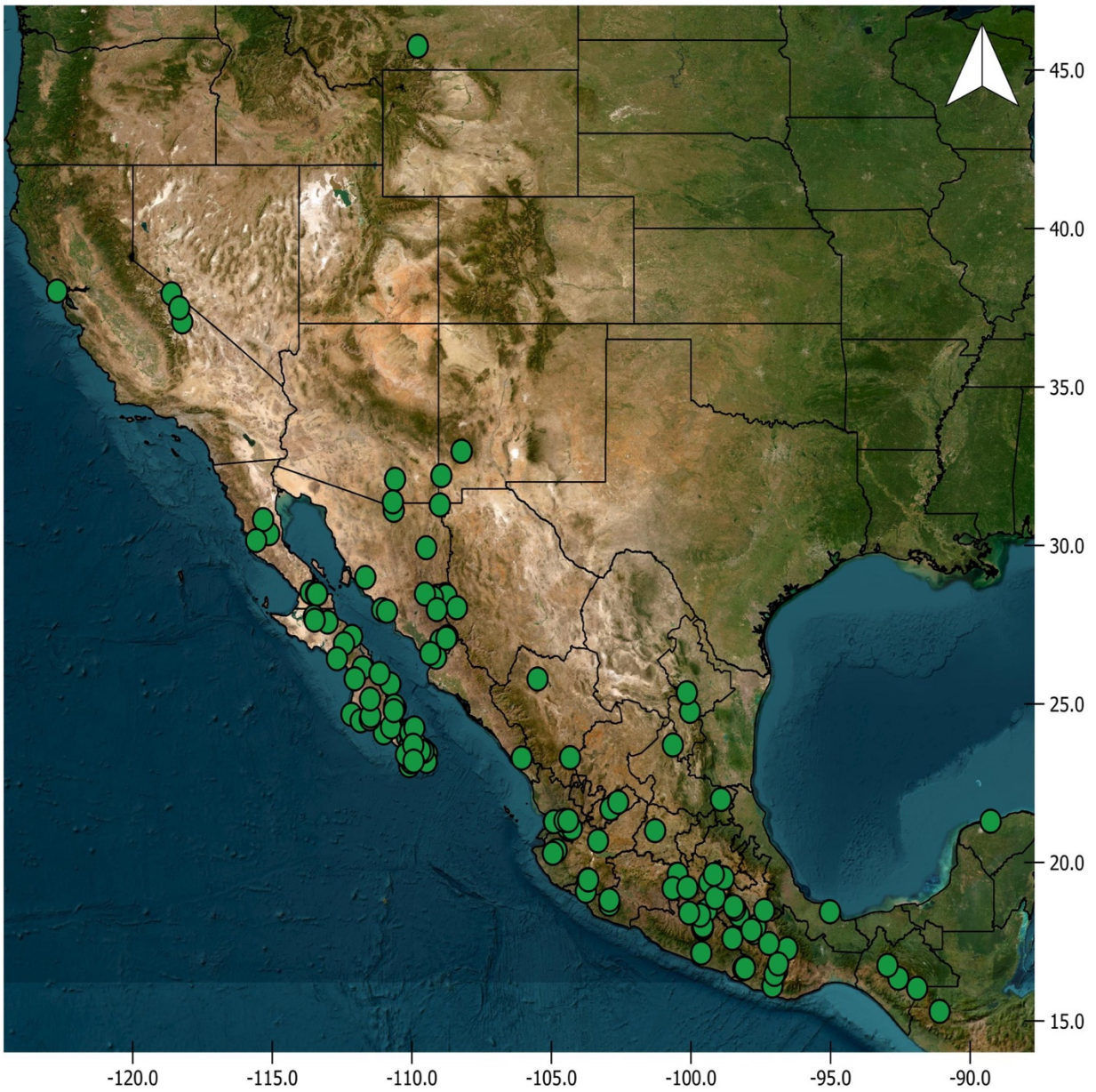


Figure 1: Localities of the accessions used to develop the phylogeny. Outlier geographically include *Dalea* from Montana, *Psorodendron* and *Psorothamnus* from eastern California and *Amorpha* from coastal California. Map made using QGIS with an ESRI layer.

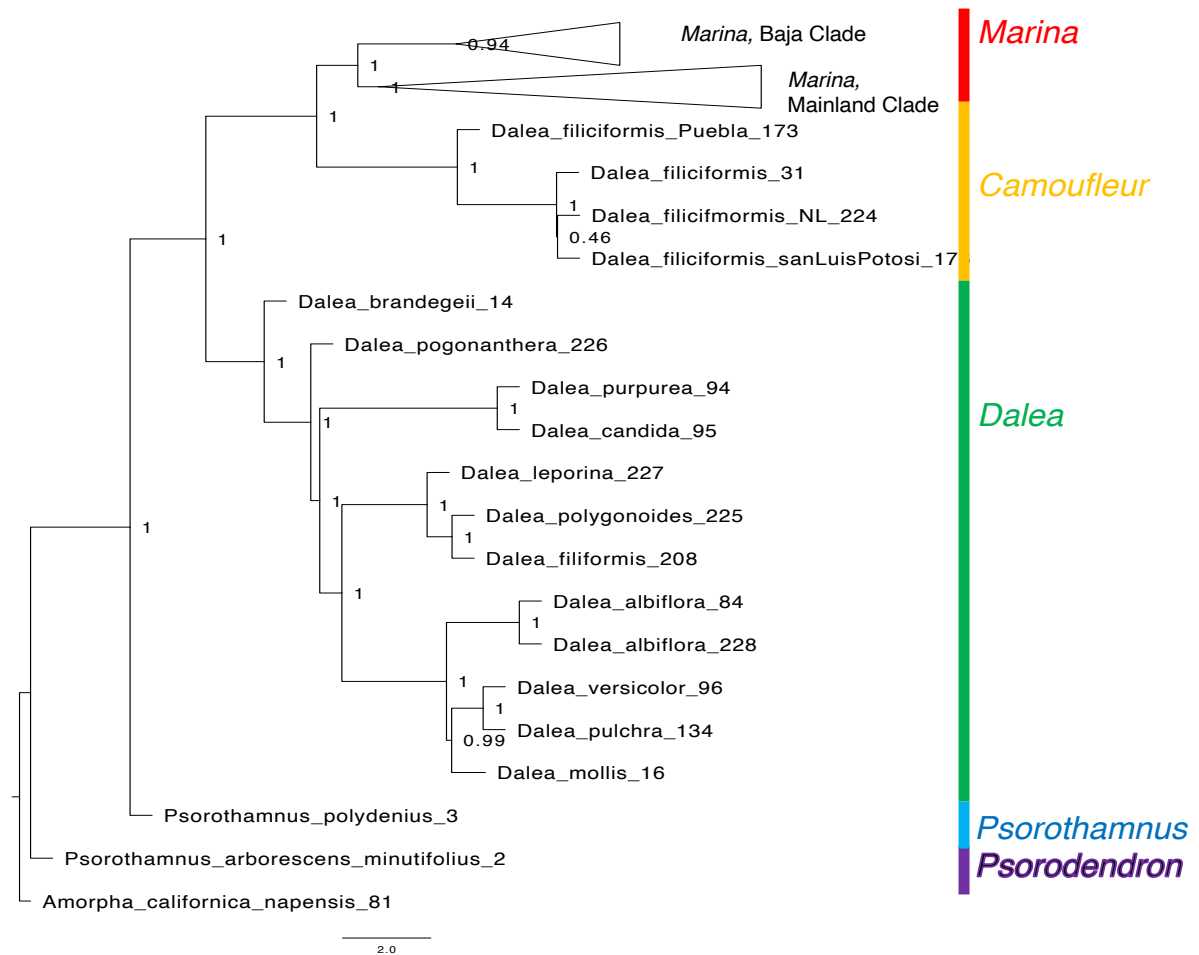


Fig. 2: Multi-species pseudocoalescent ASTRAL-III phylogeny supports previous results that *Dalea filiciformis* is separate from *Dalea*, and *Marina* and *Dalea* are monophyletic genera .



C

A

D

E

F

G

B

H

I

Og

Fig. 3 ASTRAL-III phylogeny using the multispecies pseudocoalescent model and that resolves the main monophyletic groups of *Marina* species that are the focus of this study. **A.** The Baja California *Marina* clade. **B.** The mainland *Marina* clade. **C.** Series *Chrysorrhizae* now excludes *Marina procumbens*, *M. orcuttii*, and *M. calycosa*. **D.** *Marina orcuttii* and *M. calycosa* are removed from Barneby's ser. *Chrysorrhizae* to form their own group. **E.** Series *Vetulae* remains monotypic (i.e., a clade of coalescent conspecific samples). **F.** Section *Carroa* now includes *Marina dispansa* and *M. sarodes* transferred from Barneby's ser. *Crenulatae*. **G.** Series *Crenulatae* is now monotypic. **H.** Series *Unifoliolatae* now includes *M. gracilis* and *M. procumbens*. **I.** *Marina neglecta* forms its own monotypic group and was removed from Barneby's ser. *Crenulatae*. **Og.** Outgroups include species of *Amorpha*, *Psorodendron*, *Psorothamnus*, and *Dalea*, in addition to *Camoufleur filiciformis*, the sister clade of *Marina*.

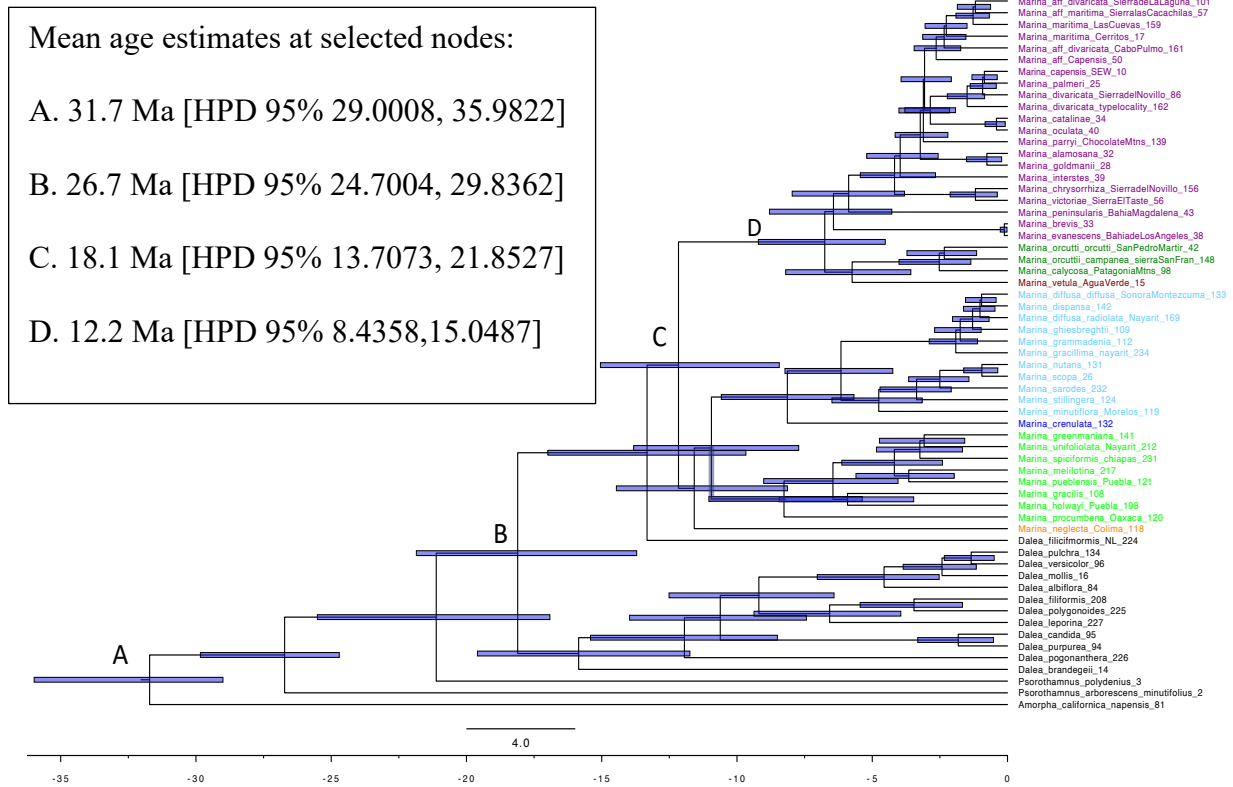


Fig. 4. Reduced single accession per taxon RAxML phylogeny. Colors correspond to subclades C-I (Fig. 3). A. Amorpheae crown clade set to  $36.9 \pm 3.0$  Ma and estimated at 31.7 Ma [HPD 95% 29.0008, 35.9822]. B. Daleoid crown clade set to  $24.7 \text{ Ma} \pm 2.7$  and estimated at 26.7 Ma [HPD 95% 24.7004, 29.8362] (see Methods & Materials). C. *Marina* crown clade (age estimated). D. Baja California crown clade (age estimated).



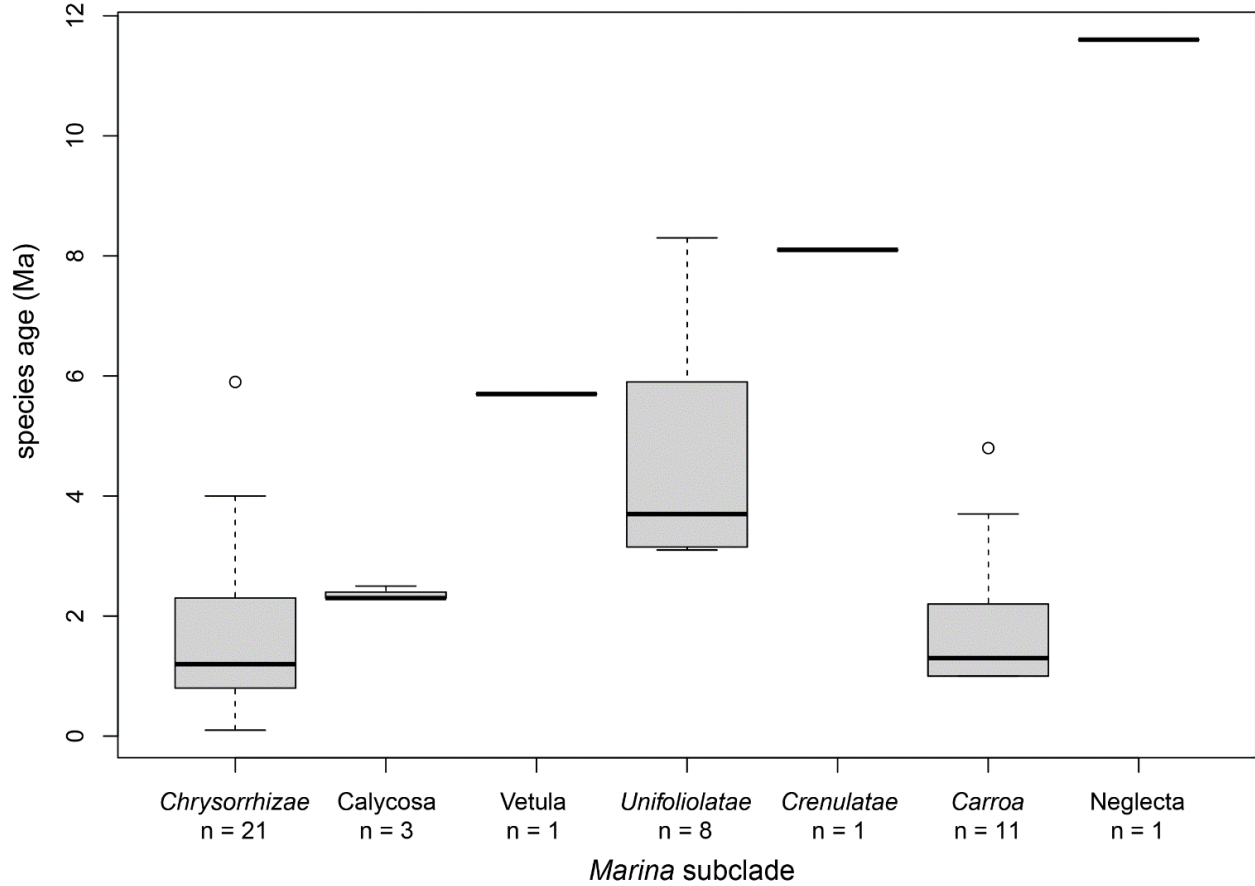


Fig. 5. Age distributions of seven main *Marina* subclades (Fig. 3, clades C-I), some of which correspond to modifications of Barneby's series. Each species age represent the mean of 10000 MCMC samples taken at likelihood stationarity. Tukey's Honestly Significant Difference post-hoc test revealed that age estimate distributions for species of subclades *Chrysorrhizae*, *Calycosa*, and *Carroa* were younger than those of the other clades.

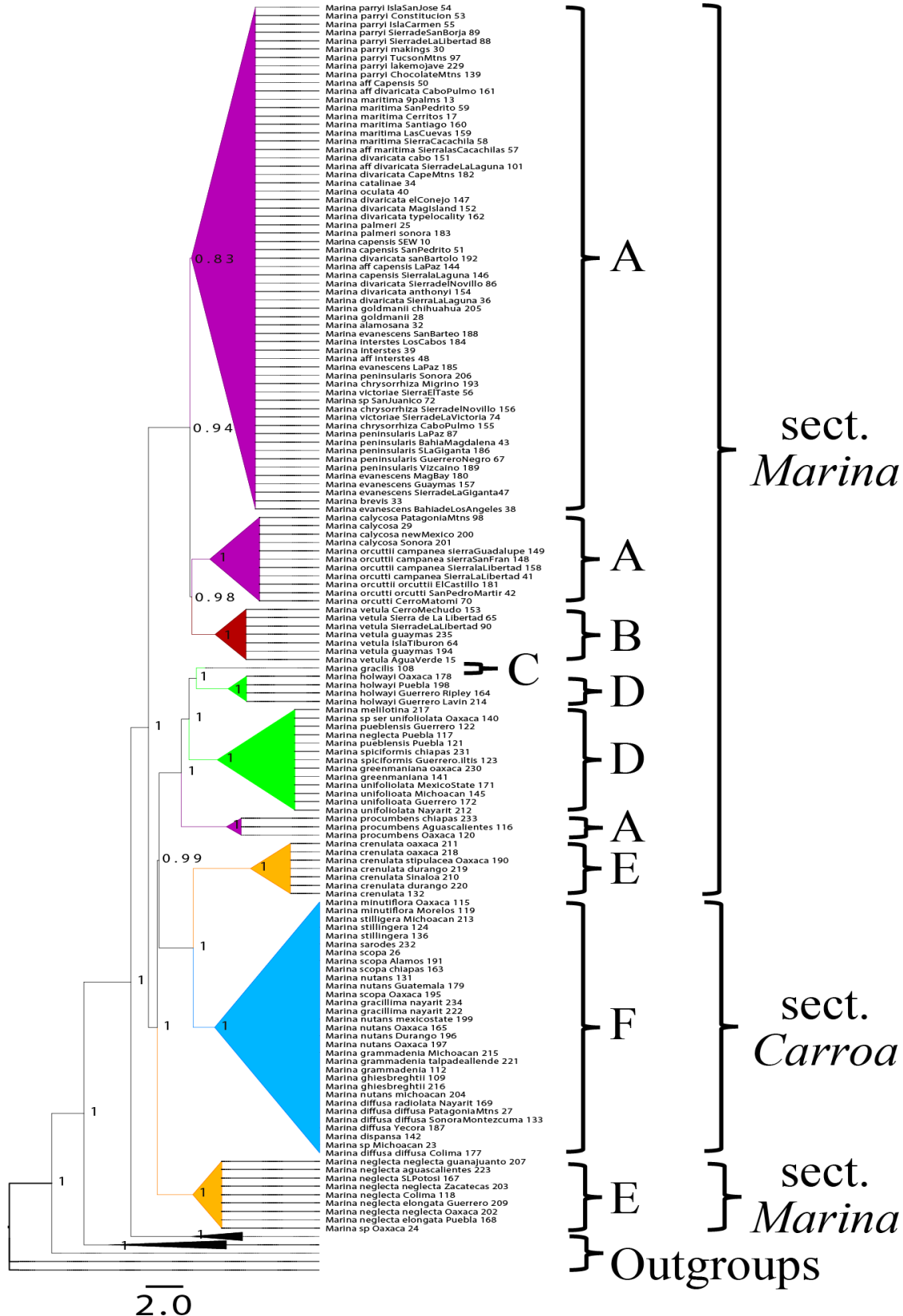


Fig. 6. *Marina* sections (labeled by name) and series (labeled by letter) representing the classification by Barneby (1977) and superimposed on our ASTRAL-III phylogeny (as in Fig. 1). A. *Marina* ser. *Chrysorrhizae* comprises three subclades on our phylogeny. B. Series *Vetulae* is monotypic and conspecific accession resolve as monophyletic. C. Barneby's *Marina* ser. *Marina* is monotypic, including only *M. gracilis*, the type species of *Marina*, and is sister a subclade of ser. *Unifoliolatae*. D. Series *Unifoliolatae* comprise two subclade in our phylogeny. E. Barneby's *Marina* ser. *Crenulatae* comprises two subclades in our phylogeny. F. Barneby's *Marina* ser. *Carroa* resolves as monophyletic in our phylogeny.

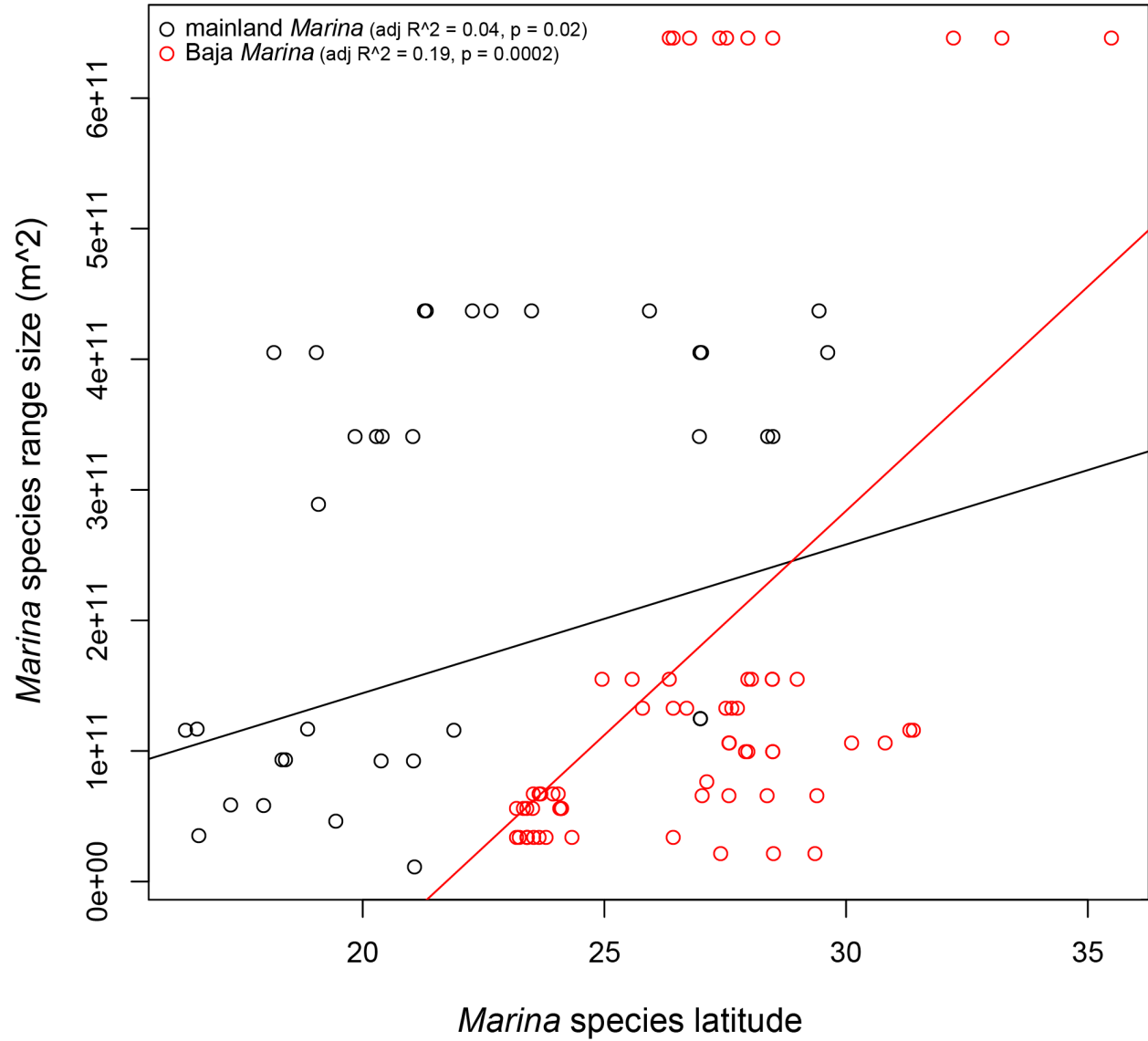


Fig. 7. Range size of *Marina* species as a function of latitude. Black data points and least squares line represent mainland *Marina* samples. Red data points and least squares line represent Baja California *Marina* samples.

| ID | TAXON                                                                                       | ACCESSION        | LOCATION                                      | HERB     | COLLECT#        | DATE       |
|----|---------------------------------------------------------------------------------------------|------------------|-----------------------------------------------|----------|-----------------|------------|
| 2  | <i>Psorothamnus arborescens</i> (A. Gray) Barneby var. <i>minutifolius</i> (Parish) Barneby | S. Winitsky 1594 | USA, California, Inyo                         | MON<br>T | Winitsky 1594   | 6-10-2020  |
| 3  | <i>Psorothamnus polydenius</i> (Torr.) Rydb. var. <i>polydenius</i>                         | S. Winitsky 1595 | USA, California, Mono                         | MON<br>T | Winitsky 1595   | 6-11-2020  |
| 10 | <i>Marina capensis</i> Barneby                                                              | S. Winitsky 1563 | Mexico, Baja California Sur, Todos Santos     | MON<br>T | Winitsky 1563   | 12-28-2019 |
| 13 | <i>Marina maritima</i> (Brandeggee) Barneby                                                 | S. Winitsky 1565 | Mexico, Baja California Sur, Cabo Pulmo       | MON<br>T | Winitsky 1565   | 1-1-2020   |
| 14 | <i>Dalea mollis</i> Benth.                                                                  | S. Winitsky 1567 | Mexico, Baja California Sur, Mulege           | MON<br>T | Winitsky 1567   | 1-10-2020  |
| 15 | <i>Marina vetula</i> (Brandg.) Barneby                                                      | S. Winitsky 1558 | Mexico, Baja California, Agua Verde           | MON<br>T | Winitsky 1558   | 12-14-2019 |
| 16 | <i>Dalea brandegeei</i> (Rose) Bullock                                                      | S. Winitsky 1559 | Mexico, Baja California Sur, Magdalena Island | MON<br>T | Winitsky 1559   | 12-20-2019 |
| 17 | <i>Marina maritima</i> (Brandeggee) Barneby                                                 | S. Winitsky 1560 | Mexico, Baja California Sur, Todos Santos     | MON<br>T | Winitsky 1560   | 12-25-2019 |
| 23 | <i>Marina</i> sp.                                                                           | MONT             | Mexico, Michoacan, Playa Azul                 | MON<br>T | Lavin 5358      |            |
| 24 | <i>Marina</i> sp.                                                                           | MONT             | Mexico, Oaxaca                                | MON<br>T | Lavin 5341      |            |
| 25 | <i>Marina palmeri</i> (Rose) Barneby                                                        | ASU0023732       | Mexico, Sonora, Cerrillos                     | ASU      | Friedman 415-94 | 10-19-1994 |

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| 26 | <i>Marina scopa</i><br>Barneby                                   | ASU0023756   | Mexico,<br>Chihuahua,<br>Mesa La<br>Lagunita<br>camp      | ASU | Martin s.n.          | 11-06-<br>1986 |
| 27 | <i>Marina diffusa</i><br>(Moric.) Barneby<br>var. <i>diffusa</i> | ASU153196    | USA,<br>Arizona,<br>Santa Cruz,<br>Patagonia<br>Mountains | ASU | Zimmerman<br>4771    | 10-20-<br>1987 |
| 28 | <i>Marina goldmanii</i><br>(Rose) Barneby                        | ASU0023727   | Mexico,<br>Sonora,<br>Yécora                              | ASU | Reina 98-<br>1764    | 09-28-<br>1998 |
| 29 | <i>Marina calycosa</i><br>(A. Gray) Barneby                      | ASU0023714   | Mexico,<br>Sonora, San<br>Lazaro                          | ASU | Reina 2002-<br>690   | 09-11-<br>2002 |
| 30 | <i>Marina parryi</i><br>(Torr. & A. Gray)<br>Barneby             | Makings 0178 | Mexico,<br>Sonora                                         | ASU | Makings<br>s.n.      | 05-01-<br>2018 |
| 31 | <i>Dalea filiciformis</i><br>Robins.et Greenm.                   | ASU0020058   | Mexico,<br>Mexico State,<br>Huixquilucan                  | ASU | Rzedowski<br>30415   | 04-15-<br>1973 |
| 32 | <i>Marina alamosana</i><br>(Rydb.) Barneby                       | ASU0023711   | Mexico,<br>Sonora, Los<br>Pilares                         | ASU | Reina G<br>2003-493  | 09-30-<br>2003 |
| 33 | <i>Marina brevis</i><br>León de la Luz                           | SD154080     | Mexico, Baja<br>California<br>Sur, Isla San<br>Jose       | SD  | Navarro136<br>1      | 10-12-<br>2000 |
| 34 | <i>Marina catalinae</i><br>Barneby                               | SD146996     | Mexico, Baja<br>Californai<br>Sur, Isla<br>Catalina       | SD  | Dominguez<br>1899    | 03-11-<br>1997 |
| 36 | <i>Marina divaricata</i><br>(Benth.) Barneby                     | SD260764     | Mexico, Baja<br>California<br>Sur, Sierra La<br>Laguna    | SD  | Vanderplan<br>k 7064 | 12-05-<br>2015 |
| 38 | <i>Marina evanescens</i><br>(Brandegees)<br>Barneby              | SD223601     | Mexico, Baja<br>California,<br>Sierra La<br>Libertad      | SD  | Rebman<br>25119      | 10-02-<br>2012 |
| 39 | <i>Marina interstes</i><br>Barneby                               | SD242171     | Mexico, Baja<br>California                                | SD  | Rebman<br>28891      | 10-10-<br>2014 |

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|    |                                                                                  |          | Sur, Sierra<br>Cacachilas                                    |    |                        |                |
| 40 | <i>Marina oculata</i><br>(Rydb.) Barneby                                         | SD255454 | Mexico, Baja<br>California<br>Sur, Isla<br>Cerralvo          | SD | Riley 180a             | 12-30-<br>2014 |
| 41 | <i>Marina orcuttii</i> (S.<br>Watson) Barneby<br>var. <i>campanea</i><br>Barneby | SD200267 | Mexico, Baja<br>California,<br>Sierra La<br>Libertad         | SD | Rebman<br>18703        | 10-28-<br>2009 |
| 42 | <i>Marina orcutti</i> (S.<br>Watson) Barneby<br>var. <i>orcuttii</i>             | SD258666 | Mexico, Baja<br>California,<br>Sierra de San<br>Pedro Martir | SD | Rebman<br>31726        | 06-09-<br>2016 |
| 43 | <i>Marina<br/>peninsularis</i> (Rose)<br>Barneby                                 | SD257864 | Mexico, Baja<br>California<br>Sur, Bahia<br>Magdalena        | SD | Leon de la<br>Luz 510  | 11-19-<br>2009 |
| 47 | <i>Marina evanescens</i><br>(Brandegees)<br>Barneby                              | SD258664 | Mexico, Baja<br>California<br>Sur, Sierra de<br>La Giganta   | SD | Rebman<br>31216        | 03-09-<br>2016 |
| 48 | <i>Marina interstes</i><br>Barneby                                               | SD179164 | Mexico,<br>Sonora,<br>Guaymas                                | SD | Felger 85-<br>376      | 03-01-<br>1985 |
| 50 | <i>Marina</i> aff.<br><i>capensis</i>                                            | SD234670 | Mexico, Baja<br>California<br>Sur, Cabo<br>Pulmo             | SD | Rebman<br>27652        | 11-13-<br>2013 |
| 51 | <i>Marina capensis</i><br>Barneby                                                | SD255902 | Mexico, Baja<br>California<br>Sur, Playa San<br>Pedrito      | SD | Rebman<br>30796        | 10-27-<br>2015 |
| 53 | <i>Marina parryi</i><br>(Torr. & A. Gray)<br>Barneby                             | SD146980 | Mexico, Baja<br>California<br>Sur, Ciudad<br>Constitución    | SD | Dominguez<br>2837      | 09-27-<br>2000 |
| 54 | <i>Marina parryi</i><br>(Torr. & A. Gray)<br>Barneby                             | SD141161 | Mexico, Baja<br>California<br>Sur, Isla San<br>Jose          | SD | Leon de la<br>Luz 8195 | 03-09-<br>1997 |
| 55 | <i>Marina parryi</i><br>(Torr. & A. Gray)<br>Barneby                             | SD265403 | Mexico, Baja<br>California                                   | SD | Leon de la<br>Luz 9149 | 04-25-<br>1998 |

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|    |                                                                |                     | Sur, Isla Carmen                                     |          |                         |                |
| 56 | <i>Marina victoriae</i><br>Leon de la Luz                      | SD260497            | Mexico, Baja California<br>Sur, Sierra El Taste      | SD       | Rebman<br>30925         | 10-31-<br>2015 |
| 57 | <i>Marina</i> aff.<br><i>maritima</i>                          | SD242172            | Mexico, Baja California<br>Sur, Sierra Cacachilas    | SD       | Rebman<br>28911         | 10-12-<br>2014 |
| 58 | <i>Marina maritima</i><br>(Brandegees)<br>Barneby              | SD256978            | Mexico, Baja California<br>Sur, Sierra Cacachilas    | SD       | Rebman<br>29931         | 04-22-<br>2015 |
| 59 | <i>Marina maritima</i><br>(Brandegees)<br>Barneby              | SD256979            | Mexico, Baja California<br>Sur, Playa San Pedrito    | SD       | Rebman<br>30821         | 10-27-<br>2015 |
| 64 | <i>Marina vetula</i><br>(Brandg.) Barneby                      | SD183249            | Mexico,<br>Sonora, Isla Tiburón                      | SD       | Wilder 06-<br>380       | 11-24-<br>2006 |
| 65 | <i>Marina vetula</i><br>(Brandg.) Barneby                      | SD225275            | Mexico, Baja California,<br>Sierra La Libertad       | SD       | Rebman<br>25073         | 10-01-<br>2012 |
| 67 | <i>Marina peninsularis</i> (Rose)<br>Barneby                   | SD250291            | Mexico, Baja California<br>Sur, Guerrero Negro       | SD       | de Groot<br>4863        | 04-02-<br>2005 |
| 70 | <i>Marina orcutti</i> (S.<br>Watson) Barneby                   | SD88720             | Mexico, Baja California,<br>Cerro Matomí             | SD       | Moran<br>20704          | 05-02-<br>1973 |
| 72 | <i>Marina</i> sp.                                              | SD202621            | Mexico, Baja California<br>Sur, Estero El Batequi    | SD       | Rebman<br>18595         | 10-22-<br>2009 |
| 74 | <i>Marina victoriae</i><br>Leon de la Luz                      | SD263189            | Mexico, Baja California<br>Sur, Sierra de La Laguna. | SD       | Leon de la<br>Luz 12292 | 09-24-<br>2015 |
| 81 | <i>Amorpha californica</i> Nutt.<br>var. <i>napensis</i> Jeps. | S. Winitsky<br>1700 | Greenhouse<br>grown seed                             | MON<br>T | Winitsky<br>1700        | 08-05-<br>2021 |



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| 84  | <i>Dalea albiflora</i> A. Gray                                       | S. Winitsky 1611 | USA, Arizona, Pima                              | MON T | Winitsky 1611     | 09-18-2020 |
| 86  | <i>Marina divaricata</i> (Benth.) Barneby                            | SD 242169        | Mexico, Baja California Sur, Sierra del Novillo | SD    | Rebman 29189      | 10-22-2014 |
| 87  | <i>Marina peninsularis</i> (Rose) Barneby                            | SD234401         | Mexico, Baja California Sur, La Paz             | SD    | Dominguez 3063    | 11-08-2001 |
| 88  | <i>Marina parryi</i> (Torr. & A. Gray) Barneby                       | SD225274         | Mexico, Baja California, Sierra de La Libertad  | SD    | Rebman 25103      | 10-02-2012 |
| 89  | <i>Marina parryi</i> (Torr. & A. Gray) Barneby                       | SD246064         | Mexico, Baja California, Sierra San Borja       | SD    | Vanderplanck 5113 | 01-27-2013 |
| 90  | <i>Marina vetula</i> (Brandg.) Barneby                               | SD225275         | Mexico, Baja California, Sierra de La Libertad, | SD    | Rebman 25073      | 10-01-2012 |
| 94  | <i>Dalea purpurea</i> Vent. var. <i>purpurea</i>                     | S. Winitsky 1601 | USA, Montana, Sweet Grass                       | MON T | Winitsky 1601     | 08-12-2020 |
| 96  | <i>Dalea versicolor</i> Zucc. var. <i>sessilis</i> (A. Gray) Barneby | S. Winitsky 1612 | USA, Arizona, Pima                              | MON T | Winitsky 1612     | 09-19-2020 |
| 97  | <i>Marina parryi</i> (Torr. & A. Gray) Barneby                       | S. Winitsky 1610 | USA, Arizona, Pima                              | MON T | Winitsky 1610     | 09-17-2020 |
| 98  | <i>Marina calycosa</i> (A. Gray) Barneby                             | S. Winitsky 1604 | USA, Arizona, Santa Cruz                        | MON T | Winitsky 1604     | 09-16-2020 |
| 101 | <i>Marina</i> aff. <i>divaricata</i>                                 | SD260496         | Mexico, Baja California Sur, Rancho Encinalito  | SD    | Rebman 31140      | 03-05-2016 |
| 108 | <i>Marina gracilis</i> Liebm.                                        | NYBG01307050     | Mexico, Guerrero                                | NYBG  | Iltis 3032        | 1981       |
| 109 | <i>Marina ghiesbreghtii</i> Barneby                                  | NYBG01307040     | Mexico, Chiapas                                 | NYBG  | Martinez s. n.    | 1985       |

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| 112 | <i>Marina grammadenia</i><br>Barneby                                          | NYBG0130705<br>9 | Mexico,<br>Jalisco                           | NYBG | Magallanes<br>3437          | 1981           |
| 115 | <i>Marina minutiflora</i><br>(Rose) Barneby                                   | NYBG0130710<br>2 | Mexico,<br>Oaxaca                            | NYBG | Barneby<br>14649            | 1966           |
| 116 | <i>Marina procumbens</i> (Sessé<br>& Moc. ex DC.)<br>Barneby                  | NYBG0130740<br>3 | Mexico,<br>Aguascalientes                    | NYBG | Lavin 5048                  | 1984           |
| 117 | <i>Marina neglecta</i><br>(B.L. Rob.)<br>Barneby var.<br><i>neglecta</i>      | NYBG0130713<br>9 | Mexico,<br>Puebla                            | NYBG | Panero 5304                 | 1994           |
| 118 | <i>Marina neglecta</i><br>(B.L. Rob.)<br>Barneby var.<br><i>neglecta</i>      | NYBG0130711<br>6 | Mexico,<br>Colima,                           | NYBG | Sanders<br>11754            | 1991           |
| 119 | <i>Marina minutiflora</i><br>(Rose) Barneby                                   | NYBG0130710<br>7 | Mexico,<br>Morelos                           | NYBG | Ripley<br>14905             | 1967           |
| 120 | <i>Marina procumbens</i> (Sessé<br>& Moc. ex DC.)<br>Barneby                  | NYBG0130740<br>4 | Mexico,<br>Oaxaca                            | NYBG | Torres 785                  | 1982           |
| 121 | <i>Marina pueblensis</i><br>(Brandegees)<br>Barneby                           | NYBG0130741<br>2 | Mexico,<br>Puebla                            | NYBG | Steinmann<br>1403           | 1998           |
| 122 | <i>Marina pueblensis</i><br>(Brandegees)<br>Barneby                           | NYBG0130741<br>4 | Mexico,<br>Puebla                            | NYBG | Lavin 5158                  | 1984           |
| 123 | <i>Marina spiciformis</i><br>(Rose) Barneby                                   | NYBG0130748<br>6 | Mexico,<br>Guerrero                          | NYBG | Iltis 3022                  | 1980           |
| 124 | <i>Marina stilligera</i><br>Barneby                                           | NYBG0130749<br>9 | Mexico,<br>Colima,                           | NYBG | Vazquez<br>1447             | 1991           |
| 131 | <i>Marina nutans</i><br>(Cav.) Barneby                                        | ARIZ270233       | Mexico,<br>Nayarit, Tepic                    | ARIZ | Gentry<br>19633             | 12-12-<br>1961 |
| 132 | <i>Marina crenulata</i><br>(Hook. & Arn.)<br>Barneby var.<br><i>crenulata</i> | ARIZ320313       | Mexico,<br>Sonora,<br>Alamos                 | ARIZ | Steinmann<br>94-38          | 04-29-<br>1994 |
| 133 | <i>Marina diffusa</i><br>(Moric.) Barneby<br>var. <i>diffusa</i>              | ARIZ406016       | Mexico,<br>Sonora,<br>Moctezuma<br>Municipio | ARIZ | Van<br>Devender<br>2010-670 | 06-15-<br>2010 |

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| 134 | <i>Dalea pulchra</i><br>Gentry                                                     | S. Winitzky<br>1605 | USA,<br>Arizona,<br>Santa Cruz                              | MON<br>T | Winitzky<br>1605        | 09-16-<br>2020 |
| 136 | <i>Marina stilligera</i><br>Barneby                                                | UCR81220            | Comala,<br>Colima                                           | UCR      | Vazquez<br>1447         | 1991           |
| 139 | <i>Marina parryi</i><br>(Torr. & A. Gray)<br>Barneby                               | UCR285255           | USA,<br>California,<br>Chocolate<br>Mountains               | UCR      | Sanders<br>43455        | 2018           |
| 140 | <i>Marina</i> sp.ser.<br><i>unifoliolata</i>                                       | CAS5766050          | Mexico,<br>Oaxaca                                           | CAS      | Lavin 5173              | 06-10-<br>1984 |
| 141 | <i>Marina</i><br><i>greenmaniana</i><br>(Rose) Barneby<br>var. <i>greenmaniana</i> | CAS452630           | Mexico,<br>Puebla                                           | CAS      | Barneby<br>13,695       | 11-07-<br>1964 |
| 142 | <i>Marina dispansa</i><br>(Rydb.) Barneby                                          | RSA305222           | Mexico,<br>Nayarit                                          | RSA      | Condit s.n.             | 05-05-<br>1905 |
| 143 | <i>Marina minutiflora</i><br>(Rose) Barneby                                        | RSA404954           | Mexico,<br>Mexico State                                     | RSA      | Rzedowski<br>31794      | 1974           |
| 144 | <i>Marina</i> aff.<br><i>capensis</i>                                              | UCR153538           | Mexico, Baja<br>California<br>Sur, La Paz                   | UCR      | Rebman<br>7059          | 2000           |
| 145 | <i>Marina unifoliata</i><br>(Robinson &<br>Greenm.) Barneby                        | RSA504276           | Mexico,<br>Michoacan                                        | RSA      | Koch 8355               | 1983           |
| 146 | <i>Marina capensis</i><br>Barneby                                                  | UCR112421           | Mexico, Baja<br>California<br>Sur, Sierra La<br>Laguna      | UCR      | Rebman<br>5801          | 1998           |
| 147 | <i>Marina divaricata</i><br>(Benth.) Barneby                                       | SD227006            | Mexico, Baja<br>California<br>Sur, La Paz                   | SD       | Leon de la<br>Luz 11036 | 03-11-<br>2011 |
| 148 | <i>Marina orcuttii</i> (S.<br>Watson) Barneby<br>var. <i>campanea</i><br>Barneby   | SD141621            | Mexico, Baja<br>California<br>Sur, Sierra<br>San Fransisco. | SD       | Rebman<br>4351          | 10-15-<br>1997 |
| 149 | <i>Marina orcuttii</i> (S.<br>Watson) Barneby<br>var. <i>campanea</i><br>Barneby   | SD142314            | Mexico, Baja<br>California<br>Sur, Sierra<br>Guadalupe      | SD       | Rebman<br>5199          | 04-28-<br>1998 |
| 151 | <i>Marina divaricata</i><br>(Benth.) Barneby                                       | SD146992            | Mexico, Baja<br>California<br>Sur, San José<br>del Cabo     | SD       | Leon de la<br>Luz 9856  | 11-11-<br>2000 |

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| 152 | <i>Marina divaricata</i><br>(Benth.) Barneby                            | SD79317  | Mexico, Baja California Sur, Magdalena Island      | SD | Beaucham 2162        | 04-08-1971 |
| 153 | <i>Marina vetula</i><br>(Brandg.) Barneby                               | SD153650 | Mexico, Baja California Sur, Cerro Mechudo         | SD | Leon de la Luz 10278 | 11-13-2003 |
| 154 | <i>Marina divaricata</i><br>(Benth.) Barneby                            | SD146993 | Mexico, Baja California Sur, Sierra de San Vicente | SD | Navarro 1379         | 10-25-2000 |
| 155 | <i>Marina chrysorrhiza</i> (A. Gray) Barneby                            | SD222530 | Mexico, Baja California Sur, Cabo Pulmo            | SD | Cadena 1213          | 01-22-1994 |
| 156 | <i>Marina chrysorrhiza</i> (A. Gray) Barneby                            | SD250655 | Mexico, Baja California Sur, Sierra del Novillo    | SD | Rebman 29215         | 10-22-2014 |
| 157 | <i>Marina evanescens</i><br>(Brandege) Barneby                          | SD121331 | Mexico, Sonora, Guaymas                            | SD | Sanders 2510         | 04-01-1982 |
| 158 | <i>Marina orcuttii</i> (S. Watson) Barneby var. <i>campanea</i> Barneby | SD194581 | Mexico, Baja California, Sierra La Libertad        | SD | Rebman 17332         | 04-27-2009 |
| 159 | <i>Marina maritima</i><br>(Brandege) Barneby                            | SD222535 | Mexico, Baja California Sur, Las Cuevas            | SD | Cadena 1201          | 01-21-1994 |
| 160 | <i>Marina maritima</i><br>(Brandege) Barneby                            | SD101439 | Mexico, Baja California Sur, Santiago              | SD | Ames 77-63           | 10-25-1977 |
| 161 | <i>Marina divaricata</i><br>(Benth.) Barneby                            | SD240081 | Mexico, Baja California Sur, Cabo Pulmo            | SD | Wilder 2013-191      | 2013       |
| 162 | <i>Marina divaricata</i><br>(Benth.) Barneby                            | SD222532 | Mexico, Baja California Sur, Magdalena Bay         | SD | Cadena 3287          | 04-13-2010 |

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| 163 | <i>Marina scopa</i><br>Barneby                                                             | CAS698290 | Mexico,<br>Chiapas                  | CAS | Sousa<br>11494     | 12-12-<br>1980 |
| 164 | <i>Marina holwayi</i><br>(Rose) Barneby                                                    | CAS452320 | Mexico,<br>Guerrero                 | CAS | Ripley<br>13736    | 11-09-<br>1964 |
| 165 | <i>Marina nutans</i><br>(Cav.) Barneby                                                     | RSA726113 | Mexico,<br>Oaxaca                   | RSA | Tenorio<br>21459   | 06-23-<br>1905 |
| 166 | <i>Marina spiciformis</i><br>(Rose) Barneby                                                | RSA529439 | Mexico,<br>Yucatan                  | RSA | Cabrera<br>10409   | 1985           |
| 167 | <i>Marina neglecta</i><br>(B.L. Rob.)<br>Barneby var.<br><i>neglecta</i>                   | RSA424303 | Mexico, San<br>Luis Potosi          | RSA | Zarate 323         | 1979           |
| 168 | <i>Marina neglecta</i><br>(B.L. Rob.)<br>Barneby var.<br><i>elongata</i> (Rose)<br>Barneby | CAS452306 | Mexico,<br>Puebla                   | CAS | Barneby<br>13688   | 11-07-<br>1964 |
| 169 | <i>Marina diffusa</i><br>(Moric.) Barneby<br>var. <i>radiolata</i><br>Barneby              | CAS458810 | Mexico,<br>Nayarit                  | CAS | Barneby<br>14052   | 10-09-<br>1965 |
| 170 | <i>Marina scopa</i><br>Barneby                                                             | UCR82365  | Mexico,<br>Nuevo Leon               | UCR | Poole 2406         | 06-03-<br>1905 |
| 171 | <i>Marina unifoliata</i><br>(Robinson &<br>Greenm.) Barneby                                | CAS478474 | Mexico,<br>Mexico State             | CAS | Barneby<br>14887   | 12-01-<br>1967 |
| 172 | <i>Marina unifoliata</i><br>(Robinson &<br>Greenm.) Barneby                                | SD89166   | Mexico,<br>Guerrero,<br>Xaltianguis | SD  | Rzedowski<br>29772 | 11-02-<br>1972 |
| 173 | <i>Dalea filiciformis</i><br>Robins.et Greenm.                                             | RSA449838 | Mexico,<br>Puebla                   | RSA | Dorado<br>1820     | 1987           |
| 174 | <i>Marina diffusa</i><br>(Moric.) Barneby<br>var. <i>diffusa</i>                           | CAS566576 | Mexico,<br>Veracruz                 | CAS | Calderon<br>1846   | 03-02-<br>1969 |
| 175 | <i>Marina gracillima</i><br>(S. Watson)<br>Barneby                                         | CAS421504 | Mexico,<br>Jalisco                  | CAS | Pringle s.n.       | 03-17-<br>1905 |
| 176 | <i>Dalea filiciformis</i><br>Robins.et Greenm.                                             | RSA675766 | Mexico, San<br>Luis Potosi          | RSA | Henrickson<br>6635 | 1971           |
| 177 | <i>Marina diffusa</i><br>(Moric.) Barneby<br>var. <i>diffusa</i>                           | UCR65506  | Mexico,<br>Colima                   | UCR | Lott 3065          | 1990           |
| 178 | <i>Marina holwayi</i><br>(Rose) Barneby                                                    | CAS468695 | Mexico,<br>Oaxaca                   | CAS | Ripley<br>14,695   | 11-16-<br>1966 |

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| 179 | <i>Marina nutans</i><br>(Cav.) Barneby                                              | CAS1237797 | Guatemala                                       | CAS  | Veliz 17951         | 11-25-<br>2006 |
| 180 | <i>Marina evanescens</i><br>(Brandege) Barneby                                      | SD234398   | Mexico, Baja California Sur,<br>Magdalena Bay   | SD   | Leon de la Luz 1244 | 12-15-<br>2009 |
| 181 | <i>Marina orcutti</i> (S. Watson) Barneby<br>var. <i>orcuttii</i>                   | SD145911   | Mexico, Baja California, El Rosario             | SD   | Rebman 5952         | 05-15-<br>1999 |
| 182 | <i>Marina divaricata</i><br>(Benth.) Barneby                                        | SD146991   | Mexico, Baja California Sur, Rancho San Antonio | SD   | Dominguez 2928      | 10-19-<br>2000 |
| 183 | <i>Marina palmeri</i><br>(Rose) Barneby                                             | SD120102   | Mexico, Sonora, Onavas                          | SD   | Rea 1276            | 10-14-<br>1986 |
| 184 | <i>Marina interstes</i><br>Barneby                                                  | SD227009   | Mexico, Baja California Sur, Sierra Cacachilas  | SD   | Narvaez 11-166      | 11-30-<br>2001 |
| 185 | <i>Marina evanescens</i><br>(Brandege) Barneby                                      | SD151858   | Mexico, Baja California Sur, La Paz             | SD   | Dominguez 2876      | 10-12-<br>2000 |
| 186 | <i>Marina peninsularis</i> (Rose) Barneby                                           | SD153652   | Mexico, Baja California Sur, Sierra la Giganta  | SD   | Leon de la Luz 3545 | 11-17-<br>2003 |
| 187 | <i>Marina diffusa</i><br>(Moric.) Barneby<br>var. <i>diffusa</i>                    | SD146995   | Mexico, Sonora, Yecora                          | SD   | Leon de la Luz 8773 | 09-21-<br>1997 |
| 188 | <i>Marina evanescens</i><br>(Brandege) Barneby                                      | SD50564    | Mexico, Baja California Sur, San Bartolo        | SD   | Moran 7116          | 01-20-<br>1959 |
| 189 | <i>Marina peninsularis</i> (Rose) Barneby                                           | SD246065   | Mexico, Baja California Sur, Vizcaino           | SD   | Vanderplanck 5261   | 02-07-<br>2015 |
| 190 | <i>Marina crenulata</i><br>(Hook. & Arn.) Barneby<br>var. <i>stipulacea</i> Barneby | ARIZ221417 | Mexico, Oaxaca, Putla                           | ARIZ | Sousa 9902          | 12-06-<br>1978 |

|     |                                                                          |            |                                                   |      |                    |                |
|-----|--------------------------------------------------------------------------|------------|---------------------------------------------------|------|--------------------|----------------|
| 191 | <i>Marina scopa</i><br>Barneby                                           | ARIZ316665 | Mexico,<br>Sonora,<br>Alamos                      | ARIZ | Jenkins 91-<br>131 | 10-30-<br>1991 |
| 192 | <i>Marina divaricata</i><br>(Benth.) Barneby                             | ARIZ255627 | Mexico, Baja<br>California<br>Sur, San<br>Bartolo | ARIZ | Sanders<br>3310    | 12-12-<br>1982 |
| 193 | <i>Marina<br/>chrysorrhiza</i> (A.<br>Gray) Barneby                      | ARIZ193147 | Mexico, Baja<br>California<br>Sur, Migrino        | ARIZ | Petryszyn<br>45    | 05-27-<br>1905 |
| 194 | <i>Marina vetula</i><br>(Brandg.) Barneby                                | UCR30118   | Mexico,<br>Sonora,<br>Guaymas                     | UCR  | Sanders<br>2623    | 1983           |
| 195 | <i>Marina scopa</i><br>Barneby                                           | ARIZ221370 | Mexico,<br>Oaxaca, Santa<br>Cruz<br>Mixtepec      | ARIZ | Sousa 6262         | 10-19-<br>1976 |
| 196 | <i>Marina nutans</i><br>(Cav.) Barneby                                   | ARIZ276759 | Mexico,<br>Durango, La<br>Posta del<br>Vergel     | ARIZ | Tenorio<br>2072    | 10-12-<br>1982 |
| 197 | <i>Marina nutans</i><br>(Cav.) Barneby                                   | ARIZ221420 | Mexico,<br>Oaxaca, Sola<br>de Vega                | ARIZ | Sousa 9976         | 12-09-<br>1978 |
| 198 | <i>Marina holwayi</i><br>(Rose) Barneby                                  | CAS468367  | Mexico,<br>Puebla                                 | CAS  | Ripley<br>14570    | 11-09-<br>1966 |
| 199 | <i>Marina nutans</i><br>(Cav.) Barneby                                   | CAS155566  | Mexico,<br>Mexico State                           | CAS  | Pringle s.n.       | 09-11-<br>1904 |
| 200 | <i>Marina calycosa</i><br>(A. Gray) Barneby                              | ARIZ334227 | USA, New<br>Mexico,<br>Hidalgo<br>County          | ARIZ | Turner 96-5        | 08-12-<br>1993 |
| 201 | <i>Marina calycosa</i><br>(A. Gray) Barneby                              | ARIZ433351 | Mexico,<br>Sonora, Agua<br>Prieta.                | ARIZ | Carnahan<br>2435   | 04-24-<br>2017 |
| 202 | <i>Marina neglecta</i><br>(B.L. Rob.)<br>Barneby var.<br><i>neglecta</i> | ARIZ269781 | Mexico,<br>Oaxaca,<br>Nochixtlan                  | ARIZ | Torres 2972        | 05-16-<br>1983 |
| 203 | <i>Marina neglecta</i><br>(B.L. Rob.)<br>Barneby var.<br><i>neglecta</i> | ARIZ245377 | Mexico,<br>Zacatecas,<br>Jalpa                    | ARIZ | Starr 666          | 08-08-<br>1983 |

|     |                                                                                            |                     |                                                |          |                           |                |
|-----|--------------------------------------------------------------------------------------------|---------------------|------------------------------------------------|----------|---------------------------|----------------|
| 204 | <i>Marina nutans</i><br>(Cav.) Barneby                                                     | ARIZ277353          | Mexico,<br>Michoacan,<br>Aguililla             | ARIZ     | Martinez<br>5372          | 11-17-<br>1983 |
| 205 | <i>Marina goldmanii</i><br>(Rose) Barneby                                                  | ARIZ314763          | Mexico,<br>Chihuahua,<br>Agua Caliente         | ARIZ     | Jenkins 91-<br>79A        | 24-09-<br>1991 |
| 206 | <i>Marina peninsularis</i> (Rose)<br>Barneby                                               | ARIZ295296          | Mexico,<br>Sonora, Las<br>Bocas                | ARIZ     | Van<br>Devender<br>92-126 | 02-01-<br>1992 |
| 207 | <i>Marina neglecta</i><br>(B.L. Rob.)<br>Barneby var.<br><i>neglecta</i>                   | CAS445051           | Mexico,<br>Guanajuato                          | CAS      | Ripley<br>13341           | 10-28-<br>1963 |
| 208 | <i>Dalea filiformis</i> A.<br>Gray                                                         | S. Winitsky<br>1628 | USA, New<br>Mexico, Gila<br>National<br>Forest | MON<br>T | Winitsky<br>1628          | 08-01-<br>2021 |
| 209 | <i>Marina neglecta</i><br>(B.L. Rob.)<br>Barneby var.<br><i>elongata</i> (Rose)<br>Barneby | ARIZ269778          | Mexico,<br>Guerrero,<br>Alpoyeca               | ARIZ     | Martinez<br>2654          | 16-09-<br>1982 |
| 210 | <i>Marina crenulata</i><br>(Hook. & Arn.)<br>Barneby var.<br><i>crenulata</i>              | MEXU618012          | Mexico,<br>Sinaloa                             | MEX<br>U | Vega 3661                 | 02-25-<br>1990 |
| 211 | <i>Marina crenulata</i><br>(Hook. & Arn.)<br>Barneby var.<br><i>crenulata</i>              | MEXU193123          | Mexico,<br>Oaxaca                              | MEX<br>U | Sousa 5220                | 02-09-<br>1976 |
| 212 | <i>Marina unifoliata</i><br>(Robinson &<br>Greenm.) Barneby                                | MEXU621747          | Mexico,<br>Nayarit, Santa<br>Maria del Oro     | MEX<br>U | Acevedo<br>1088a          | 02-01-<br>1991 |
| 213 | <i>Marina stilligera</i><br>Barneby                                                        | MEXU478891          | Mexico,<br>Michoacan                           | MEX<br>U | Martinez<br>4317          | 10-10-<br>1983 |
| 214 | <i>Marina holwayi</i><br>(Rose) Barneby                                                    | MEXU392546          | Mexico,<br>Guerrero                            | MEX<br>U | Lavin 5159                | 1984           |
| 215 | <i>Marina grammadenia</i><br>Barneby                                                       | MEXU451487          | Mexico,<br>Michoacan                           | MEX<br>U | McVaugh<br>22761          | 1965           |
| 216 | <i>Marina ghiesbreghtii</i><br>Barneby                                                     | MEXU193786          | México,<br>Oaxaca                              | MEX<br>U | Boege 2096                | 12-25-<br>1972 |



|     |                                                                                        |                     |                                                |          |                    |                |
|-----|----------------------------------------------------------------------------------------|---------------------|------------------------------------------------|----------|--------------------|----------------|
| 217 | <i>Marina melilotina</i><br>Barneby                                                    | MEXU99189           | Mexico,<br>Guerrero,<br>Mexcala                | MEX<br>U | Moore 5198         | 10-03-<br>1949 |
| 218 | <i>Marina crenulata</i><br>(Hook. & Arn.)<br>Barneby var.<br><i>stipulacea</i> Barneby | MEXU216331          | Mexico,<br>Oaxaca                              | MEX<br>U | Sousa 7050         | 02-04-<br>1977 |
| 219 | <i>Marina crenulata</i><br>(Hook. & Arn.)<br>Barneby var.<br><i>crenulata</i>          | MEXU754589          | Mexico,<br>Durango                             | MEX<br>U | Tenorio<br>8093    | 1985           |
| 220 | <i>Marina crenulata</i><br>(Hook. & Arn.)<br>Barneby var.<br><i>crenulata</i>          | MEXU648144          | México,<br>Durango,<br>Tamazula                | MEX<br>U | Tenorio<br>8398    | 03-17-<br>1985 |
| 221 | <i>Marina<br/>grammadenia</i><br>Barneby                                               | MEXU399693          | Mexico,<br>Zacatecas                           | MEX<br>U | Magallanes<br>3437 | 12-06-<br>1981 |
| 222 | <i>Marina gracillima</i><br>(S. Watson)<br>Barneby                                     | MEXU281405          | Mexico,<br>Nayarit                             | MEX<br>U | Delgado<br>456     | 01-24-<br>1977 |
| 223 | <i>Marina neglecta</i><br>(B.L. Rob.)<br>Barneby var.<br><i>neglecta</i>               | UCR117808           | Mexico,<br>Aguascaliente<br>s                  | UCR      | Provance<br>1244   | 1999           |
| 224 | <i>Dalea filiciformis</i><br>Robins.et Greenm.                                         | E. Castillon s.n.   | Mexico,<br>Nuevo Leon,<br>Galeana              | CFNL     | Castillon<br>s.n.  | 08-05-<br>2021 |
| 225 | <i>Dalea<br/>polygonoides</i> A.<br>Gray                                               | S. Winitsky<br>1629 | USA, New<br>Mexico, Gila<br>National<br>Forest | MON<br>T | Winitsky<br>1629   | 08-01-<br>2021 |
| 226 | <i>Dalea<br/>pogonantha</i> A.<br>Gray var.<br><i>pogonantha</i>                       | S. Winitsky<br>1623 | USA, New<br>Mexico, Gila<br>National<br>Forest | MON<br>T | Winitsky<br>1623   | 08-01-<br>2021 |
| 227 | <i>Dalea leporina</i><br>(Aiton) Bullock                                               | S. Winitsky<br>1630 | USA, New<br>Mexico, Gila<br>National<br>Forest | MON<br>T | Winitsky<br>1630   | 08-01-<br>2021 |
| 228 | <i>Dalea albiflora</i> A.<br>Gray                                                      | S. Winitsky<br>1631 | USA, New<br>Mexico, Gila<br>National<br>Forest | MON<br>T | Winitsky<br>1631   | 08-01-<br>2021 |

|     |                                                                          |                     |                                               |          |                              |                |
|-----|--------------------------------------------------------------------------|---------------------|-----------------------------------------------|----------|------------------------------|----------------|
| 229 | <i>Marina parryi</i><br>(Torr. & A. Gray)<br>Barneby                     | S. Winitzky<br>1613 | USA, Nevada,<br>Lake Mead                     | MON<br>T | Winitzky<br>1613             | 2020           |
| 230 | <i>Marina greenmaniana</i><br>(Rose) Barneby<br>var. <i>greenmaniana</i> | NYBG0130706<br>6    | Mexico,<br>Oaxaca                             | NYBG     | Breedlove<br>60038           | 1983           |
| 231 | <i>Marina spiciformis</i><br>(Rose) Barneby                              | CAS443489           | Mexico,<br>Chiapas                            | CAS      | Laughlin<br>2601             | 10-24-<br>1966 |
| 231 | <i>Marina orcutti</i> (S.<br>Watson) Barneby<br>var. <i>orcuttii</i>     | S. Winitzky<br>1617 | USA,<br>California,<br>Riverside<br>County    | MON<br>T | Winitzky<br>1617             | 04-11-<br>2021 |
| 232 | <i>Marina sarodes</i><br>Barneby                                         | ARIZ383635          | Mexico,<br>Sonora,<br>Rancho Santa<br>Barbara | ARIZ     | Van<br>Devender<br>2006-1118 | 10-03-<br>2006 |
| 233 | <i>Marina procumbens</i> (Sessé<br>& Moc. ex DC.)<br>Barneby             | CAS443488           | Mexico,<br>Chiapas                            | CAS      | Laughlin<br>1640             | 08-23-<br>1966 |
| 234 | <i>Marina gracillima</i><br>(S. Watson)<br>Barneby                       | ARIZ339033          | Mexico,<br>Nayarit, El<br>Ocotillo            | ARIZ     | Jenkins 96-<br>146           | 12-14-<br>1996 |

Table 1: Accessions used in the phylogenies inferred.

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EVIDENCE FOR RECOGNIZING A MONOTYPIC MEXICAN GENUS THAT  
ACCOMMODATES THE LEGUME SPECIES

DALEA FILICIFORMIS (FABACEAE)

Contribution of Authors and Co-Authors

Manuscript in Chapter Two

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# Evidence For Recognizing a Monotypic Mexican Genus that Accommodates the Legume

## Species *Dalea filiciformis* (Fabaceae)

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**Abstract**— *Dalea filiciformis* since its inception has been included in the genus *Dalea*. Barneby treated *D. filiciformis* as a taxonomically isolated species of *Dalea* and thought that it harbored many traits that carried the “stamp of age,” plesiomorphic states not just within *Dalea* but within the legume tribe Amorpheae, to which *Dalea* belongs. In contrast, initial genetic evidence suggested *Dalea filiciformis* belonged to *Marina*, the sister genus of *Dalea* and of which Barneby thought harbored the highest number of derived states within Amorpheae. To resolve these contrasting perspectives, we conducted an analysis of diverse traits bearing on the taxonomic position of *Dalea filiciformis*. This included a genomic analysis of multiple conspecific samples of *Dalea filiciformis* and a representative sampling of *Dalea*, *Marina*, *Psorothamnus*, and *Psorodendron*, the genera of the daleoid subclade of Amorpheae. We find

that *Dalea filiciformis* has indeed retained many plesiomorphic traits with respect to *Dalea*. Yet genetic evidence strongly suggests *D. filiciformis* represents the sister clade of *Marina* with *Dalea* resolving as sister to the subclade comprising *D. filiciformis* and *Marina*. We therefore classify *Dalea filiciformis* into its own monotypic genus.

**Keywords**— Amorpheae, bioclimatic variables, gypsum, Leguminosae, Mexico, phylogenomics.

A solid taxonomic foundation of tribe Amorpheae (Barneby 1977) permits us to detail a study of *Dalea filiciformis* Robins. et Greenm. and thereby come to definitive conclusions about the taxonomic classification of this enigmatic species. The relevant taxonomic history is now at a point where it can be said confidently that the papilionoid legume tribe Amorpheae is sister to the Dalbergioid clade (Lavin et al. 2001; McMahon and Hufford 2005) and comprises 10 genera and 277 species (LPWG 2021). Amorpheae is geographically distinctive among legume tribes for being confined to the western hemisphere and having a center of diversity in and around Mexico (Polhill 1981). Barneby's (1977) circumscription of tribe Amorpheae was affirmed by Polhill (1981) in a tribal classification system of the legume family revised from especially that of Bentham (1865). Subsequently, McMahon and Hufford (2004) and Pineros-Urrego et al. (2023) using DNA sequence data from select loci, and Becklund and Ayers (2022) and Winitzky et al. (Chapter 1) using phylogenomics, validated the circumscription of Amorpheae or revised the generic classification to arrive at the current 10 formally recognized Amorpheae genera: *Amorpha* L., *Apoplanesia* C. Presl, *Errazurizia* Phil., *Eysenhardtia* Kunth, *Parryella* Torr. & A. Gray, and *Pictarena* Becklund in the amorphoid clade, and *Psorodendron* Rydb., *Psorothamnus* Rydb., *Dalea* L., and *Marina* Liebm. in the daleoid clade. Barneby's (1977) phenotypic diagnosis of tribe Amorpheae still stands (e.g., McMahon and Hufford 2005): epidermal glands

throughout foliage, flower, and fruit, simple basifixed hairs, fundamentally pinnately compound leaves (albeit in some species reduced to unifoliate or trifoliate leaves), determinate terminal racemes or spikes, and a mostly single-seeded indehiscent dry nut-like legume fruit that is continuous with the receptacle and disperses with the marcescent calyx, which is sometimes modified to aid fruit dispersal (Barneby 1977). A tendency to independently evolve from the standard papilionoid floral architecture to a more simplified or reduced floral form is also diagnostic of Amorpheae, a tendency perhaps more pronounced in the amorphoid clade (McMahon 2005). For example, the name *Amorpha* (amorphous) derives from the papilionoid flower of this genus, which lacks keel and wing petals (Lewis et al. 2005).

Barneby's (1977) circumscription of Amorpheae represented a major revision to prior classifications of constituent genera (e.g., Bentham 1865) by disentangling this distinctive papilionoid legume clade from genera now belonging to tribe Psoraleae, such as *Psoralea* L., *Pediomelum* Rydb., *Psoralidium* Rydb., and *Rupertia* J.W.Grimes, to name a few genera. Psoraleae, like Amorpheae, are marked by a single seeded indehiscent fruit that disperses with a marcescent calyx, and epidermal glands throughout foliage, flower, and fruit. But this is where the similarity ends. Psoraleae genera consistently produce traits not found in Amorpheae, such as palmately compound leaves and axillary pseudoracemose inflorescences (Barneby 1977; McMahon and Hufford 2004). Detailed anatomical and phytochemical investigations have demonstrated that the epidermal glands are structurally different between Amorpheae and Psoraleae and sequester different secondary compounds (e.g., Dreyer 1975; Turner 1986). Regardless, any similarities in epidermal glands between Psoraleae and Amorpheae are likely

the product of convergent evolution because epidermal glands in general are thought to evolve in response to insect predation (Turner 1986).

The taxonomic history behind Amorphaeae and its distinction from tribe Psoraleeae is complex, and Barneby (1977) and Polhill (1981) provide the details in this regard. Suffice it to say that Barneby's (1977) circumscription of tribe Amorphaeae lays the foundation for our study of *Dalea filiciformis* and the distinction of this species from both *Dalea* and *Marina*. McMahon and Hufford's (2004) and McMahon's (2005) recognition of the daleoid subclade (*Psorodendron*, *Psorothamnus*, *Dalea*, and *Marina*) as sister to the amorphoid clade (the other six genera of Amorphaeae) provides additional taxonomic foundation for us to focus on genera of the daleoid subclade to address our question related to the taxonomic placement of *Dalea filiciformis*.

The "daleoid Amorphaeae" derives from Barneby (1977) where he generally used daleoid to refer to *Dalea* and *Marina* and other legume taxa with a floral form marked by petals, mainly the wing and keel petals, which are perched along the staminal column rather than directly on the rim of the hypanthium, the latter floral condition being ubiquitous in legumes. According to Barneby (1977), *Dalea filiciformis* harbors mostly "primitive" (ancestral) character states, such as an ovary with two collateral ovules, leaflets lacking oblique lineoles, and hairs of the calyx and foliage that are spiral and turn rusty or yellowish when dry. Yet *Dalea filiciformis* also has a floral morphology whereby the wing and keel petals are perched on the staminal column, a decidedly advanced character state in Barneby's view of Amorphaeae.

The enigmatic taxonomic position of *Dalea filiciformis* has been underscored beginning with Barneby (1977), who classified it in a taxonomically isolated position as the sole member of

*Dalea* subgen. *Psoropteris* Barneby, and referred to *D. filiciformis* as “the most primitive surviving species” and a “primitive relict”. A relict species is a species with an old age estimate that persists despite the extinction of close relatives (Stebbins and Major 1965). A McMahon and Hufford (2004), McMahon (2005), and Pineros-Urrego et al (2023) resolve *Dalea* as paraphyletic with *Dalea filiciformis* grouping with a clade of *Marina* species and *Dalea* samples as sister to the *Marina* plus *D. filiciformis* clade. Our goal in this study is to firmly resolve the phylogenetic relationship of *Dalea filiciformis* with species of *Marina* and determine whether it derived from within the *Marina* clade or is sister to it.

## MATERIALS AND METHODS

### ***Taxon Sampling***—

*Dalea* comprises five subgenera: *Psoropteris* Barneby, *Theodora* Barneby, *Dalea*, *Parosela* (Cav.) Barneby, and *Asprolea* Barneby (Barneby 1977). *Dalea filiciformis* belongs to the monotypic subg. *Psoropteris*. *Marina* comprises sect. *Marina* with 32 species and sect. *Carroa* (K.B.Presl) Barneby with 8 species (Barneby 1977). *Psorothamnus* includes four species now that five species are now recognized in the recently resurrected *Psorodendron* (Pineros et al 2023). DNA samples come from all these taxa with the exception of the monotypic *Dalea* subg. *Asprolea*, represented by the rare Oaxacan *Dalea trifoliata* Zuccarini. In addition to these daleoid samples, one amorphoid sample representing *Amorpha californica* var. *napensis* was used as an outgroup.

***DNA Extraction, Amplification and Sequencing —***

DNA was isolated from field collections of silica-dried leaf material and herbarium specimens using Qiagen DNeasy Plant Mini Kits (Qiagen, Valencia, CA, USA). Libraries were prepared in the Evolutionary Genetics Laboratory in the Museum of Vertebrate Zoology at UC Berkeley using the KAPA hyper-prep protocol. Qubit dsDNA BR (broad range) Assay Kit (Thermo Fisher Scientific, Waltham, MA, USA) was used to quantify DNA fragments. DNA fragments were diluted before sonication. A QSonica was used for fragmentation, set at 40% amplitude, 15-15 pulse for 2:30 minutes. Most DNA isolates were extracted from degraded herbarium specimens and already sufficiently fragmented and near the ideal range of 300-500 bp. Double-sided size selection was performed, followed by end repair, A-tailing, and adapter ligation. Indexing PCR attached samples to identifiable indexes. Samples were again quantified using a Qubit dsDNA HS (high sensitivity) Assay Kit and some samples were reamplified. Samples were enriched for targeted capture of hundreds of low-copy nuclear loci using the Angiosperms353 bait set (Johnson et al 2019), which was purchased from Arbor Biosciences (Ann Arbor, MI, USA). Libraries were pooled and whole genome shotgun sequencing of enriched multiplexed libraries was performed on a single lane of an Illumina HiSeq4000 at GeneWiz (South Plainfield, New Jersey).

***Assembly and Phylogenetic Inference —***

Raw sequences were assembled using de novo and reference guided assembly in the software program HybPiper (Johnson et al 2016). Sequences were aligned in data matrices using MAFFT (Kazutaka 2019). Densely sampled phylogenetic trees using a maximum likelihood (RaxML, Stamatakis 2014), a Bayesian (EXABayes, Aberer et al 2014), and pseudocoalescent

(ASTRAL-III, Zhang et al 2018) approaches were inferred. Winitsky (Chapter 1) provides great detail to the settings of the used in this study.

### ***Fieldwork* —**

The first and second authors conducted fieldwork a region of gypsum outcrops in the vicinity of Galeana, Nuevo Leon, Mexico, where *Dalea filiciformis* is abundant. This fieldwork provided the opportunity to compare other gypsophile species of *Dalea* with *Dalea filiciformis*. The second author has published multiple new species within the daleoid clade (Estrada et al 2004, 2008, 2011, 2014, 2016, 2020) and collected additional *D. filiciformis* populations used in this study.

### ***Herbarium Studies* —**

Select herbaria with holdings of important historical and recent collections of *Dalea filiciformis*, specifically ARIZ, CAS, MOBOT, RSA, SDNHM, UC/JEPS, UCR, were targeted for analysis of morphological variation within this species, especially regarding morphologies that vary along a north-south gradient. Comparisons of traits considered by Barneby (1977) to be evolutionarily significant among daleoid Amorpheae genera and sections were made for *Dalea filiciformis*, *Marina*, and *Dalea* (Table 1).

### ***Climatic Comparisons Among Genera of Daleoid Amorpheae* —**

To determine how the habitat of *Dalea filiciformis*, as proxied by 19 standard bioclimatic variables (O'Donnell and Ignizio 2012), differed from the other four genera of daleoid Amorpheae, we analyzed 14,865 herbarium collections of daleoid Amorpheae genera. This included 176 vetted herbarium localities for *Dalea filiciformis*, 1124 vetted herbarium localities for *Marina* species, 9960 GBIF-cleaned herbarium localities for *Dalea* species (other than *Dalea*



*filiciformis*), 2021 GBIF-cleaned herbarium localities for *Psorodendron*, and 1584 GBIF-cleaned herbarium localities for *Psorothamnus*. Vetting localities for collections of *Dalea filiciformis* and all *Marina* species was undertaken by the first author. GBIF-cleaned herbarium localities were obtained using R (R Core Team 2023) and the R library *rgbif* (Chamberlain 2017).

## RESULTS

### ***Phylogenetics* —**

Phylogenies based on a concatenated data matrix of 1,452,811 base pairs of orthologous nuclear loci were congruent at almost all nodes and highly supported using both maximum likelihood (ML) and Bayesian inference (BI) approaches. High clade support was consistently revealed among these different approaches for the clades corresponding to daleoid Amorpheae genera, in addition to the clade of *Dalea filiciformis* samples (Fig. 1). Little incomplete lineage sorting (ILS) and discordance across species was detected by the pseudocoalescent method employed (Fig. 1) and at the generic level there was no gene tree discordance across the nuclear loci used.

Our phylogenomic analysis resolved with high clade support the conspecific accessions of *Dalea filiciformis* and the congeneric samples for each of *Marina* and *Dalea* (with *D. filiciformis* excluded). Our samples of *Psorodendron*, form a clade that is sister to all other daleoid Amorpheae. Samples of *Psorothamnus*, form a clade that is sister to the clade comprising *Dalea filiciformis*, *Marina*, and *Dalea*. We resolved all these relationships with high clade support (Fig. 1).

### ***Morphology* —**

Our review of the morphological evidence is consistent with taxonomic history in that *Dalea filiciformis* exhibits few if any of the consistently present synapomorphies that are used to identify the genus *Marina* (Table 1). Furthermore, *Dalea filiciformis* shares what could be considered derived character states with species of *Dalea* (Fig. 2). The most visible of these are the spiral hairs of all *Dalea* species including *D. filiciformis* that are most conspicuous on the foliage and calyx, which dry a tawny or yellowish color (fulvescent trichomes; Fig. 2D). Such hairs are not found in other genera of Amorpheae, which like all species of *Marina*, have straight basifixed hairs that remain unchanged when dry on herbarium specimens.

In contrast to *Dalea filiciformis* (Fig. 2), all *Marina* species have leaflets where the upper surface is marked by epidermal glands that are confluent into sinuous pallid lineoles, which ascend obliquely from the midrib. All other Amorpheae, including *Dalea filiciformis* and indeed all *Dalea* species, have leaflets with epidermal glands often densely arranged but that are not confluent into lineoles (Fig. 2C). All Amorpheae including *Dalea filiciformis* produce an ovary with 2 collateral ovules (exceptionally 3-7), whereas *Marina* species produce an ovule with 1 ovule. All *Dalea* species including *D. filiciformis* have prominent rib-like venation on the calyx tube that is continuous along the midrib from the tube to the tip of the calyx lobe and then continuous with the prominent marginal veins of the calyx lobes (Fig. 2D). All *Marina* species also have a calyx with prominent venation but the ribbed veins on the calyx tube fade out soon after reaching the calyx lobe. In sum, including *Dalea filiciformis* within the genus *Marina* would result in a genus phenotypically undiagnosable especially regarding apomorphic character states.

## TAXONOMIC TREATMENT

*New Combinations—*

CAMOUFLEUR S.E. Winitzky & E. A. Estrada gen. nov. *Dalea* subg. *Psoropteris* Barneby,  
 Memoirs of the New York Botanical Garden, 27: 147. 1977 (Leguminosae, Papilionoideae,  
 Amorpheae, daleoid Amorpheae)

Mainly subshrubs but also shrubs and herbs, in any case mature plants branching in broom-like fashion. Leaves pinnately compound with leaflets minutely pallid-dotted but dots never confluent into lineoles. Hairs of foliage and calyx spirally twisted and drying tawny to yellowish. Inflorescences of loosely-flowered ascending racemes. Flower enveloped by clasping membranous bracts, with five petals of which the wing and keel petals (the two inner pairs) are epistemonous. Calyx pedicellate, with teeth elongate and plumose, ribs confluent distally into a gallery of pointed arches, the point of each arch leading to a calyx tooth and excurrent as a conspicuous mucro. Keel blades imbricately adherent into a conventional keel enclosing the anthers at dehiscence, gland sprinkled but lacking a gland cluster at junction with claw. Ovary with two collateral ovules. Pod charged on either face with 2 distinct crescents of blister-glands (like that of *Marina*). Diagnosis distilled from Barneby (1977) and herbarium studies.

Typus Generis: *Camoufleur filiciformis*

CAMOUFLEUR FILICIFORMIS comb. nov. (Robins. & Greenm.) S.E. Winitzky. *Dalea filiciformis*

Robins. & Greenm., Proc. Amer. Acad. 29: 382. 1894. TYPE: MEXICO. Mexico, San Luis Potosi, Villar, "Collected upon limestone hills," 14 September 1893, *C. G. Pringle 5472* (holotype: GH, photo!; isotypes: none).

*Parosela filiciformis* (Robins. & Greenm.) Rose, Contrib. U. S. Nat. Herb. 8: 303. 1905.

*Marina filiciformis* (Robins. & Greenm.) Piñeros-U. & F. González, comb. nov. *Caldasia* 45, no. 1 (2023).

Herbaceous, suffruticose, or (southward) becoming shrubby and up to 2 m tall, when herbaceous the stems rarely over 5 dm long, dying back yearly to the crown of a taproot up to 3 cm diam, when shrubby, branching and broomlike, glabrous to the pedicels, the young stems purplish or glaucescent, densely micro-tuberculate, the old wood gray and furrowed, the foliage greenish-glaucous, the thick-textured leaflets dotted or pustular beneath; *leaf-spurs* 0.2-1 mm long; *stipules* narrowly subulate, livid, 0.3-1.5 mm long, deciduous; *intrapetiolar glands* 0 or minute, impressed; *post-petiolar glands* small, impressed or scarcely prominent; *main cauline leaves* 1.5-4 (4.5) cm long, shortly petioled or sessile, with subterete, narrowly grooved, punctate rachis and (11) 13-29 orbicular, ovate, broadly oblong-ovate, or cordate, emarginate or very obtuse, flat leaflets 1-3 mm long; *peduncles* leaf-opposed and terminal to the main stem and (when present) some lateral branches, (1) 2-12 cm long; *spikes* racemiform, always laxly often remotely (5) 8-20-flowered, the flowers ascending on erect, hirsutulous pedicels 0.6-1.2 mm long, the glabrous axis becoming 3 - 20 ( 27) cm long, the flowers elevated well beyond the leafy parts of the stem; *bracts* broadly ovate-acuminate, spathaceous, submembranous, wrapped around the young flower-buds but thrown off long before anthesis, commonly livid or purplish about the obscure keel, brownish or pallid toward the margins, glabrous and gland-sprinkled dorsally, glabrous within, sometimes minutely puberulent at tip; *calyx* jointed to the pedicel, deciduous with the pod, 6.7-10 mm long, a little accrescent after early anthesis, hirsute with straight, lustrous, spiral hairs up to 1-1.8 mm long, the shallow tube 2.2-3 mm long, a little oblique at mouth, the ribs prominent, often purplish, the submembranous intervals charged with

3-5 uniseriate, orange or livid blister- glands, the narrowly lance-acuminate or -caudate, 1-2 (3)-spurred, plumose teeth unequal, the dorsal one longest, (3.7) 4-7.6 mm long, all  $\pm$  stellate in age; *petals* concolorous or nearly so, commonly opening dull pinkish-purple or lavender, drying brownish or livid, rarely soft blue drying brown, all coarsely many-veined (the veins branching distally), the blade of the banner gland-sprinkled, those of wings and keel glandless (or the latter with a few small glands on blade, or one at apex, or both), the inner ones elevated only 0.5-1.5 mm above the hypanthium; *banner* 4.1-6.2 mm long, the claw (1.5) 1.8-2.5 mm, the spade-shaped, commonly acute blade open at base, 3-4.6 mm long, 2.8-4 mm wide; *wings* 5.1-6.6 mm long, the claw 1.5-2 mm, the obliquely ovate, obtuse blade 3.6-5 mm long, 2.2-3.6 mm wide; *keel* 7.3-11.3 mm long, the claws 2.6-3.3 mm, the broadly ovate-elliptic blades (4.8) 5.2-8.8 mm long, (3) 3.2-5 mm wide; *androecium* (6.6) 7.5-10 mm long, the longest filament free for (2.9) 3.2-4 mm, the bluish, gland-tipped anthers 1-1.35 mm long; *pod* harp-shaped, strongly compressed, 3-3.5 mm long, the style-base lateral or latero-terminal, the dorsal keel slender but distally prominent, the valves submembranous and glabrous proximally, papery and hirsute distally, charged with blister-glands arranged in 2 oblique crescents; *seed*  $\pm$  2.6 mm long;  $x = \pm 8$  (Rice et al 2015; Fig. 4).

***Etymology***—Camoufleur means to hide or disguise, referring to both the genus' mix of apomorphic characters, but also its ability to blend into its surroundings – despite growing in open landscapes. The specific epithet filiciformis refers to fern-shaped, presumably of the leaves, perhaps likened to the fronds of some *Pellaea* species.

***Additional Specimens Examined*** – **Mexico.** – TAMULIPAS: 10 km al SW de Altamira, *Sandoval 1966* (MO) NUEVO LEON: San Francisco, *Hinton 22696* (ARIZ), Santa Rita, *Hinton*

18169 (MO), El Charco, *Fishbein* 2956 (ARIZ). SAN LUIS POTOSI: Ojo de Agua de García, *McVaugh* 18210 (MO), Minas de San Rafael, *Purpus* 4834 (MO, UC), Cedral *Ripley & Barneby* 13,296 (UC, CAS), *Johnston* 7585 (UC), Matchuala, *Henrickson* 6635 (RSA), Matchuala, *Shreve* 8704 (ARIZ), Vallejo, *Ozment* 664 (MO) ESTADO DE MEXICO (D.F.): Lomas, *Lyonnet* 354 (MO), Santa Fe, *Pringle* 8522 (UC), Mpio. de Huixquilucan, *Rzedowski* 30415 (ASU), *Rzedowski* 25891 (ARIZ). MORELOS: Moyotepec, *Ripley & Barneby* 13,704 (CAS). PUEBLA: Molcaxac, *Gonzalez* 12426 (MO), Tehuacan, *Sousa* 6171 (ARIZ), *Purpus* 1204 (UC), *H. S. Gentry* 20368 (ARIZ), Izucar de Matamoros, *Ripley & Barneby* 14,569 (CAS), Axusco, *Dorado* 1820 (RSA), Acatzinco, *Amable* 3570 (MO). OAXACA: Tamazulapam, *Ripley & Barneby* 13,655 (CAS), *Lavin* 5174 (MO), San Pablo Huitzo, *Ripley & Barneby* 14,659 (CAS), Huajuapán de León, *Breedlove* 59675 (MO), *Breedlove* 39204 (MO), *Sousa* 12458 (MO) HIDALGO: Barrancas de Tolantongo, *Magana* 6231 (MO), El Salto, *Pringle* 11959 (MO). AGUASCALIENTES: Aguascalientes, *Rose* 7706 (NY).

#### KEY TO THE FIVE DALEOID GENERA (AMORPHEAE, FABACEAE)

1. Flower papilionaceous and with five well developed petals, the inner pairs of which (the keel and wing petals) are inserted on the rim of the hypanthium like the banner petal.

2. Flowers sessile; pods enclosed or mostly so within the calyx *Psorothamnus*

2. Flowers pedicellate; pods exserted or mostly so from calyx *Psorodendron*

1. Flower papilionaceous or appearing somewhat radial or with some petals reduced, the inner pairs of which (the keel and wing petals) are perched on the staminal column; if one or both inner pairs of petals lacking, then the plant annual.

3. Ovary with a solitary ovule; ribs of calyx not confluent distally into pointed arches produced into a mucro or subulate to caudate tooth but tapering out into a flat, herbaceous blade and appearing externally in the form of alternating I and Y; leaflets, always above and usually both sides, marked with sinuous, pallid lineoles ascending from the midrib at an oblique angle *Marina*
3. Ovary with 2 collateral ovules (but only one maturing into a seed); ribs of calyx commonly confluent distally into a gallery of pointed arches, the point of each arch leading to a calyx-tooth and excurrent as a distinct mucro (if this is obscure then calyx strictly sessile); leaflets green or minutely pallid-dotted, but the dots never confluent into lineoles.
4. Calyx sessile or pedicellate; inflorescence usually spicate but also short racemose; pod on either face with blister-glands not arranged as 2 distinct crescents *Dalea*
4. Calyx pedicellate; inflorescence loosely flowered and long racemose; pod on either face bearing 2 distinct crescents of blister-glands *Camoufleur*

## DISCUSSION

Conspecific sampling of *Camoufleur filiciformis*, a vast increase in informative genetic data relative to earlier studies, and agreement across methods of phylogenetic inference allows for a confident taxonomic placement of *Camoufleur filiciformis*. We argue that *Camoufleur filiciformis* is overall ecologically, geographically, and phenotypically most like the genus *Dalea*, in agreement with Barneby's (1977) classification. Yet our phylogenetic results agree with McMahon and Hufford (2004) and McMahon (2005) that *Camoufleur filiciformis* is most closely related to *Marina*. Our phylogenomic analysis of hundreds of nuclear loci strongly resolved

*Dalea filiciformis* as sister to *Marina*, and not nested within it (Fig. 1). Furthermore, our phylogenomic results resolve a coalescent clade of all conspecific accessions of *Camoufleur filiciformis*, which suggests that this species has attributes perhaps involving a combination of a geologically old age, a historically low effective population size, and having consistently low ploidy levels of its genome (e.g., Naciri and Linder 2015; Lavin and Pennington 2022). These results suggest *Camoufleur filiciformis* has indeed retained many plesiomorphic daleoid Amorpheae traits, as enumerated by Barneby (1977) and lacks many of the traits that apomorphically diagnose *Marina*, such as leaflets with both surfaces bearing epidermal glands in lineole fashion and flower each with a calyx with continuous venation and an ovary with one ovule. Because of the ecological, geographic, and phenotypic similarity of *Camoufleur filiciformis* to species of *Dalea*, and its strongly supported sister relationship with *Marina*, we opt to segregate *Camoufleur filiciformis* as its genus to emphasize, as did Barneby (1977), its taxonomically isolated position within the *Dalea-Marina* clade.

### ***Cytological Differences—***

Barneby (1977) relied heavily on base chromosome numbers to reconstruct his scheme of higher-level relationships among genera and infra-generic taxa of daleoid Amorpheae. Especially noted by Barneby was the base chromosome number of *Camoufleur filiciformis*,  $x=8$ , that matched counts found among some *Dalea* species but that differed from the counts of base chromosome numbers made for *Marina* species,  $x=10$ . Indeed, a base chromosome number of  $x=10$  was found for species of *Psorothamnus* (including *Psorodendron* in Barneby 1977) so the aneuploid reduction suggested by base chromosome counts of  $x=7$  and 8 in *Dalea* provided evidence for retaining *Camoufleur filiciformis* in *Dalea*.



Since Barneby (1977), many more base chromosome numbers are now available. Of the 84 *Dalea* species sampled so far, 67 species have a base count of  $x=7$ , five species have a base count of  $x=8$ , and this includes *Camoufleur filiciformis*. Three species of *Dalea* are apparently tetraploid with a base count of  $x=14$  (Rice et al. 2015). Ten species of *Marina* have a base count of  $x=10$  and nine accessions of *Psorothamnus arborescens* var. *minutifolius* have a base count of  $x=20$  (Rice et al 2015). These additional chromosome numbers essentially support Barneby's (1977) classification of *Marina* to exclude *Camoufleur filiciformis*.

### ***Ecological Differences—***

Many *Dalea* species including *Camoufleur filiciformis* grow on gypsum (Fig. 3), but no *Marina* demonstrate a predilection for this substrate (e.g., as measured by an increase in abundance on gypsum) or show evidence of being restricted to gypsum. The rosette scrublands of northeastern Mexico and the gypsum grasslands of the Mexican state of San Luis Potosi have been identified as hotspots of endemism that should be prioritized for conservation (Sosa and De-Nova 2012). These areas harbor many narrowly distributed *Dalea* taxa. Many *Dalea* species inhabit gypsum outcrops and grasslands that can be dominated also by *Camoufleur filiciformis*. Certain *Dalea* species are known as calciphiles from throughout their range, whereas other *Dalea* species are known from sites with or without gypsum. *Dalea* thus includes both obligate and facultative gypsophiles (or gypsoclines; Meyer 1986). The following *Dalea* species are known predominantly from gypsum: *Dalea neomexicana* var. *megaladenia* Barneby, *Dalea eriophylla* S. Watson, *Dalea radicans* S. Watson, *Dalea nana* var. *carnescens* (Rydb.) Kearney & Peebles, *Dalea parrasana* Brandege. During fieldwork in the gypsum outcrops of the Galeana district of Nuevo León, Mexico, many *Dalea* grew sympatrically with *Camoufleur filiciformis*, including

*Dalea hospes* (Rose) Bullock, *Dalea melantha* S. Schauer var. *melantha*, *Dalea saffordii* (Rose) Bullock, and *Dalea gypsophila* Barneby, the last of which is locally endemic to Galeana and restricted to gypsum. Johnston (1941) noted that if the soil contained enough gypsum such that the substrate was mostly white, gypsophiles including *Camoufleur filiciformis* could be found. However, if there was over an inch of non-gypsum soil, known gypsophiles tended to be absent (Johnston 1941). Johnston (1941) noted that populations of *Camoufleur filiciformis* not growing on gypsum from Puebla (one of which is included in the phylogeny here) had morphological distinctions and perhaps should be recognized as a distinct taxon. Moore (2014) notes that gypsum communities are often independently derived from local taxa, which follows the pattern here with the *Dalea*-rich gypsum outcrops of northwest Mexico emerging within a center of diversity for the genus. Gypsum plant communities often include clades of closely related species, exemplified by species of *Mentzelia* sect. *Bartonia* and *Nama* (Moore 2014). This is true of *Dalea* with most gypsum tolerant taxa belonging to subgenus *Parosela*.

Of the gypsophile species of *Dalea*, *Camoufleur filiciformis* has the widest geographic range, but commonly restricted to gypsum across that range. Johnston (1941) noted that *Camoufleur filiciformis* when not growing on gypsum soils phenotypically differs from forms growing on gypsum. Whether this represents ecotypic or taxonomic variation is yet unknown. Our herbarium studies of *Camoufleur filiciformis* from throughout its geographical distribution reveals high levels of ecological and morphological variation that somewhat correspond to populations restricted to gypsum versus those found inhabiting other substrates. The taxonomic implications of this will be the focus of future research.

*Intraspecific Variation* —

Throughout its geographic range *Camoufleur filiciformis* grows in open grasslands, but its edaphic preferences change throughout its distribution. North of the Trans-Mexican Volcanic Belt, *Camoufleur filiciformis* is most common on gypsum substrates and occasionally on limestone. Southwards in Oaxaca and Puebla, *Camoufleur filiciformis* grows on diverse substrates and appears to have little edaphic affinity. Morphological differences among herbarium specimens of *Camoufleur filiciformis* represent mostly population variation found along this north-south gradient where gypsum and limestone predominate to the north.

Morphological differences between northern and southern populations include plant growth habit. Plants from the northern part of the range are herbaceous with stems dying back each year. Plants from the south retain their stems year after year and mature into shrubs. Generally plants within the same species do not vary in this way, and deeper investigation into taxonomic boundaries is warranted. Plants on gypsum have a thick taproot, whereas plants from the south have a branching root system. In the north, plants produce flowers with rose to purple petals; in the south, plants have flowers that produce pink petals with brown veins to blue petals with dark blue veins. Petal color, however, is difficult to assess on herbarium specimens because most light-colored petals fade to brown. Specimens representing the northern morph include *Ripley & Barneby 13,296* (UC), *Henrickson 6635* (RSA), *Purpus 4834* (MO,UC), *Hernandez 6231* (MO), *Hernandez 01966* (MO), *Rose 7706* (NY), *Pringle 8522* (UC), *Johnston 7585* (UC), and *Pringle 11959* (UC). In addition to the above, southern populations of *Camoufleur filiciformis* tend to have smaller flowers and leaves with fewer leaflets. Specimens representatives of the southern morph include *Dorado 1820* (RSA), *Breedlove 39204* (CAS), *Sousa 12458* (MO), *Breedlove 59875* (CAS) and *Lavin 5174* (MO). Specimens representing a

combination of the northern and southern morphs include *Hinton 18169* (MO), *McVaugh 18210* (MO), *Ozment 664* (MO), and *Purpus 1204* (UC). The phylogeny showing relationships among conspecific samples of *Camoufleur filiciformis* resolves no pattern consistent with northern versus southern samples so perhaps ecotypic variation explains the northern versus southern morphs.

### ***Geographical Distribution* —**

(Fig. 5) Arid grassy flats, gullied knolls and barren, eroded hillsides, sometimes in crevices of cliffs or shelving rock-faces, 1410-2210 m ( $\pm$  4700-7370 ft), on a variety of soils but mostly on gypsum and limestone, less often on mixed alluvia, volcanic ash, and perhaps other porous soils, local but widespread over the arid lands of the Mexican Plateau from Galeana district in the Sierra Madre Oriental, Nuevo Leon, to southeastern Durango, south to the Valley of Mexico (Estado and Distrito Federal), and throughout the desert valleys of Puebla and adjoining Morelos to the north and central Oaxaca to the south.

*Camoufleur filiciformis* is ecologically and geographically distinguished from other Amorpheae genera with its predilection to open dry habitats in central Mexico, as described above. The amorphoid subclade of tribe Amorpheae includes three monotypic genera: *Parryella*, *Apoplanesia*, and *Pictarena*. *Parryella* and *Pictarena* inhabit the arid southwestern USA just north of the Mexican border (Polhill 1981; Becklund and Ayers 2022), whereas *Apoplanesia* inhabits seasonally dry tropical forests of southern Mexico and adjacent Central America (e.g., Polhill 1981). *Errazurizia* species diversity is centered outside of mainland Mexico in southwestern USA, the Baja California peninsula, and northern Chile. *Amorpha* is most abundant and diverse north of Mexico at northern latitudes in the USA and Canada. *Eysenhardtia* is most

abundant and species diverse in Mexico and adjacent USA, but *Eysenhardtia* is generally inhabits seasonally dry woodlands and forests.

Among the daleoid Amorpheae, *Psorodendron* with five species occurs in the Baja California peninsula, the Sonoran Desert, and disjunct in the northern Great Basin.

*Psorothamnus* with four species occurs mainly in the Chihuahuan and Sonoran Deserts, and the Great Basin. *Dalea* comprises 192 species (LPWG 2021) distributed throughout all of Mexico and extending northwards into the southwestern Canadian prairies and south into Central America especially in pine-oak woodlands. A second *Dalea* radiation occurs in the mid elevation Andes and inter-Andean valleys of Peru, Bolivia, Ecuador, and Colombia with a few taxa reaching northern Chile and Argentina. A high level of species diversity of Mexican *Dalea* is underscored by 18 *Dalea* species having been newly described since 2000, six of these in Mexico by Estrada et al. (2004, 2008, 2011, 2014, 2016, 2020). We note that *Dalea* (like *Marina*) includes a species or two that have become naturalized beyond their historic ranges (e.g., Cuba and Venezuela). *Marina* is the second most diverse Amorpheae genus, and its 40 species all occur in Mexico, with four them extending into the southwest USA, three into Central America. Many *Marina* species and varieties are found in close geographic proximity, with many of these with overlapping geographic distributions especially in the Sierra Madre Occidental and the Baja California peninsula. *Marina* species are notably lacking from the northern Sierra Madre Oriental, where *Camoufleur filiciformis* is common on gypsum outcrops. *Marina* and *Camoufleur filiciformis* geographically overlap only in the Mexican states of Puebla to Oaxaca.

Comparisons of 19 standard bioclimatic variables (O'Donnell and Ignizio 2012) taken from herbarium localities for 14,865 specimens generally showed that the five genera of daleoid Amorpheae occupy different elevational zones and therefore climatic regimes, but that *Camoufleur filiciformis* accessions occupy sites that are climatically more similar to *Dalea* accessions than to *Marina* accessions. *Camoufleur filiciformis* accessions (n = 176) average close to 2000 m in elevation, whereas *Dalea* accessions (n = 9960) occupy sites just over 1000 m and the other daleoid Amorpheae genera occupy sites less than 1000 m (Fig. 6). This likely relates to *Camoufleur filiciformis* accessions occupying sites with precipitation regimes that are more similar to *Dalea* than to *Marina*. For example, *Camoufleur filiciformis* and *Dalea* accessions do not differ with respect to bioclimate variables such as mean annual precipitation (#12; O'Donnell and Ignizio 2012), precipitation of wettest month (#13), precipitation of wettest quarter (#16), and precipitation of warmest quarter (#18), in addition to mean temperature of wettest quarter (#8). In contrast, because *Marina* tends to occupy low elevation drier and hotter sites, *Camoufleur filiciformis* accessions show less climatic similarities with *Marina* accessions. The three bioclimatic variables that are similar among localities for *Camoufleur filiciformis* and *Marina* accessions include minimum temperature of coldest month (#6), mean temperature of coldest quarter (#11), and precipitation seasonality (#15, the coefficient of variation for mean monthly precipitation; O'Donnell and Ignizio 2012). Such climatic similarities of *Camoufleur filiciformis* and *Marina* accessions are trivial because they relate to temperatures during the coldest month or quarter, but this reflects that *Marina* and *Camoufleur filiciformis* accessions do not occur at high latitudes like many other Amorpheae genera. Climatic similarities of *Camoufleur filiciformis* localities with *Dalea* localities are more profound and include mean

annual precipitation. In sum, the combination of an ecological predilection to open dry habitats and a geographical distribution in central Mexico renders *Camoufleur filiciformis* accessions occupying sites that are climatically more similar to *Dalea* than to *Marina* accessions. This parallels what we have described for phenotype.

***Taxonomic History of Camoufleur filiciformis* —**

Although Robinson and Greenman (1894) described *Dalea filiciformis* from an 1893 collection by Cyrus Guernsey Pringle from the Mexican state of San Luis Potosi (Fig. 7), Barneby (1977) noted that a specimen of *Dalea filiciformis* had been collected in 1791 by Tadeusz Hänke “somewhere in southern Mexico.” Given the widespread distribution of this species in central Mexico and its occurrence in and around Mexico City, Barneby wondered why it had not been described earlier.

Barneby considered *Dalea filiciformis* to be the most “primitive” species within the daleoid taxa because it combines the characters he hypothesized to be ancestral within the group: lax raceme, deciduous bracts, five petals, woodiness, a short androecial column, and overlapping keel petals. Due to this unique suite of characters, he put *Dalea filiciformis* in the monotypic subgenus *Psoropteris*. Rydberg found affinities between *Dalea filiciformis* and other taxa, placing it with sympatric *Dalea melantha* var. *berlandieri* (A. Gray) Barneby as well as the Sonoran Desert *Marina calycosa* (A. Gray) Barneby. All of these taxa have similar pedicels, lax racemes, and similar ecological affinities, such as being a strong calciphile (*Dalea melantha* var. *berlandieri*) and preferring rocky outcrops (*M. calycosa*), but these species are not closely related.

Using mostly McMahon and Hufford's (2004) data and results, Piñeros-Urrego et al. (2023) transferred *Dalea filiciformis* into the genus *Marina*. Piñeros-Urrego et al. acknowledged traits recognized by Barneby (1977) that are shared by *Dalea filiciformis* and *Marina* species, including pedicellate flowers and harp-shaped pods with two crescents of blister glands. However, pedicellate flowers occur also in a few *Dalea* species, which belong to different subgroups of the genus (and to species of *Psorodendron* and *Psorothamnus kingii* (S. Watson) Barneby). The morphological character most distinctively shared by *Dalea filiciformis* and *Marina* is the pod with a crescent pattern of glands on either face, but this does not occur in all *Marina* species. Given the paucity of distinctive morphologies shared consistently by *Dalea filiciformis* with *Marina* species, it is not surprising that Barneby ultimately classified *D. filiciformis* into the genus *Dalea*.

### **Conclusion —**

Our phylogenetic results are consistent with those of McMahon and Hufford (2004). However, we clearly resolve *Camoufleur filiciformis* as sister to and not nested within *Marina*. With this phylogenetic result, *Camoufleur filiciformis* clearly cannot remain in the genus *Dalea* if the criterion of monophyly is to be implemented such that a classification of daleoid Amorpheae genera reflects evolutionary history. However, transferring *Camoufleur filiciformis* to *Marina* would dissolve the distinctiveness of *Marina* as a cohesive group whose distinction is supported by visibly conspicuous synapomorphies, in addition to geographic and ecological distinctions. Placing *Camoufleur filiciformis* into the newly described monotypic *Camoufleur* is ultimately consistent with Barneby's (1977) classification and perspective that *Camoufleur filiciformis* represents an evolutionarily and taxonomically isolated lineage among daleoid Amorpheae genera.



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Table 1. Comparing apomorphic traits of *Camoufleur* with those of *Dalea* and *Marina*.

|                                          | Marina                                                                            | Dalea                                         | Camoufleur                                    |
|------------------------------------------|-----------------------------------------------------------------------------------|-----------------------------------------------|-----------------------------------------------|
| Ovule count                              | 1                                                                                 | 2                                             | 2                                             |
| Flowers                                  | Pedicellate                                                                       | Usually sessile                               | Pedicellate                                   |
| Pod glands                               | 2+ distinct crescents of blister-glands in some species, glands various in others | Various                                       | 2 distinct crescents of blister glands        |
| Leaflet glands                           | In sinuous pallid lineoles on upper surface that ascend from midrib               | Dotted (not lineolate)                        | Dotted (not lineolate)                        |
| Calyx ribs                               | Discontinuous distally, ending in calyx lobes                                     | Continuous distally and forming closed arches | Continuous distally and forming closed arches |
| Raceme internodes                        | Loose                                                                             | Dense to loose                                | Loose                                         |
| Chromosome number                        | 10                                                                                | 7 (8 or 14)                                   | 8                                             |
| Vestiture of fulvescent spiral trichomes | Absent                                                                            | Present                                       | Present                                       |

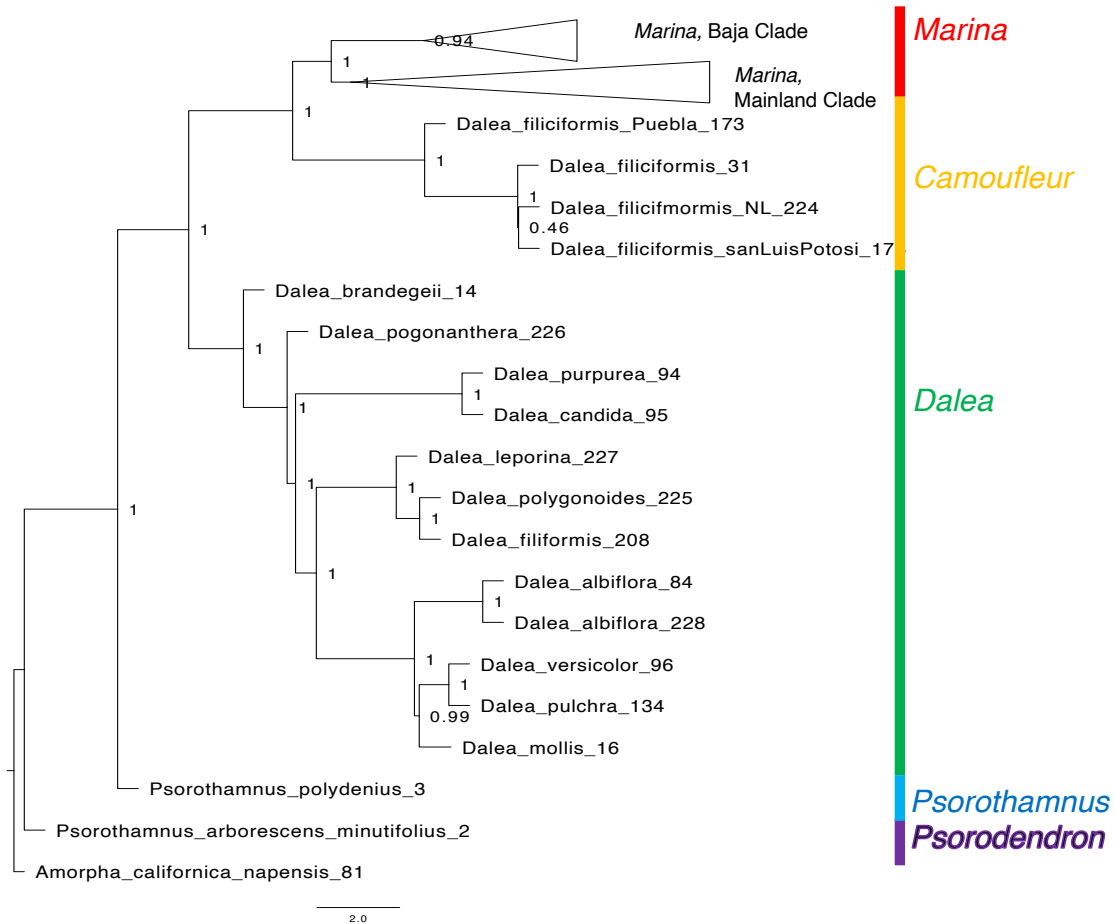


Fig. 1. ASTRAL-III phylogeny derived from a pseudocoalescent approach that uses individual gene trees inferred with RaXML to infer a species tree. All phylogenetic methods reveal strong support for *Dalea filiciformis* as sister to *Marina*.



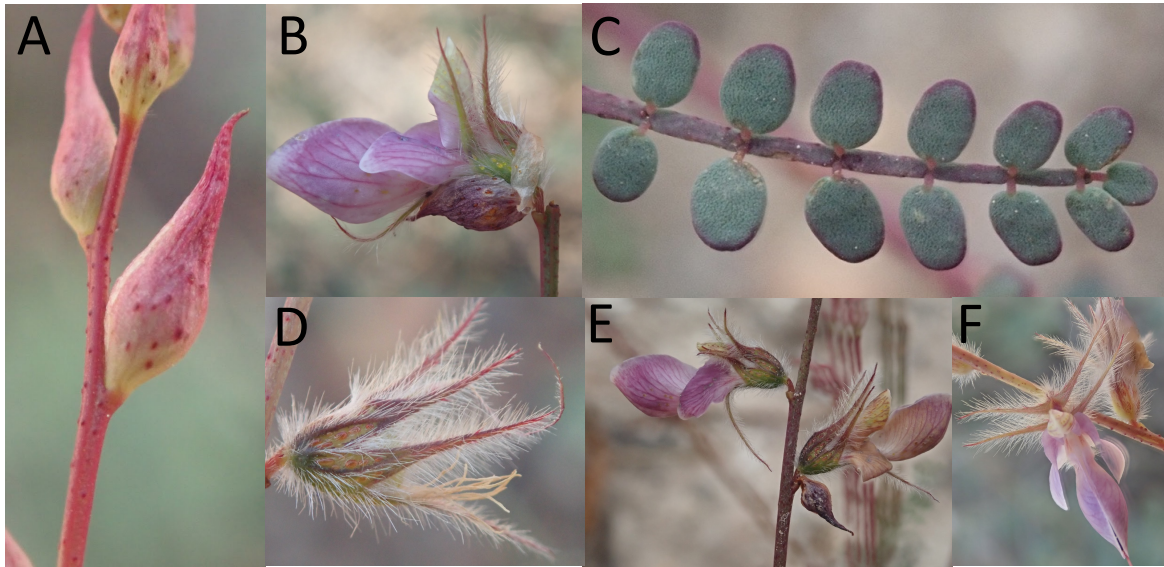


Fig. 2. Diagnostic characters of *Camoufleur filiciformis*. A. Spathaceous floral bracts (3X). B. Nervature of the petals - similar to *Psorothamnus* (3X). C. Fern-shaped leaflets lacking oblique lineoles (3X). D. Spiral hairs that change color when dry. E. Pedicellate flowers born along a loose raceme and calyx with ribs that converge at the calyx lobes. F. Front view of flower illustrating spreading calyx lobes. Photos by S. Winitsky.

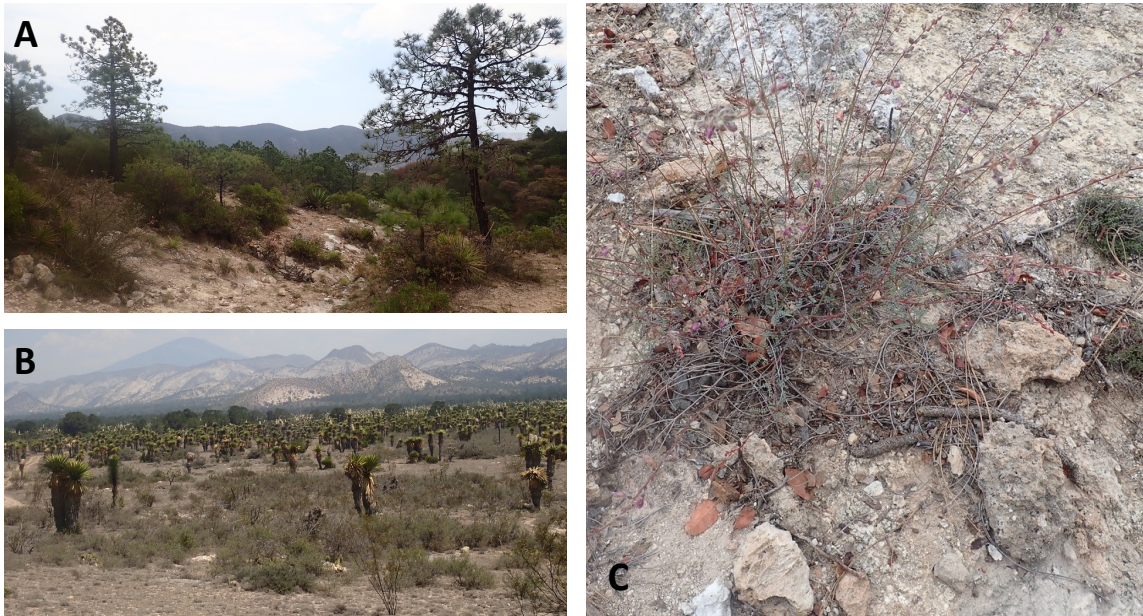


Fig. 3. Main habitat of *Camoufleur filiciformis*. A. Gypsum outcrops (white surface patches) in open understory near Galeana, Nuevo Leon. B. Gypsum outcrops (white surface patches) among stands of *Yucca*, also near Galeana, Nuevo Leon. C. *Camoufleur filiciformis* growing on gypsum, becoming camouflaged when leaflets abscise. Photos by S. Winitsky.

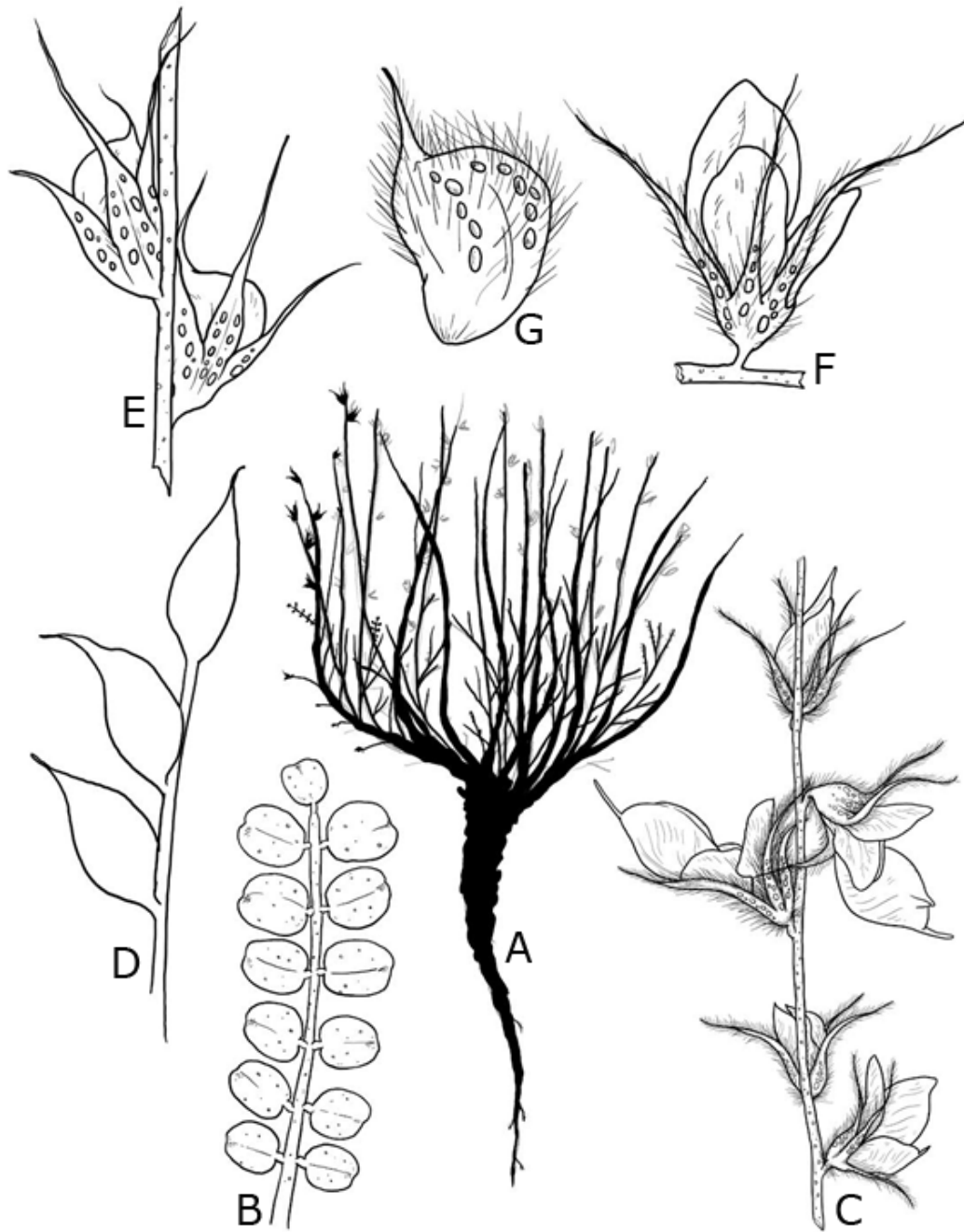


Fig. 4. *Camoufleur filiciformis* (illustration by Nayl Gonzalez). A. Tap-root growth habit (0.1X). B. Leaf (3X). C. Inflorescence section (2X). D. Spatheaceous floral bracts (2X). E. Calyx in fruit (2X). F. Calyx at anthesis (2X). G. Fruit (3X).

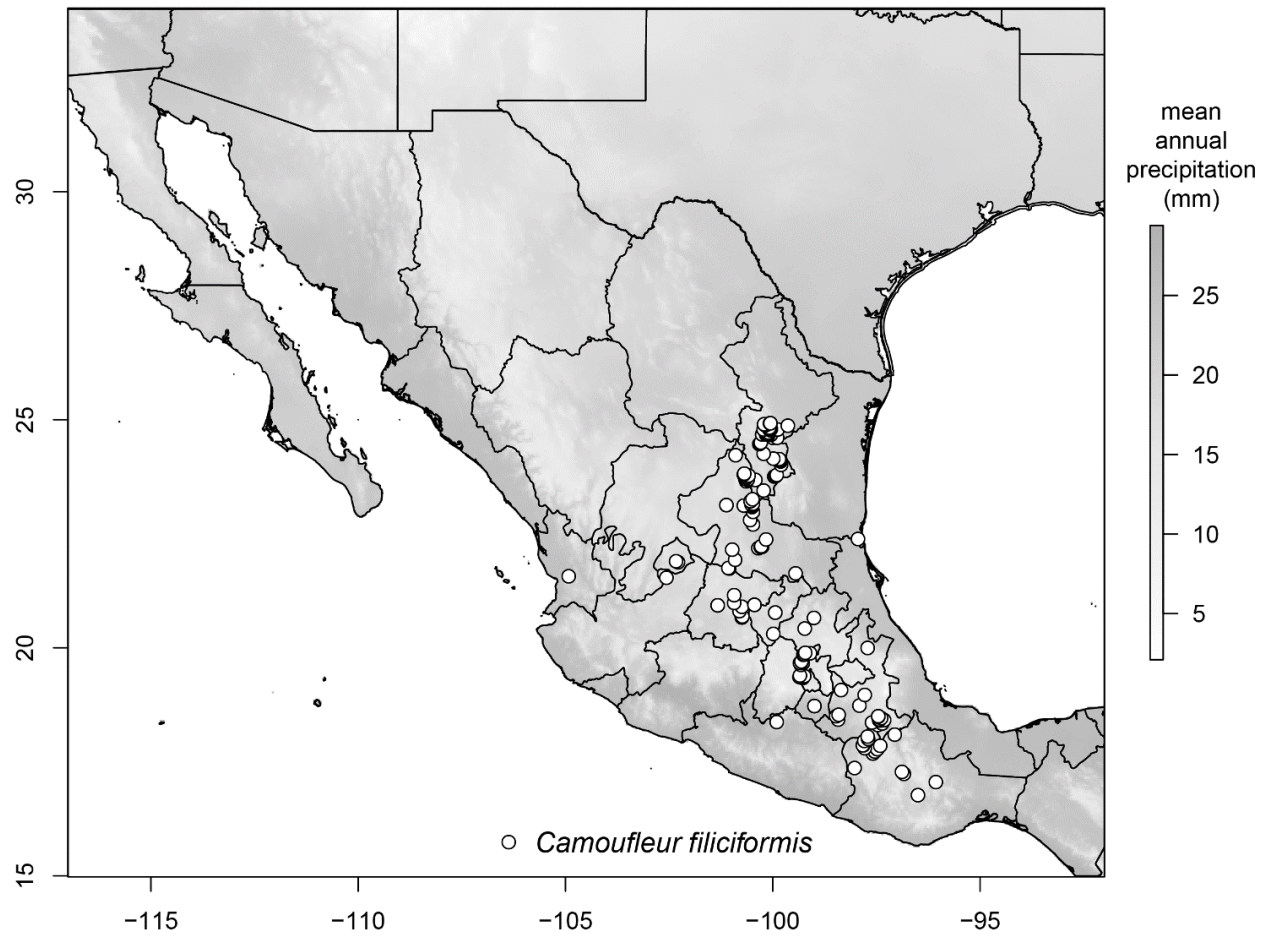


Fig. 5. Geographic distribution of *Dalea filiciformis*, endemic to Mexico from southern Nuevo Leon in the north to central Oaxaca in the south. We derived these site occurrences from 176 herbarium specimens vetted for geographical coordinates.



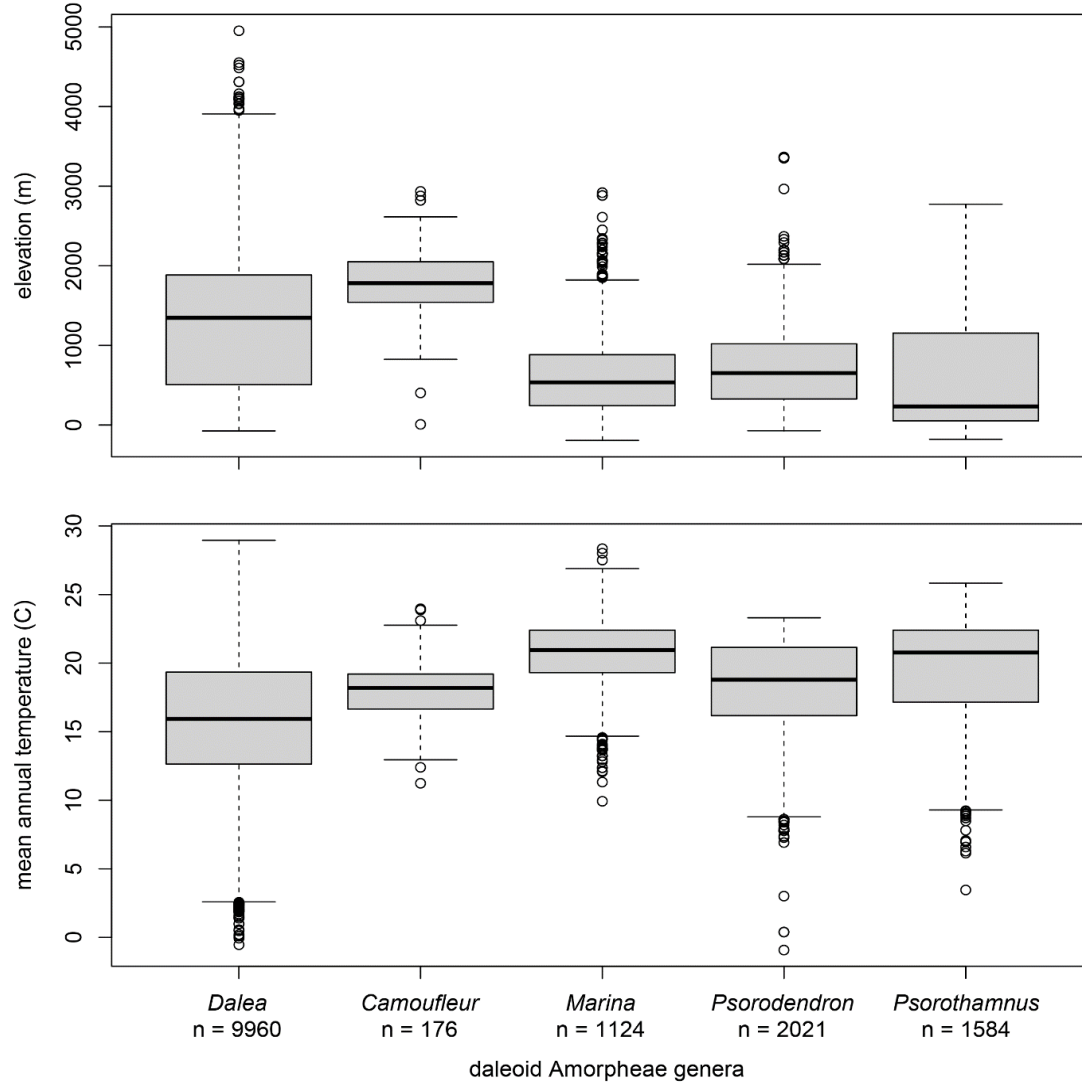


Fig. 6. Comparisons of elevation and mean annual temperature among the genera of daleoid Amorpheae. We obtained these data from vetted geographical coordinates of 14,865 herbarium specimens and occurrence records of daleoid Amorpheae. Top panel. Elevation (m). Bottom panel: mean annual temperature (C). Tukey's Honestly Significant Difference test suggests all pairwise comparisons significantly differ excepting *Marina* and *Psorodendron* for elevation *Camouffleur* and *Psorodendron* for mean annual temperature.

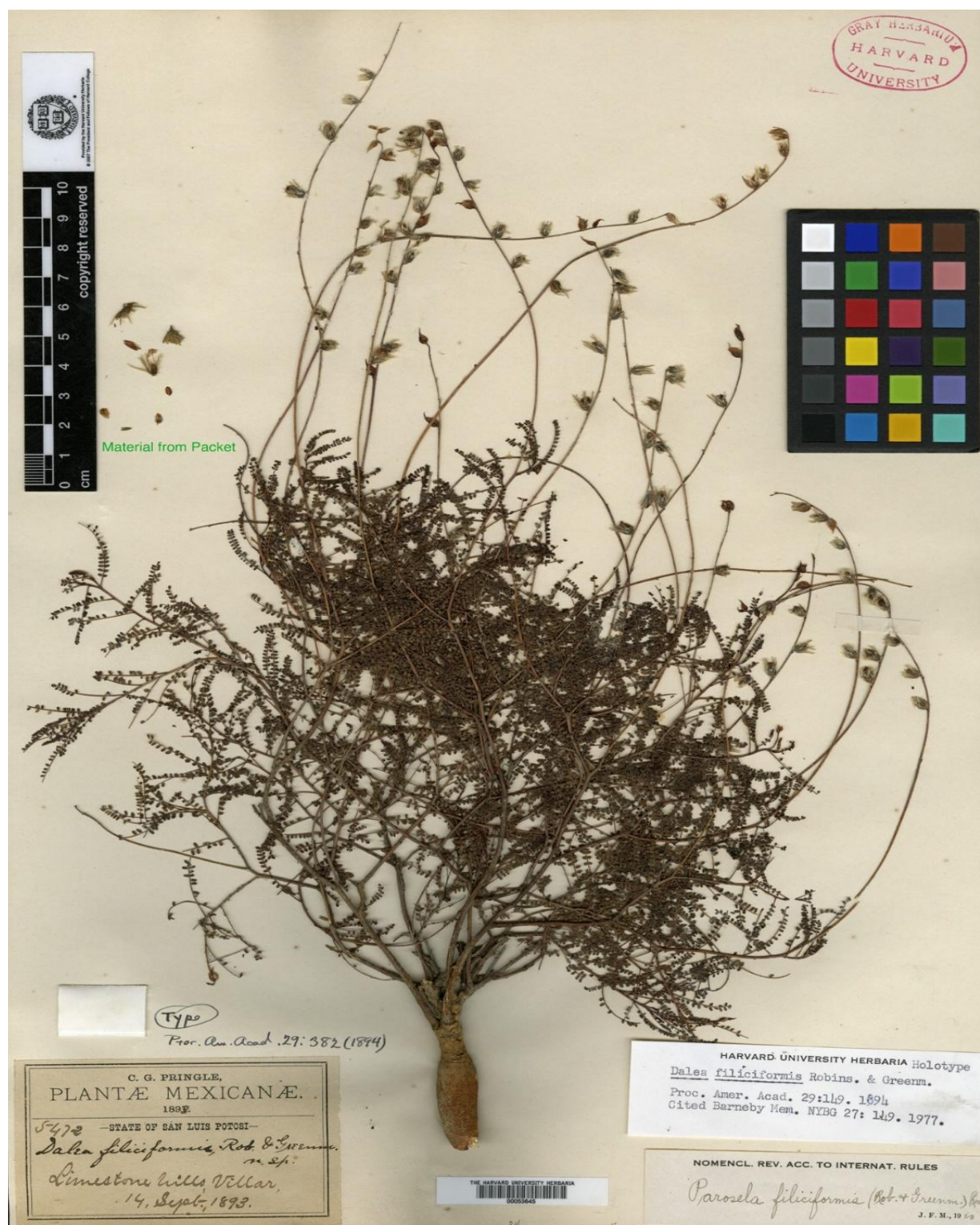


Fig. 7. Type specimen of *Dalea filiciformis* (GH) from San Luis Potosi, Mexico.  
 ([https://kiki.huh.harvard.edu/databases/specimen\\_search.php?mode=details&id=33565](https://kiki.huh.harvard.edu/databases/specimen_search.php?mode=details&id=33565))

SIX NEW SPECIES AND ONE NEW COMBINATION IN THE GENUS MARINA  
(FABACEAE: AMORPHEAE), SERIES CHRYSORRHIZAE FROM BAJA CALIFORNIA  
SUR, SONORA AND SINALOA, MEXICO.

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Manuscript in Chapter Three

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SIX NEW SPECIES AND ONE NEW COMBINATION IN THE GENUS *MARINA*  
(FABACEAE: AMORPHEAE), SERIES CHRYSORRHIZAE FROM BAJA CALIFORNIA  
SUR, SONORA AND SINALOA, MEXICO.

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ABSTRACT:

Five new endemic species and one new combination of *Marina* are described from the Cape Region of Baja California Sur and a single species of *Marina* is described from across the Gulf of California in coastal Sonora and Sinaloa. All seven are in the taxonomic series *Chrysorrhizae*, distinguished by a flower with a gland-sprinkled banner and keel petals longer than the banner, and a fruit with crescentic rows of glands along each valve. The taxonomy of the genus *Marina* has been revisited with phylogenomic target capture methods. Our earlier phylogenomic studies found that multiple species complexes are not resolved as monophyletic, which prompted a reanalysis of morphological, ecological, and taxonomic data. We present phylogenetic, morphological, and ecological support for these newly described taxa as well as a dichotomous key, range map, and botanical photographs or illustrations to aid biologists in their identification. Many of these species are still only known from a few populations and need further fieldwork and surveying to verify that they are indeed narrowly restricted geographically and ecologically. There are historic specimens representing the taxa described here with locality information that should be revisited to assess current population numbers, as well as surveys of suitable habitat that could harbor new populations.

Keywords: Amorpheae, Baja California Sur, Cape Region, endemism, Fabaceae, *Marina*, phylogenomics, Sonora, Sinaloa, taxonomy

*Marina* series *Chrysorrhizae* contains 18 species, which recently have been represented by 72 accessions in a phylogenomic analysis to assess the morphological and geographic diversity within each of these densely sampled species (Winitsky et al. Chapter 1; Figure 1). This study resulted in removing three species from series *Chrysorrhizae*, *Marina procumbens* (Sessé & Moc. ex DC.) Barneby, *Marina orcuttii* (S. Watson) Barneby, and *Marina calycosa* (A. Gray) Barneby. This left series *Chrysorrhizae* restricted to the southwest USA, Sonora, northern Sinaloa, Baja California and with most taxonomic diversity found in Baja California Sur. One widespread *Chrysorrhizae* species, *Marina parryi* (Torr. & A. Gray) Barneby, extends into the Sonoran and Mojave deserts of Arizona, California, and southwestern Nevada.

Two species complexes of Baja California Sur, centered on *Marina divaricata* (Benth.) Barneby and *M. maritima* (Brandege) Barneby, long have been confusing for field botanists. Many populations do not fit the original descriptions of morphology and geographic distributions of *Marina divaricata* and *M. maritima*. *Marina divaricata* has glabrous stems and calyces (Figure 2) and is found in the lowlands and mountains of the Cape region and Magdalena plain. *Marina maritima* has canescent stems and calyces (Figure 3) and is restricted to the immediate coast. Identifications thus far have mostly been based on this glabrous versus canescent distinction, but it has been challenging following Barneby (1977) to morphologically circumscribe any accessions that do not easily fit in one of those categories.

Intermediates between *Marina maritima* and *M. divaricata* were identified by Barneby (1977), who lacked sufficient specimens and locality data to circumscribe additional taxonomic

entities at that time. Decades of subsequent fieldwork (Rebman et al 2016, Leon de Luz et al 1989) revealed additional critical population variation in Baja California species of *Marina*, which warranted a phylogenomic investigation with the intent of improving species circumscriptions and a knowledge of species interrelationships. By testing current species circumscriptions using phylogenomic approaches (Winitsky et al Chapter 1), *Marina divaricata* and *Marina maritima* were found to be polyphyletic (Figure 1). Additionally, we found that populations previously called *Marina peninsularis* (Rose) Barneby from Sonora and Sinaloa represented an overlooked taxon (Figure 1).

By applying a species concept that integrates ecological, genetic, geographical, morphological, and perhaps other kinds of variation into circumscribing species as evolving lineages (e.g., Monro 2022), we describe new species to resolve the non-monophyly detected after a comprehensive phylogenetic analysis of the series *Chrysorrhizae* (Winitsky et al. Chapter 1). Although monophyly is not a necessary criterion for circumscribing a species (e.g., Fazekas et al. 2009; Naciri and Linder 2015; Freudenstein 2017; Lavin and Pennington 2022), we found that we could apply our species concept to monophyletic groups because such groups were revealed during fieldwork to be distinctive ecologically, geographically, and morphologically.

## MATERIALS AND METHODS

### Taxon Sampling.

*Marina* ser. *Chrysorrhizae* was extensively sampled, with multiple conspecific representatives of each peninsular taxon. The narrowly endemic species *Marina brevis* León de la Luz, *Marina oculata* (Rydb.) Barneby and *Marina catalinae* Barneby, are each represented by a single accession. The Sonoran species *Marina minor* (Rose) Barneby repeatedly yielded

insufficient quantities of DNA extract to be included in the study. Fourteen accessions of *M. divaricata*, six accessions of *M. peninsularis*, and seven accessions of *M. maritima* were included to cover the range of variation in morphology, geographic disjunctions, and ecological preferences for each of these. *Camoufleur filiciformis*, sister genus to *Marina*, was used as an outgroup (Winitsky et al. Chapter 3).

#### DNA Extraction, Amplification, and Sequencing.

DNA was isolated from field collections of silica-dried leaf material and herbarium specimens using Qiagen DNAeasy Plant Mini Kits (Qiagen, Valencia, CA, USA). Library preparation, target enrichment (Johnson et al 2019) and sequencing followed the methods outlined in Winitsky et al. (Chapter 1).

#### Assembly and Phylogenetic Inference.

Raw sequences were assembled using de novo and reference guided assembly and densely sampled phylogenetic trees using maximum likelihood, Bayesian, and pseudocoalescent approaches were inferred. Winitsky et al. (Chapter 1) provides details for the phylogenomic approach used in this study.

#### Fieldwork.

The third author has been leading field expeditions throughout the Baja California peninsula over the past thirty years, which has led to a vast increase in *Marina* specimens that generated the hypotheses explored in this study. The first author took two trips by road to study *Marina* in habitat. The first expedition targeted already described narrow endemic taxa to understand the existing diversity within the genus throughout the peninsula. The second

expedition allowed the first author to visit populations that were not conforming to monophyletic groups for ecological, geographic, and morphologic differences in the field.

#### Herbarium Studies.

Herbaria with extensive *Marina* collections, as well as those housing types, were visited to explore the morphological variation within the genus: ARIZ, CAS, HCIB, MOBOT, RSA, SDNHM, UC/JEPS, UCR. The first and third author collaborated on morphological study at SDNHM, where the third author serves as curator.

### RESULTS

Once three taxa are excluded, *Marina* ser. *Chrysorrhizae* is supported as monophyletic by three different phylogenetic methods. *Marina peninsularis* (Figure 1) resolves as two distinct clades neatly divided by the Gulf of California. The type of *M. peninsularis* is from the Magdalena Bay, collected during the H.M.S. Sulphur expedition in 1839 by George Barclay, so the peninsular accessions will all remain *M. peninsularis*. Sand dune accessions of *M. peninsularis* from Sonora and northern Sinaloa represent an undescribed taxon that is sister to *M. chrysorrhizae* and *M. victoriae*.

The fourteen accessions of *Marina divaricata* (some of these are labeled as *M. capensis* because of their small flowers on Figure 1) resolve into four distinct clades. One clade includes populations from near the type locality at the Magdalena Plain, which represents the type concept and will remain *M. divaricata*. A second clade comprises populations in mountain and lowland habitats from La Paz to Cabo San Lucas that are more morphologically similar to *M. capensis*, a narrow endemic near Todos Santos and has been previously described as *Dalea*

*anthonyi*. A third clade comes from a single population in Cabo Pulmo that has the prostrate, entangled habit of *Marina maritima* but is completely glabrous. A fourth clade has canescent stems and glabrous calyces, a combination noted but left undescribed from a *Purpus* specimen by Barneby (1977) and is found throughout the Sierra La Laguna. *Marina divaricata* of Magdalena Bay is sister to a clade that includes true *M. capensis* of San Pedrito, *M. palmeri* of Sonora and the *M. divaricata* clade from the Cape that will be resurrected to a species that was previously used to describe them, *Dalea anthonyi*, but now within the genus *Marina*. The other two glabrous calyx clades (of Cabo Pulmo and Sierra la Laguna) were more closely related to *M. maritima* and each of these will receive a new name and circumscription.

*Marina maritima* was described from around the entire Cape region but restricted to the immediate coast. This circumscription will remain, as coastal populations form a monophyletic group and are phenotypically and otherwise distinct from populations in the Cape mountains and arroyos of the east Cape. *Marina maritima* forms a paraphyletic group and two species will need to be described to reconcile our genetic, ecological, geographic, and morphological data. Each of these two species described herein are narrowly endemic, known from only a few populations. In addition, sister to the clade comprising all four undescribed taxa and *Marina maritima* is a single accession labeled “Marina\_aff\_Capensis\_50”, which is also morphologically distinct, having much smaller leaves with less leaflets, a glabrous stem, and pubescent calyces. This population also has a unique growth form, with the branches stiffly dichotomously branching. Both the first and third author have visited this population in the field, but it is still only known from this one locality.

## Taxonomic Treatment.

*Marina arenaria* S.E. Winitzky & J. P. Rebman sp. nov.

*Type.* MEXICO, Sonora. AC Sanders 9206, 04 Sept 1989. Holotype: SD129347, isotypes: NY, UCR) Huatabampo, Playa Huatabampito c. 14 km (airline) SSE of Huatabampo. Coastal dunes and flats immediately behind the beach, 26.7 -109.6, 5 meters. (Figure 4).

*Description.* Perennial, orange-yellow taproot. Many-stemmed, diffuse, occasionally prostrate. Pilose throughout with long wavy hairs that are loosely appressed, 0.3-0.4 mm long along stem, leaflets, and rachis. Stems cylindrical, stramineous, with occasional sunken red or amber glands - darkening to brown- barely raised from epidermis 0.1-0.2 mm long and .05-0.1 mm wide. Stems long, flexible, and repeatedly branching. Foliage is pale green, leaflets lineolate above with livid- or orange-punctate beneath, papillose-hispid on both sides, stipules lance-acuminate; 0.9-1.2 mm long, thinly herbaceous becoming red-margined and crumpled, fragile, deciduous, charged at base with a pair of brown glands; *leaves* 1-2 cm long, reddish and gland charged petiole, 1-1.5 mm, with narrowly margined, glandular rachis and 6-9 (11) pairs of obovate, bluntly gland-tipped with a large orange linear gland, loosely folded leaflets 1.5-2.5 mm long; *peduncles* are leaf-opposed and 0.8-2.5 cm long; *racemes* loose; *inflorescence* 6-22 flowers; *bracts* readily deciduous, reddish and lanceolate, 1-1.5 mm, thinly herbaceous, glandular; *pedicels* 0.1-0.3 mm long, at the base of pedicel and below calyx there are two pairs of fusiform, orange glands; *calyx* 1.8-3.0 mm long, pilosulous with somewhat appressed hairs, the tube 1.0-1.5 mm, pleated, with thick, red ribs, the orifice contracting near the mouth, intervals charged with a chain of 5-13 small, round to elliptic, honey-colored glands, the calyx teeth slightly unequal, the dorsal one 1.0-1.5 mm long, the ventral pair a little shorter (0.8-1.0 mm) and slightly broader, all gland-tipped; *petals* bicolor, pink above fading to white except for a

dark yellow spot completely covered with orange glands on the banner, the eglandular inner petals perched above hypanthium rim; *banner* 1.3-2.0 mm; *wings* 3.0-4.0 mm; *keel* 3.5-4.5 mm; *androecium* 10-merous, the connective gland-tipped, the dark red anthers 0.25-0.35 mm long; *pod* obovate in profile, 1.7-2.2 mm long, hairs throughout fruit, curly hairs throughout except on glands, three rows of dark large glands; *seeds* not examined.

*Diagnosis.* *Marina arenaria* (Figure 5) differs from *Marina peninsularis* (Figure 6) in corolla color: *M. arenaria* having a light pink to yellow corolla with darker banner and *M. peninsularis* having a bright magenta-purple except for the yellow eyespot on the banner (Table 1). The leaf pubescence differs with *M. arenaria* having long wavy hairs that are loosely appressed as opposed to *M. peninsularis*' spreading-incurved, stiff white hairs (Figure 6). Barneby included the Sonoran taxon within *M. peninsularis*, but noted a difference in stem glands, *M. peninsularis* has very distinct grain like glands throughout the stem, but "in the isolated population from coastal Sonora (known only from young specimens) these glands are apparently almost lacking." (Barneby 1977). The type of *M. peninsularis* is from Magdalena Bay. *Marina chrysorrhiza* and *Marina arenaria* are sister phylogenetically but they differ morphologically (Table 1). *M. arenaria* has pilose leaflets (Figure 5) and *M. chrysorrhiza* has quite glabrous leaflets, sometimes thinly pilosulous beneath (Table 1).

*Additional accessions.* **Van Devender 93-274**, 15 March 1993, (UCR76481) Sonora, Gulf of California, Camahuiroa between Agiabampo and Las Bocas on the Gulf of California, 26.51667 -109.26667.

*Endemism, Habitat, Distribution.* *M. arenaria* is only known from sand dunes and adjacent to dunes in sparse Sinaloan thornscrub from Playa Huatabampito to Las Bocas, Sonora,



with an additional observation from Santa Maria, along the same dune system, crossing the border into Sinaloa. These plants bloom opportunistically following rains. Fieldwork is needed to confirm that none of the other populations previously identified as *Marina peninsularis*, represent *M. arenaria*. Many of these dunes are highly disturbed.

*Associated taxa.* *Cenchrus ciliare* L. (Link), *Heliotropium curassavicum* L., *Asclepias subaphylla* Woodson, *Croton californicus* Mull. Arg.

*Etymology.* *arenaria*- from Latin, meaning sand, referring to the plants' sand dune habitat.

*Common name.* Sand Marina

*Marina cabopulmensis* S. E. Winitsky & J. P Rebman sp. nov.

*Type.* MEXICO, Baja California Sur, Benjamin Wilder 2013-191 with Charlie de la Rosa, 10 November 2013. (Holotype: SD240081), Canyon just inland of Cabo Pulmo. Desert scrub with *Croton magdalenae*, *Bursera epinnata*, *Euphorbia hindsiana*, *Lysiloma divaricatum*. 23.4298 -109.46111, 94 meters (308ft). Figure 7.

*Description.* Perennial prostrate shrub, orange-yellow taproot. Glabrous throughout the entire plant. Stem cylindrical densely warty with red and yellow circular glands, glaucous. Stems flexuous. Foliage is light green, leaflets lineolate above with orange-punctate glands dorsally and ventrally; *stipules* 2.1 mm, triangular, densely glandular; *petiole* 0.3- 0.5 mm, with crenulate, emarginate at leaflet tip narrowly margined, rachis with small yellow glands; *leaves* 2.5-4.5 cm, 6-12 pairs of emarginate, obovate leaflets, large glands around the margins, two rows following the midrib, smaller ones scattered; *leaflets* 1.8-2.7 mm long; drought deciduous; *peduncles* are leaf-opposed; *racemes* loose, flowers ascending, approx. 15-20 per inflorescence; *flowers* showy,

large, 0.9-1.1 cm; *bracts* leaflike, 3.3 mm, yellow glands scattered throughout, not extending past calyx, lanceolate readily deciduous; *pedicels* 0.9 mm long; *calyx* 3.5-4 mm long, glabrous, occasionally 1-2 glandular hairs on margins, pleated, with thick, red ribs, intervals charged with 1 to 3 large elliptic, sometimes bleeding together, honey-colored glands, the calyx teeth unequal, dorsal lobe far exceeding others, all ribs fading out at calyx lobes, red (fading to yellow) gland-tipped; *petals* bicolored, purple above and white below, dark red, maroon spot, sometimes green or yellow, on banner *banner* 1-1.5 mm banner yellow inside, purple on margins, covered with 3 rows of yellow glands, 1 mm. *wings*: 2.0-2.4 mm, white below, purple above, small yellow glands throughout *keel*: 3.0-3.5 mm, bicolored, small yellow glands; *androecium* 10-merous; *pod* obovate in profile, 3.1 mm glabrous, papery margin, charged with 2 rows of gland-crescents, glands not overlapping; *seeds* not examined.

*Diagnosis.* *M. cabopulmensis* differs from the nearby prostrate shrub *M. maritima* by its glaucous stems (Figure 8). It differs from *M. divaricata* by having 1-2 glands per calyx rib interval, larger flowers, and very conspicuous leaf glands. The combination of these characters and its warty stems (rather than striped) glabrous and shiny red, fading to silver calyx, separates it from any other cape taxa described here (Figure 8).

*Additional Accessions.* **Winitzky 1744**, from type locality with Isaac Lichter Marck, Wren Annetta Marck, December 15, 2022, along trails behind and upslope of the town of Cabo Pulmo, following the trail called "Junior's" down into the arroyo. Growing in a riverbank of a dry arroyo - covering the bare parts of the cliffs. 23.43551 N, -109.44958 W. **M.E. Jones 24052** 23 January 1923, San Jose del Cabo, CAS 173009, RSA 55219, SD25457, UC400508. **Annetta**

**Carter 2234** 17 December 1947, Broad arroyo, and sand dunes near the ocean; 19.2 km southwest of San Jose del Cabo, UC 916062.

*Endemism, Habitat, Distribution.* Although there are few recent collections of this plant, and it is currently only known in the vicinity of Cabo Pulmo, historic specimens, with imprecise locality information, suggest that this plant was more common throughout what is now called the “tourist corridor” of Los Cabos. Any habitat that remains intact from this region, especially arroyos near the coast should be surveyed for undocumented populations. All historic occurrences have been from river drainages, growing along exposed arroyo slopes.

*Associated Taxa.* *Bouteloua reflexa* Swallen, *Euphorbia hindsiana* Benth., *Olneya tesota* A. Gray, *Pachycereus pecten-aboriginum* (Engelm. ex S. Watson) Britton & Rose, *Melochia tomentosa* L., *Indigofera fruticosa* Rose, *Bursera fagaroides* (Kunth) Engl., *Bursera microphylla* A. Gray, *Forchhammeria watsonii* Rose.

*Phenology.* November- January.

*Etymology.* Named for the National Park Cabo Pulmo, Baja California Sur, where the type locality of this taxon is found.

*Common Name.* Cabo Pulmo Marina.

*Marina cacachilensis* S. E. Winitsky & J. P. Rebman

*Type.* MEXICO, Baja California Sur, Rebman 25429 with John & Fran Reynolds, 21 January 2013 (holotype: SD228875), La Paz Municipality. Sierra Cacachila; east of La Paz and west of El Sargento; in a canyon upstream from Las Canoas Ranch. Granitic substrates. Cape Region canyon vegetation with *Brahea brandegeei*, *Lysiloma candida*, *Sebastiania bilocularis*, *Cyrtocarpa edulis*, *Eucnide cordata*, *Hechtia montana*, *Pachycereus pringlei*, and *Euphorbia*

*californica*. Prostrate herbaceous perennial, flowers purple; rare. 24.09725, -110.06676. 480 m.

Figure 9.

*Description.* Perennial, yellow taproot. The stems often leafless, branched and trailing, forming low, entangled masses up to many meters across, densely strigose with dark brown to black glands, the leaflets glabrous except on margins and a couple stray hairs (0.1-0.2 mm) along midrib; *main cauline leaves* 1.8-4 cm long, the leaflets 5-12 pairs, obovate with obcordate tips, 3.8-4.8 mm long, faint, small glands on abaxial side of leaflet, mostly noticeable along the margin, rachis glands minute and yellow under strigose hairs; *stipules* long narrow, lance-acuminate, 1.8 mm long, thinly herbaceous and crumpled, deciduous; *racemes* dense; *flowers* ascending, approx. 24-39 per inflorescence, showy, large, 0.9-1.1 cm; *bracts* 4.4 mm long, readily deciduous, leaflike halfway, then tapering, covered dense straight hairs, hairs (0.4-0.5 mm), extending past calyx *pedicel*; 1.9-3.1 cm; *calyx* 1.8-3.0 mm long, glabrous except for orifice, pleated, with thick ribs, intervals have (1)2(3) small, round clear to bright red glands, the calyx teeth equal, all gland-tipped; *petals* almost solidly purple, less bicolored than related *Marina* and with a green eye covered in yellow glands, on the banner; *keel* 8.8-9.7 mm; *wing*; 4.2-5.1 mm; *banner* 2.7-3.7 mm; *androecium* 6.5 mm, the anthers  $\pm$  0.8 mm long; *pod* 3.4 mm, glabrous, obovate, two crescents of dark glands, pod readily turns black in age.

*Diagnosis.* *Marina cacachilensis* is most similar to *Marina maritima* because of its entangled, clumping habit, its stem pubescence, its flower size and dense raceme (Figure 10). Geographically and ecologically, they differ because *Marina maritima* grows along the immediate coast in the Cape Region and in dense sand and *Marina cacachilensis* grows in the

Cacachilas mountains in bare, open areas, but not sand dunes. Morphologically, *M. cacachiensis* are easily distinguished by glabrous calyces and mostly purple flowers.

*Additional Accessions.* **Sophia Winitsky 1742** with Isaac Marck & Wren Annetta Marck, Cacachilas Mountains, in a “dead zone” along a fault, between the Ranch House and la Cueva del Delfin, along the road, 24.06755 N, -110.06311 W. **Sophia Winitsky 1743** with Isaac Marck & Wren Annetta Marck, Cacachila Mountains, north of la Cueva del Delfin along the road, 24.10188, -110.060032. **Jon Rebman 27323**, Sierra Cacachilas, SE of La Paz & W of El Sargento; N of Hwy 286 between La Paz & San Juan de Los Planes; along the canyon up from Las Canoas, 24.08846, -110.06403, SD236996 **Jon Rebman 28911**, Sierra las Cacachilas: north of Hwy. 286 between La Paz & San Juan de los Planes; west of El Sargento; along a canyon between Rancho Dos Hermanos and Las Canoas Canyon, 24.07743, -110.05968, SD242172. **Jon Rebman 29931**, Sierra las Cacachilas: north of Hwy 286 between La Paz & San Juan de los Planes; west of El Sargento; on Remigio's ranch along a canyon near the start of the trail to Cerro Las Tinajas (El Llano), 24.07953, -110.10992 SD256978.

*Endemism, Habitat, Distribution.* This taxon is known only from the Cacachilas mountains of Baja California Sur, which are situated west of El Sargento, southeast of La Paz and northeast of highway 286. It is locally abundant, forming dense patches throughout the mountains, but only in openings, but never within dense overstory of the nearby shrublands. The large shrubs of the surrounding vegetation are not found in these openings, allowing lower growing herbaceous perennials to fill them in. These areas have been called “kill zones” and are areas of granite with chemically different soil than what supports the surrounding vegetation

(Hollingsworth et al 2020). The currently documented populations of *Marina cacachilensis* are on privately owned land and are not at immediate risk of development or other threats.

*Associated Taxa.* *Brahea brandegeei* (Purpus) H.E. Moore, *Lysiloma candidum* Brandege, *Lysiloma divaricatum* Benth., *Pachycereus pecten-aboriginum* (Engelm. ex S. Watson) Britton & Rose, *Pachycereus pringlei* (S. Watson) Britton & Rose, *Bursera microphylla* A. Gray, *Jatropha cinerea* (Ortega) Mull. Arg., *Jatropha vernicosa* Brandege, *Diospyros californica* (Brandegee) I.M. Johnst., *Stenocereus thurberi* (Engelm.) Buxb., *Sebastiania bilocularis* S. Watson, *Cyrtocarpa edulis* (Brandegee) Standl., *Eucnide cordata* Kellogg ex Curran, *Hechtia montana* Brandege, *Euphorbia californica* Benth., *Pluchea parvifolia* (A. Gray) R.K. Godfrey, *Parkinsonia florida* (Benth ex Gray) S. Watson, *Distimake aureus* (Kellogg) A. R. Simoes & Staples, *Bahiopsis tomentosa* (A. Gray) E.E. Schill & Panero, *Gossypium* L. sp., and *Melochia tomentosa* L.

*Phenology.* blooming opportunistically throughout the year, collections in flower from April, October, December, January.

*Etymology.* This taxon is named for the Sierra de las Cacachilas near the Pichilingue Peninsula, which hosts many endemic taxa as well as disjunctions from the Sierra la Laguna and *Karwinskia humboldtiana*, which is commonly known as Cacachila.

*Common Name.* Cacachilas Marina.

*Marina leondelaluzii* S.E. Winitsky & J.P. Rebman sp. Nov.

*Type.* MEXICO. Baja California Sur, Jon Rebman 31140 with Michael Rebman, Kathleen Mitchell, & Scott Landis, 05 March 2016 (holotype: SD 260496) La Paz, Rancho Encinalito: northeastern foothills of the Sierra de La Laguna, east of San Antonio de la Sierra,

southwest of San Bartolo; private ranch owned by Kathleen Mitchell & Scott Landis; along the trail near the truck parking area, granitic substrates, Oak Woodland with *Quercus albocincta*, *Quercus tuberculata*, *Dodonaea viscosa*, *Indigofera fruticosa*, *Bouteloua repens*, *Melinis repens*, & *Sida* sp., prostrate perennial, flowers purple & white; rare. Note dense white strigose pubescence on stems, 23.69013 -109.92318, 835 meters (2739ft). Figure 11.

*Description.* Perennial ascending shrub, orange-yellow taproot. Stem strigose, hairs 0.1-0.2 mm. Stem cylindrical with reddish, oval, elevated glands (2 mm). Stems stiff. Foliage is light green, leaflets lineolate; *stipules* 0.6-0.7 mm, dark purple, triangular, not tapering; *leaves* 1.3-2.6 cm; *petiole* 0.9 mm; *rachis* glands yellow, elongate, scattered, not margined; *leaflets* darkened by glands reddish along leaflet margins, wavy from glands, truncate, 7-12 pairs of folded, obovate, truncate leaflets, adaxial face glabrous with strigose on margins and along the abaxial midrib, one large gland at tip on adaxial face. abaxial face glandular, the margins and midrib have larger glands (0.1mm) and lighter colored, smaller glands scattered between, 1.8-2.4 mm long; drought deciduous; *peduncles* are leaf-opposed, short; *racemes* compressed, dense, flowers ascending, approx. 5-18 per inflorescence; *flowers* smaller with keel jutting upward, 6.7-7.3 mm; *bracts* short (2.3-3.5mm) and deciduous, acuminate but not extending beyond calyx, glandular and less densely strigose than inflorescence stem; *pedicels* 0.4-0.5 mm long; *calyx* 3.0-3.5 mm long, dark, glabrous calyx tube with dense hairs on orifice, intervals charged with 2-3 small elliptic, honey-colored glands, which are harder to see due to the darker calyx color. The calyx teeth slightly unequal, dorsal lobe exceeding others, ribs elevated but similarly colored to rest of calyx, gland-tipped; *petals* bicolored; *banner* 2.4-2.8 mm, white eye in center but yellow from glands; *wings* 3.8-4.1 mm, white below, purple above, small yellow glands throughout; *keel* 6.0- 6.4 mm,

bicolored, small yellow glands, keel angled upward; *androecium* 10-merous, not gland tipped; *pod* not examined; *seeds* not examined.

*Diagnosis.* This taxon is sister to *Marina cacachilensis* however it has a different growth form, upright rather than the entangled creeping and mounding *Marina cacachilensis* or *Marina maritima*. Additionally, it is not found in the Cacachilas mountains, like *M. cacachilensis*, or near the coast, like *M. maritima*. *Marina anthonyi* is the most similar taxon that is found in this region but *M. leondelaluzii* differs by having strigose stems, having less flowers per inflorescence (18 maximum) and dark colored calyces (Figure 12).

*Additional Accessions.* **Leon de la Luz 9856** La Paz, Rancho San Antonio de la Sierra, 23.684571 -109.939761, SD146992. **Navarro 1374** La Paz, Aprox. 1 km al S del Rancho San Antonio de La Sierra, 23.65 -110, SD146994. **Cadena 1180** La Paz, Sierra La Laguna - Sierra La Victoria: Rancho San Antonio de la Sierra 23.75 -109.93333, SD26124. **Leon de la Luz 9856**, San Jose del Cabo, Camino a Palo Escopeta, 23.13333 -109.65, SD203832. **Dominguez 2928**, La Paz, Rancho San Antonio de la Sierra, 23.666667 -109.983333, SD146991. **Purpus 515**, Arroyo de San Felipe, UC81948. This accession (Purpus 515) was also noted in Barneby's monograph for having "the tomentulose stems of *M. maritima* with a calyx only shortly puberulent around the mouth, suggesting that intergradient populations may exist in greater numbers than are now known." (Barneby 1977).

*Endemism, Habitat, Distribution.* This taxon is endemic to the northern part of the Sierra La Laguna, in the cape region of Baja California Sur. The known populations are all within five miles of each other, near Rancho San Antonio, south of Highway 1, southwest of San Bartolo and southeast of San Antonio. *Marina leondelaluzii* is found throughout oak woodlands,



often on eroded slopes in hilly landscapes. Due to its narrow distribution, this region should be surveyed for additional populations.

*Associated Taxa.* *Lysiloma microphyllum* Benth., *Polygala* L. spp., *Behria tenuiflora* Greene, *Quercus albocincta* Trel., *Quercus tuberculata* Liebm., *Dodonaea viscosa* Jacq., *Indigofera fruticosa* Rose, *Bouteloua repens* (Kunth) Scribn. & Merr., *Melinis repens* (Willd.) Zizka, & *Sida* L. sp.

*Phenology.* Opportunistically flowering throughout October -March.

*Etymology.* *Marina leondelaluzii* is named for Dr. Jose Luis Leon de la Luz of the Northeastern Center of Biological Investigation (HCIB), La Paz, Mexico, who has contributed immensely to our knowledge of the Baja California flora in the fields of taxonomy, floristics, and ecology. Specifically, to the genus *Marina*, he has contributed two new narrowly endemic taxa (Leon de la Luz 2002) and his floristic work in the Sierra la Laguna has provided essential locality and morphological information for this description.

*Common Name.* Jose Luis' Marina.

*Marina tomentosa* S.E. Winitsky & J.P. Rebman sp. nov.

*Type.* MEXICO. Baja California Sur, Reymundo Domínguez Cadena 2362, 03 May 2001 (holotype: SD00040851, isotype: HCIB 16307), Los Cabos, La Ribera, carr. Between the Hotel Punta Colorada and Rancho Las Lagunas, sand dunes, cape shrubland and grassland with *Bursera microphylla*, *Jatropha cinerea*, *Stenocereus gummosus*, 23.5, -109.58333, 50 meters (164ft). Figure 13.

*Description.* Prostrate perennial herb, yellow taproot. The stems strigose, 1 mm, variable, reddish glands, 0.1-0.4 mm; *main cauline leaves* 1-6 cm long; *petiole* 0.2-0.8 mm, rachis with

orange grain-like glands (0.2-0.4 mm) under strigose hairs; *leaflets* pubescent (0.1-0.3mm) along margins and midrib of abaxial side, margins strigose, 6-14 pairs oblong, emarginate, truncate, 1.6-3.0 mm, no glands on adaxial side, very glandular underneath with larger glands along the midrib and margins and at the tip (0.2-0.4 mm) and smaller glands (0.1 mm) throughout; *stipules* dark purple triangular, not tapering, 0.6 mm long; *peduncles* 2 cm, leaf-opposed; *racemes* dense; *flowers* ascending, approx. 23-42 per inflorescence, 0.6-0.9 cm; *bracts* 1.8-2.3 mm, long acuminate, 0.4 mm wide, leaflike bracts with long tapering tails, pairs of glands, long curly spreading hairs on bracts; *pedicel* 1.9-3.1 cm; *calyx* 2.0-3.0 mm long, wavy, spreading, tangled hairs, with thick ribs, intervals have 1 small, round clear gland, occasionally with a second smaller one, calyx lobes longer than other taxa, not uneven, 1-2 mm long, all gland-tipped; *petals* bicolored; *keel* 5.8-6.0 mm; *wing* 3.8-4.2 mm; *banner* 2.1-2.3 mm, eye yellow, white with some purple; *androecium* 10-merous; *pod* 2.5mm sparse hairs, 2 crescents, each row of 3 glands, two smaller glands on inner margin; *seed* not examined.

*Diagnosis.* *Marina tomentosa* is most similar to *M. maritima*, but the calyces differ by having densely covered in curly hairs, whereas calyces of *M. maritima*, *M. cacachilensis* and *M. leondelaluzii* have pubescence beginning at some point along the calyx, or can be restricted to the orifice, but not covering the entire calyx. It differs from *M. anthonyi*, *M. cabopulmensis* and *M. divaricata* by having strigose stems (Figure 14). The single gland per calyx rib interval is also diagnostic.

*Additional Accessions.* **Winitzky 1747** Near the town of Santiago overlooking the river, in a wide bank 23.51520 N, -109.69025 W, **G. P. Lewis 2038** 6 km S of Santiago on road to San José del Cabo 23.42, -109.72, NY 0130795. **Turner77-63** 3 miles by road north of the turn-off

to Santiago 23.5152, -109.69025, SD00070926. **Cadena 1201** low elevation in the east Cape, SE of the town of Las Cuevas 23.53769, -109.67182, SD222535.

*Endemism, Habitat, Distribution.* This taxon is endemic to the eastern Cape of Baja California Sur, specifically along riverbanks parallel to Hwy 1 between Agua Caliente and Santa Cruz. It is also found in sandy areas to the southeast of the highway, near Las Cuevas. Growing, sometimes in highly disturbed, dunes within cactus shrubland and grasslands. The roadside populations have been highly disturbed by cars, trash and erosion, the *Marina* has persisted in these conditions and appears to invade recently disturbed settings.

*Associated Taxa.* *Bursera fagaroides* (Kunth.) Engl., *Bursera microphylla* A. Gray, *Colubrina viridis* (M.E. Jones) M.C. Johnst., *Stenocereus gummosus* (Engelm) A.C. Gibson & K.E. Horak, *Lysiloma candidum* Brandegees, *Jatropha cinerea* (Ortega) Mull. Arg., *Lippia palmeri* S. Watson, *Nahuatlea arborescens* (Brandegee) V.A. Funk, *Abutilon californicum* Benth., *Boerhavia xantii* S. Watson.

*Phenology.* Blooms opportunistically, seen in flower May – January.

*Etymology.* *Marina tomentosa* is named for its very fuzzy calyx, which distinguishes it from other species of *Marina*.

*Common Name.* Fuzzy Marina, Marina mullida

*Marina rebmanii* S.E. Winitzky sp. nov.

*Type.* MEXICO. Baja California Sur, Jon Rebman 27652 with Alfonso Medel Narvaez, Jose Luis Leon de la Luz, John LaGrange, 13 November 2013, (holotype: SD00040852, isotype: ARIZ418217), Cabo Pulmo vicinity: southeastern Cape region, between La Ribera and Bahia Los Frailes; along an arroyo approximately 4 miles south of La Ribera & south of the main road

(Camino Cabo Este), Mostly granitic substrates. Cape Lowland vegetation with *Tecoma stans*, *Lysiloma candidum*, *Pachycereus pringlei*, *Fouquieria diguetii*, *Bursera microphylla*, *Ambrosia monogyra* & *Parkinsonia florida*. Herbaceous perennial, prostrate growth habit, flowers blue & white; uncommon. Note rather large flowers, 23.52848, -109.57486, 60 meters (197ft). Figure 15.

*Description.* Prostrate perennial herb, yellow taproot. Stems glabrous, slightly ribbed, red, elevated glands (0.3 mm) throughout; *main cauline leaves* 0.8-1.6 cm long, rachis not margined, small yellow under strigose hairs; *leaflets* glabrous except a couple sparse hairs along the leaf margins (0.2 mm), 4-8 pairs obovate, lineolate, 4.0-4.7 mm, no glands adaxial, abaxial has small glands, mostly around margins, gland tipped leaf that extends beyond leaf (0.2 mm), appearing drought deciduous; *stipules* gland at base and tip dark purple triangular, not tapering, 0.3-0.8 mm long; *peduncles* up to 10 cm long, leaf-opposed; *petiole* 0.3-0.7 mm; *racemes* dense; *flowers* ascending, approx. 22-70 per inflorescence, 4.8-6.5 mm; *bracts* early deciduous, lacking on mature inflorescences, long acuminate 2.6-4.1 mm, leaflike at base and narrowing halfway up, some strigose hairs but much less strigose than the calyces, making the yellow glands more visible on the bracts; *pedicel* 0.3-0.7 mm; *calyx* 2.4-2.8mm, strigose throughout calyx, especially on ribs and orifice, intervals have (1)2(3) glands, calyx lobes equal; *petals* bicolored; *keel* 4.5-7.1 mm; *wing* 2.0-3.1; *banner* 0.8-1.3mm, eye purple & yellow, glandular; *androecium* 10-merous, gland tipped, golden gland between anther sacs; *pod* not examined; *seed* not examined

*Diagnosis.* *Marina rebmanii* differs from *M. cacachilensis*, *M. divaricata*, *M. leondelaluzii*, *M. cabopulmensis* and *M. anthonyi* because it has hairs throughout the calyx and down the ribs of the calyx. *M. tomentosa* and *M. maritima* both have pubescent calyces and are

found nearby, and would be most easily confused for *M. rebmanii*. *M. maritima* is nearby on the immediate coast and *M. tomentosa* is found in arroyos directly north of *M. rebmanii*. *M. maritima* has an entangled, clumping growth form that differentiates it from *M. rebmanii*, which is a prostrate perennial but does not form mounds. *M. rebmanii* differs from *M. tomentosa* by having an extra calyx gland per rib interval and less leaflets (4-8 pairs, rather than 6-14) per leaf (Figure 16). Both, *M. maritima* and *M. tomentosa* have strigose stems that readily differentiate them from the glabrous stem of *M. rebmanii* (Figure 16).

*Additional Accessions.* **Winitzky 1748** 4.5 miles south of La Ribera, in the center of a wash, sand and gravel, 23.52833 N, 109.57486 W.

*Endemism, Habitat, Distribution.* *Marina rebmanii* grows in sand and granite throughout a wide wash south of La Ribera. This taxon is restricted to one arroyo in cape lowland vegetation. Due to its narrow distribution and potential threats to the existing populations, it should be prioritized for additional surveying. There are cows grazing throughout this region and some plants have clear herbivore damage. There are also tire tracks from 4WD vehicles throughout the wash.

*Associated Taxa.* *Tecoma stans* L. Juss. ex Kunth., *Lysiloma candidum* Brandege, *Pachycereus pringlei* (S. Watson) Britton & Rose, *Fouquieria diguetii* (Tiegh.) I.M. Johnst, *Bursera microphylla* A. Gray, *Ambrosia monogyra* (Torr. & A. Gray) Strother & B.G. Baldwin, *Parkinsonia florida* (Benth ex A. Gray) S. Watson, *Tamarix ramosissima* Ledeb., *Abutilon californicum* Benth. & *Jatropha cinerea* (Ortega) Mull. Arg.

*Phenology.* November- January.

*Etymology.* This *Marina* honors the botanist Dr. Jon Rebman who has collected many of the *Marina* specimens used for this research and has spent decades conducting floristic and taxonomic research to improve our knowledge of the biodiversity of the peninsula.

*Common name.* Rebman's Marina.

*Marina anthonyi* (Brandege) S. E. Winitzky comb. nov.

*Type.* Lectotype designated by Barneby: MEXICO, Baja California Sur, T. S. Brandege 129 San Jose del Cabo, 3 Sept 1890 (holotype: UC15153, isotype: CAS, F) paratype, Anthony 352 (UC33331, F, MEXU, CAS, US). Figure 17.

*Parosela anthonyi* (Bdg.) Rose, Contrib. U. S. Nat. Herb. 12: 272. 1909.

*Dalea divaricata* ssp. *anthonyi* (Bdg.) Wiggins, Contrib. Dudl. Herb. 3: 50. 1940.

*Dalea anthonyi* Bdg., Erythea 7: 2. 1899. No. 129, Proc. Cal. Acad., ser. 2, vol iii, 126.

*Taxonomic History.* Two previously described names, which are currently included in *Marina divaricata* based on Barneby's taxonomy, could be applied to this taxon. *Dalea anthonyi* Brandege and *Parosela variegata* Rydb. were both described to address the variation of specimens similar to *Marina divaricata*, but found in the Cape Region, BCS with notable morphological differences. Both taxa had type localities of San Jose del Cabo, an area that is much more developed than the time of their collection and description. Due to development and lack of specific locality information, it is not possible to revisit the type locality and expect to find similar habitat as existed in 1899-1919 (the time of description). For species to conform to monophyletic groups, given the phylogenetic evidence now available (Winitzky chapter 1), either *Marina capensis* Barneby, of San Pedrito, BCS, and *Marina palmeri* (Rose) Barneby, of Sonora and northern Sinaloa, need to be included in *Marina divaricata*. Or *M. divaricata* of the

type locality, Magdalena Bay populations needs to be distinct from the Cape populations. *P. variegata* was described to differentiate the glabrous individuals found throughout the Cape mountains from *D. anthonyi* with hirsutulous foliage, but at this time, we cannot support this distinction with phylogenetic analyses, and they will remain one entity with variable pubescence. Barneby lectotypified *D. anthonyi*, to conform to the subglabrous calyx referenced in the protologue, changing the type from an Anthony (#352) collection to a Brandegee (#129) collection. Both UC and CAS house isotypes of these collections and there is varying pubescence across all four specimens. Here, we return to the name *Anthonyi* because it predates *Variegata*.

*Description.* Plants achieve a stature of 2 m in some places, and become bushy in outline or can be diffuse and trailing. Frutescent, growing in dense clumps, up to a meter wide. The stems glabrous, slightly ribbed, red, elevated glands (0.3 mm) throughout; *main cauline leaves* 3-5 cm long, rachis ribbed, golden grain like glands; *leaflets* pubescence variable, almost glabrous to long wavy hairs (up to 0.5 mm) on both leaflet faces, 6-20 pairs, oval, slightly obcordate, lineolate, leaf margins crenulate, 2.4-4.5 mm, small glands throughout abaxial side, prominent gland at tip, glands around margin and midrib are slightly larger than those scattered throughout blade. Glands on adaxial side only have marginal glands, drought deciduous; *stipules* narrow linear, brown, papery, tapering, 2.5 mm; *peduncles*; 2-6 cm long, leaf-opposed; *petiole* 0.6-0.1 cm *racemes* loose; *flowers* ascending, 5.3-7.2 mm approx. 30-60 per inflorescence, infr. 5-6 cm long; *bracts* early deciduous, lacking on mature inflorescences, long, acuminate 2.6-4.1 mm, leaflike at base and narrowing halfway up, some strigose hairs; *pedicel* 0.3-0.7 mm, ribbed and covered in glands; *calyx* 2.0-2.8 mm, glabrous until orifice, intervals have 3-5 small glands,

calyx lobes unequal- lower lobe 0.5 mm longer than other lobes; *petals* bicolored; *keel* 4.0-4.8 mm; *wing* 2.2-3.5 *banner*; 1.6-2.5 mm, eye densely glandular, yellow eye with dark glands; *androecium* 10-merous; *pod* obovate, two crescents of glands, glabrous, 1.5-1.9 mm; *seed* not examined.

*Diagnosis.* The characters distinguishing *M. anthonyi* from *M. divaricata* are the longer leaves, more obvious abaxial glands, occasional curved hairs, long inflorescence bracts with very long, tapering tips (Figure 18). The flowers are showier, and the plant habit is ascending or trailing, but never low, crooked shrubs, like are found in the Magdalena plain. The calyx has one larger, odd sepal, whereas true *M. divaricata* has equal calyx lobes. These two taxa do not geographically overlap. The glabrous stem differentiates *M. anthonyi* from *M. maritima*, *M. cacachilensis*, *M. leondelaluzii* and *M. tomentosa* all of which also inhabit the cape region. *M. anthonyi* is distinct from *M. rebmanii* by having a glabrous calyx. *M. anthonyi* could most easily be confused for *M. cabopulmensis*, especially individuals with a trailing habit, but *M. cabopulmensis* has fewer glands per calyx rib interval, smaller leaflets (1.8-2.7 mm versus 2.4-4.5 mm) and a glaucous stem (Figure 18).

*Additional Accessions.* **Winitzky 1749** within the Sierra La Laguna reserve, southeast of San Antonio along the mountain road and then a short walk up the wash, 23.65027 N, -109.92284 W, **Jon Rebman 29189** Sierra del Novillo: approx. 15 miles southeast of La Paz & northeast of the jctn. Of Hwy. 1 & Hwy 19; in a canyon & mesa above Rancho Las Calabazas on the northeast side of the Sierra, 23.94127 -110.17766, SD00040845. **Reid Moran 7290** April 30, 1959, Near canyon mouth, El Chorro, 23.44008 -109.80775, SD00070883. **Moran 6942** 2 km below San Bartolo, 23.7333 -109.8333, SD00070890. **H S Gentry 4392** La Laguna, Sierra



Laguna UC 709025. **Annetta Carter 2680**, Rancho San Bernardo, east side of Sierra de la Victoria, MICH1171736. **Reid Moran 6942** Cape Region, cañon 2 km below San Bartolo, on canyon wall, 23.7333, -109.8333, SD50565. **Annetta Carter and Francia Chisaki 3521** Los Cabos, El Ancón Grande; S side of La Carrerita; Sierra El Taste, 23.1833 -109.917, MICH1171735 . **Annetta Carter and Roxana Ferris 3340** East side of Sierra de la Victoria, 23.49194 -109.79861, TEX00272361, **Brandegge 125** Sierra de la Laguna, UC81958. **Vanderplank 7034** Sierra La Laguna, Arroyo La Junta, main arroyo from Rancho Paredecitos downstream, 23.66137, -110.09183, SD260764, RSA0150917. **Sanders 3310** 17 km NW of San Bartolo, Sierra de la Laguna, 23.78 -109.95, NY01307021, ARIZ255627. **Rebman 7059** Arroyo Santa Cruz; drainage area, 24.15528 -110.10889, UCR 153538, SD00070892. **Rebman 5801** Sierra de la Laguna: NE of Todos Santos: vicinity of Valle La Laguna at top of the Sierra; NE of Cañon La Burrera and Rancho Corral Grande, 23.55056, -109.98306, UCR 112421, BCMEX10857, SD145382, HCIB13793. **José Juan Pérez Navarro 1379** La Paz, Sierra de San Vicente, San Vicente de la Sierra, 23.16667 -110.03333, SD00070884, HCIB15249. **John H. Thomas 7844** The Cape Region, Potrero de Almenta, Arroyo de Almenta, eastern slopes of the Sierra de la Victoria. Inland from Caduano, RSA0112476, NY01307025, MICH1171738, USF78297.

*Endemism, Habitat, Distribution.* *Marina anthonyi* is found throughout the Cape region of Baja California Sur, most commonly in the pine oak forests of the Cape mountains (up to 1800 meters), but also occurs throughout lowland scrub, along washes and riverbanks. It occurs from San Lucas del Cabo to La Paz, generally in soil of granitic origin. It is the most widespread

of the newly described taxa and the majority of specimens found in the cape region previously called *M. divaricata* represent *M. anthonyi*.

*Associated Taxa.* *Lysiloma divaricatum* Benth., *Quercus tuberculata* Liebm., *Brahea brandegeei* (Purpus) H.E. Moore, *Nahuatlea arborescens* (Brandege) V.A. Funk, *Haematoxylon brasiletto* Karst., *Bouteloua repens* (Kunth) Scribn. & Merr., *Croton magdalenae* Millsp., *Salvia similis* Brandege, *Antigonon leptopus* Hook. & Arn., *Ricinus communis* L., *Ambrosia ambrosioides* (Cav.) W.W. Payne, *Washingtonia robusta* H. Wendl., *Jatropha cinerea* (Ortega) Muell. Arg., *Jatropha cuneata* Wiggins & Rollins, *Stenocereus thurberi* (Engelm.) Buxb., *Bursera microphylla* A. Gray & *Pachycereus pringlei* Britton & Rose.

*Phenology.* September – January.

*Etymology.* Named by T. S. Brandege for Alfred Webster Anthony, an ornithologist who traveled extensively and collected the original type assigned to this taxon in San Lucas del Cabo.

*Common Name.* Anthony's Marina, Sierra de la Laguna Marina

Key to Marina Series *Chrysorrhizae*.

Because all of the species described herein belong to *Marina* series *Chrysorrhizae*, a key is provided to distinguish among these 22 species. Series *Chrysorrhizae* now includes about half the described species diversity of the genus *Marina*. As distilled from Barneby (1977), *Marina* ser. *Chrysorrhizae* is diagnosed relative to other series of *Marina* by floral pedicels relatively short and firm (not capillary); calyx-teeth often gland-spurred marginally but not glandular dorsally; dorsal tooth of calyx not over twice as long as tube; banner and usually keel blades gland-sprinkled; keel petals not attached to the staminal column and nearly as long to much longer than banner, blades overlapping along external margins and adherent by their faces;

valves of pod charged with glands arranged in crescentic patterns; and by being most abundant and species diverse around the Gulf of California.

1. Plants endemic to islands in the Gulf of California.

2. Calyx glabrous except for the thinly ciliate orifice..... *M. oculata*

2. Calyx pilosulous from base upward..... *M. catalinae*

1. Plants not endemic to islands on the gulf coast

3. Androecium 5-merous..... *M. evanescens*

3. Androecium 10-merous

4. Vexillum to 2.4 mm, plants ephemeral..... *M. brevis*

4. Vexillum at least 2.5 mm, plants annuals to shrubs

5. Stem pubescence widely divergent

6. Leaflets pubescent both faces

7. 1-2 glands in calyx rib interval..... *M. goldmanii*

7. 4-7 glands in calyx rib interval

8. Corolla color bright pink- magenta..... *M. peninsularis*

8. Corolla color light pink to yellow..... *M. arenaria*

6. Leaflets dorsally glabrous ..... *Marina chrysorrhiza*

5. Stems glabrous or pubescent, if pubescent, hairs appressed never widely divergent

9. Glands in each calyx interval 4-7

10. raceme greater than 2.5 cm

11. Flowers greater than 3 mm ..... *Marina parryi*

11. Flowers less than 3.2 mm

- 12. Herbaceous, plant of Baja California Sur .....*Marina capensis*
- 12. Suffruticose, plant of Sonora Mexico .....*Marina palmeri*
- 10. Racemes less than 2.5 cm
  - 13. 8-18 flowers .....*Marina interstes*
  - 13. 5-7 flowered .....*Marina victoriae*
- 9. Glands in each interval of calyx 1-4, concentrated above middle of tube or just below its orifice
  - 14. Stems pubescent throughout
    - 15. Entire calyx tomentose .....*M. tomentosa*
    - 15. Calyx entirely glabrous up to the orifice, or pubescence begins halfway towards calyx lobes
      - 16. Not prostrate or mounding, upright, plant of oak woodlands, not of Cacachilas mountains or coast .....*M. leondelaluzii*
      - 16. Mound forming up to meters wide, prostrate
        - 17. Plant of immediate coast and sand, bicolored, leaflets pubescent  
.....*M. maritima*
        - 17. Plant not on immediate coast, of Cacachilas mountains, usually solidly purple, can be slightly bicolored, leaflet hairs mostly along margins  
.....*M. cacachilensis*
- 14. Stems glabrous
  - 18. Plants of Mainland Mexico- Sonora, Durango, Sinaloa, Chihuahua

19. Glabrous or nearly so, the intervals between the ribs firm, charged at or just below the orifice with 1-2 brown blister-glands .....*M. minor*
19. Densely pilosulous, the intervals membranous, charged at and near the middle with  $\pm$  3 small, yellow glands .....*M. alamosana*
18. Plants restricted to the Baja California Peninsula
20. Glabrous calyx
21. Calyx rib interval glands 2-4
22. Plant of the Magdalena Bay to Conejo Point, BCS, with almost equal calyx lobes and leaves 1-3.5 cm .....*M. divaricata*
22. Plant of the Cape Region with abaxial calyx lobe much exceeding other lobes, leaves 3-5 cm, keel .....*M. anthonyi*
21. Calyx rib interval glands 1-2(3) .....*M. cabopulmensis*
20. Pubescent calyx .....*M. rebmanii*

## DISCUSSION

Description of overlooked biodiversity is imperative for targeted and efficient conservation efforts to take place. Taxonomy should incorporate new information and reflect our collaborative knowledge of our planet, and therefore, when undescribed diversity is illuminated via phylogenetics, taxonomic follow up is essential to ensure that gained evolutionary understanding is not lost. Especially in regions affected by growing tourism, dense grazing and resource extraction, data on narrowly endemic taxa should be prioritized to increase chances of their survival. *Marina arenaria*, *Marina rebmanii* and *Marina tomentosa* are each only known from less than five populations and should be surveyed for additional populations in suitable

habitat (Figure 19, Figure 20). *Marina leondelaluzii* and *Marina cabopulmensis* should also be surveyed to better understand their ranges because additional populations of both are likely and more information will add to the species concepts introduced here (Figure 20). *Marina cacachilensis* and *Marina anthonyi* have many populations on protected lands for the time being and many of these populations are undisturbed (Figure 20).

Based on morphological study in the herbarium and field, *Marina* of Baja California Sur was identified as a group that needed systematic revision that incorporates the diversity seen since its monograph. We extensively sampled this group to infer a phylogeny based on 266 low copy nuclear regions that illuminated previously unknown evolutionary relationships. Based on this phylogenetic insight and targeted field and museum study, we introduce six new species and one resurrected species to the series *Chrysorrhiza* of the genus *Marina*. Here, we have presented the accumulated data we have for each species, how to identify them and the areas we would like to prioritize for further investigation.

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Table 1: Comparison of morphological characters among *Marina arenaria*, *M. peninsularis*, and *M. chrysorrhiza*.

| character                       | <i>M. arenaria</i>                                                                                                   | <i>M. peninsularis</i>                                                                                                                                                                                                            | <i>M. chrysorrhiza</i>                                                                                                                                                                                                                            |
|---------------------------------|----------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Life history                    | Perennial                                                                                                            | Perennial                                                                                                                                                                                                                         | Annual, short-lived perennial                                                                                                                                                                                                                     |
| Corolla color                   | light pink to yellow<br>with darker banner                                                                           | bright magenta-purple except for the yellow, gland-charged eyespot on the banner                                                                                                                                                  | bicolored, the banner with a small, yellow, the wings and keel vivid purple in inner half, pallid externally                                                                                                                                      |
| Leaf pubescence                 | long wavy hairs, loosely appressed, 0.3-0.4 mm long divergent hairs on stem (0.3-0.4mm)                              | pilosulous throughout with spreading-incurved, or subdeflexed, stiff white hairs up to 0.2-0.35 mm long                                                                                                                           | quite glabrous or thinly pilosulous beneath                                                                                                                                                                                                       |
| Stem glands and pubescence      | scattered, sparse grain like amber glands                                                                            | the stems terete, stramineous, prominently verrucose with protuberant or grain like, mostly livid glands                                                                                                                          | sparsely charged with low blister-glands, sometimes almost smooth,                                                                                                                                                                                |
| Fruit glands                    | Obovate, 2 mm pod, hairy throughout fruit, curly hairs everywhere except on glands, three rows of dark large glands. | obovate in profile, 1.7-2.2 mm long, the style-base terminal but eccentric, the prow prominent but very slender, the valves hyaline in lower half, thinly papery and pilosulous distally, charged with 2 vertical gland-crescents | 1.8-2 mm long, obliquely triangular-obovate in profile, the style-base strongly eccentric, the prow prominent but subfiliform, the valves hyaline in lower half, thence papery, thinly pilosulous, and charged with 2 subvertical gland-crescents |
| Calyx rib glands and pubescence | 5-13, inconspicuous and under dense                                                                                  | 5-7 small, elliptic, pale yellow or                                                                                                                                                                                               | a chain of $\pm$ 5-6 small, honey-colored                                                                                                                                                                                                         |

| character                 | <i>M. arenaria</i>                                                                                | <i>M. peninsularis</i>                                                                 | <i>M. chrysorrhiza</i>                                                                        |
|---------------------------|---------------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------|
|                           | tomentose hairs                                                                                   | hyaline glands                                                                         | glands,                                                                                       |
| Corolla dimensions        | <i>banner</i> 1.3-2.0 mm,<br><i>wings</i> 3.0-4.0 mm<br><i>keel</i> : 3.5-4.5 mm                  | <i>banner</i> 2.7-4 mm long<br><i>wings</i> 2.6-3.2 mm<br><i>keel</i> (3.2) 3.5-4.7 mm | <i>banner</i> 1.6-2.6 mm long<br><i>wings</i> :2.5-3 mm long<br><i>keel</i> :(2.7) 3.3-4.5 mm |
| Leaflet #                 | 6-20 pairs                                                                                        | 6-10 pairs                                                                             | 6-12 pairs                                                                                    |
| Leaflet length            | 2.1-3.4 mm                                                                                        | (1.5) 2-4.5 (5) mm                                                                     | 1-4 mm                                                                                        |
| Leaflet gland pattern     | small glands (0.05-0.1) amber throughout, and then one large 0.4-0.5 linear gland at tip of leaf. | bluntly gland-tipped                                                                   | charged dorsally at or just below apex with a large yellow or orange gland                    |
| Flowers per inflorescence | 6-22                                                                                              | 10-25                                                                                  | 4-12                                                                                          |

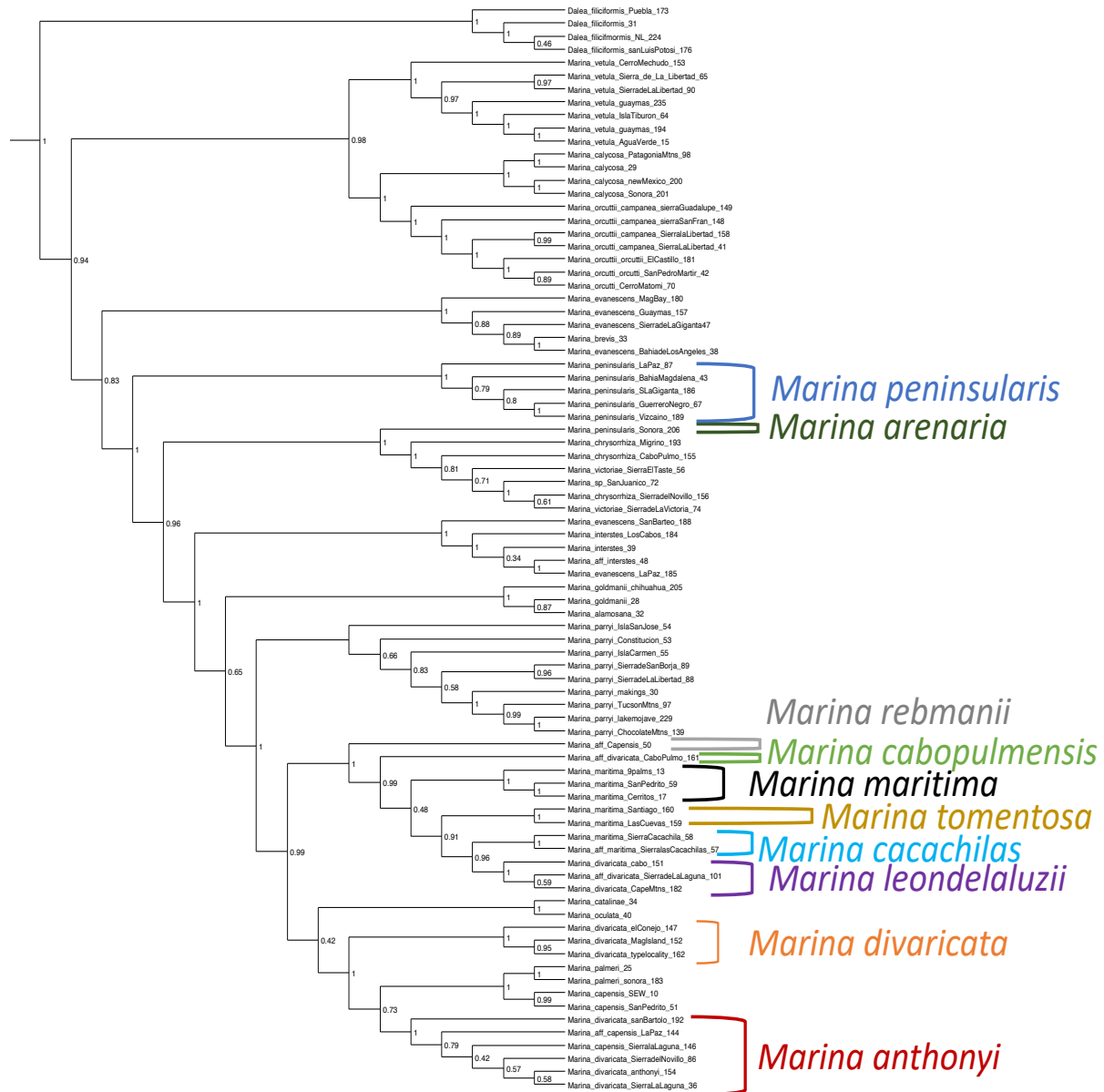


Figure 1: ASTRAL-III phylogeny of the Baja California taxa of *Marina* (series Chrysorrhizae and Vetulae), using *Dalea filiciformis* as an outgroup. New taxa identified on the left as well as species these taxa have previously been included in: *Marina peninsularis*, *Marina divaricata*, and *Marina maritima*.

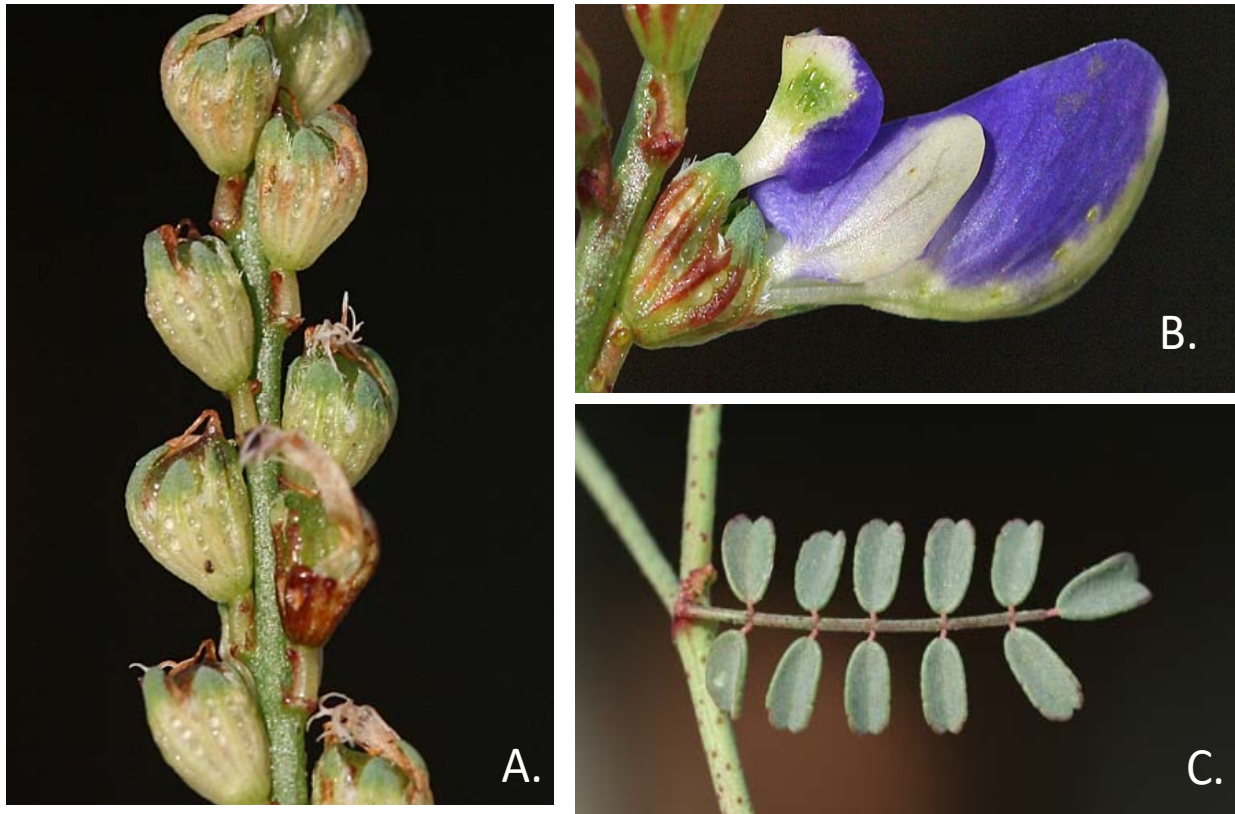


Figure 2: Diagnostic traits of *Marina divaricata* A. Glabrous calyces with many glands per rib interval. B. Flower with green eyespot and red ribs on calyx. C. Small, dainty, notched leaflets, and glabrous, green stem (photos by Jon Rebman).

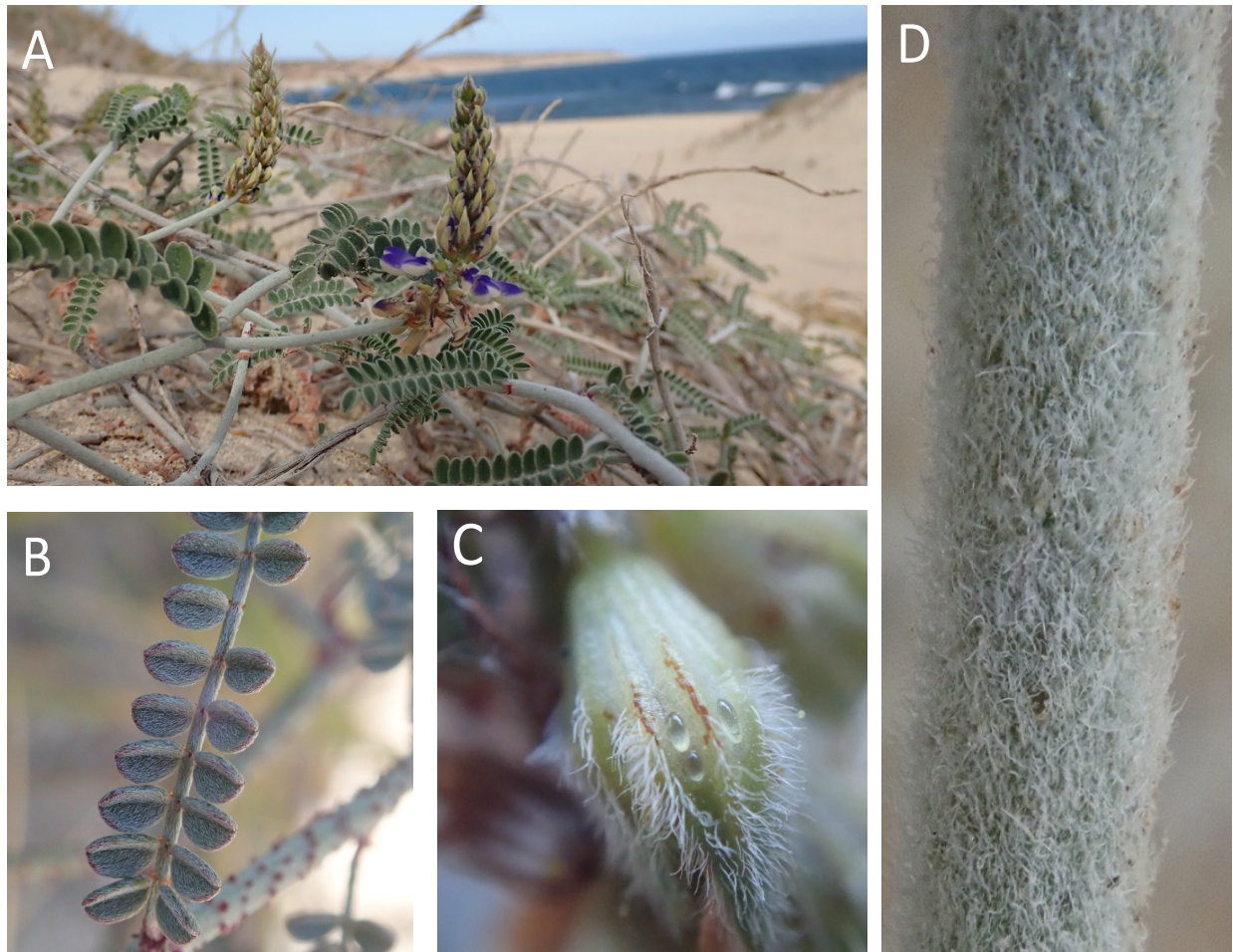


Figure 3: Diagnostic traits of *Marina maritima* A. Plant habit – prostrate in sand. B. Leaf pubescence. C. Calyx rib interval glands 1-2, calyces pubescent. D. Canescent stems.



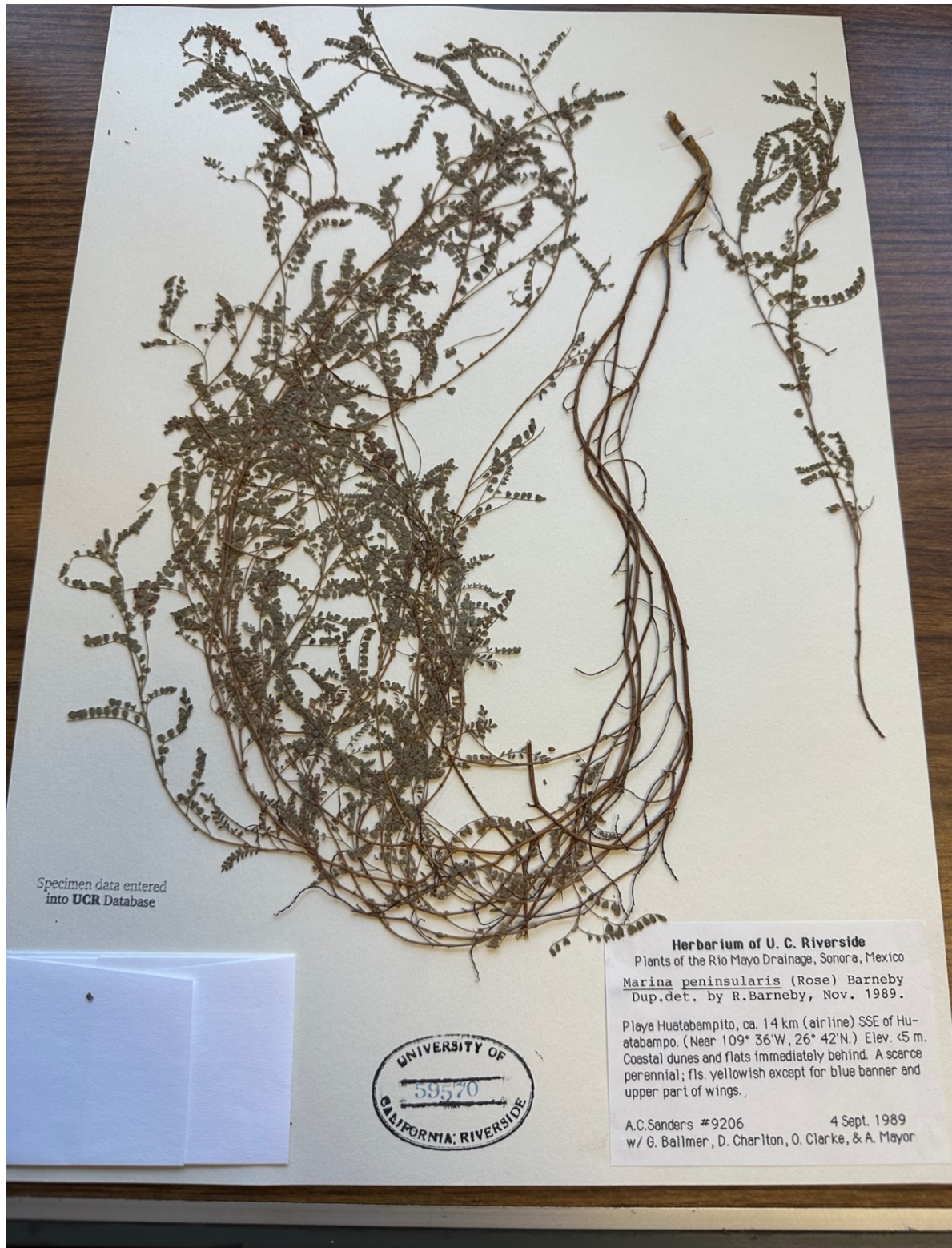


Figure 4: Holotype: SD129347 *Marina arenaria* S.E. Winitzky & J. P. Rebman *sp. nov.*

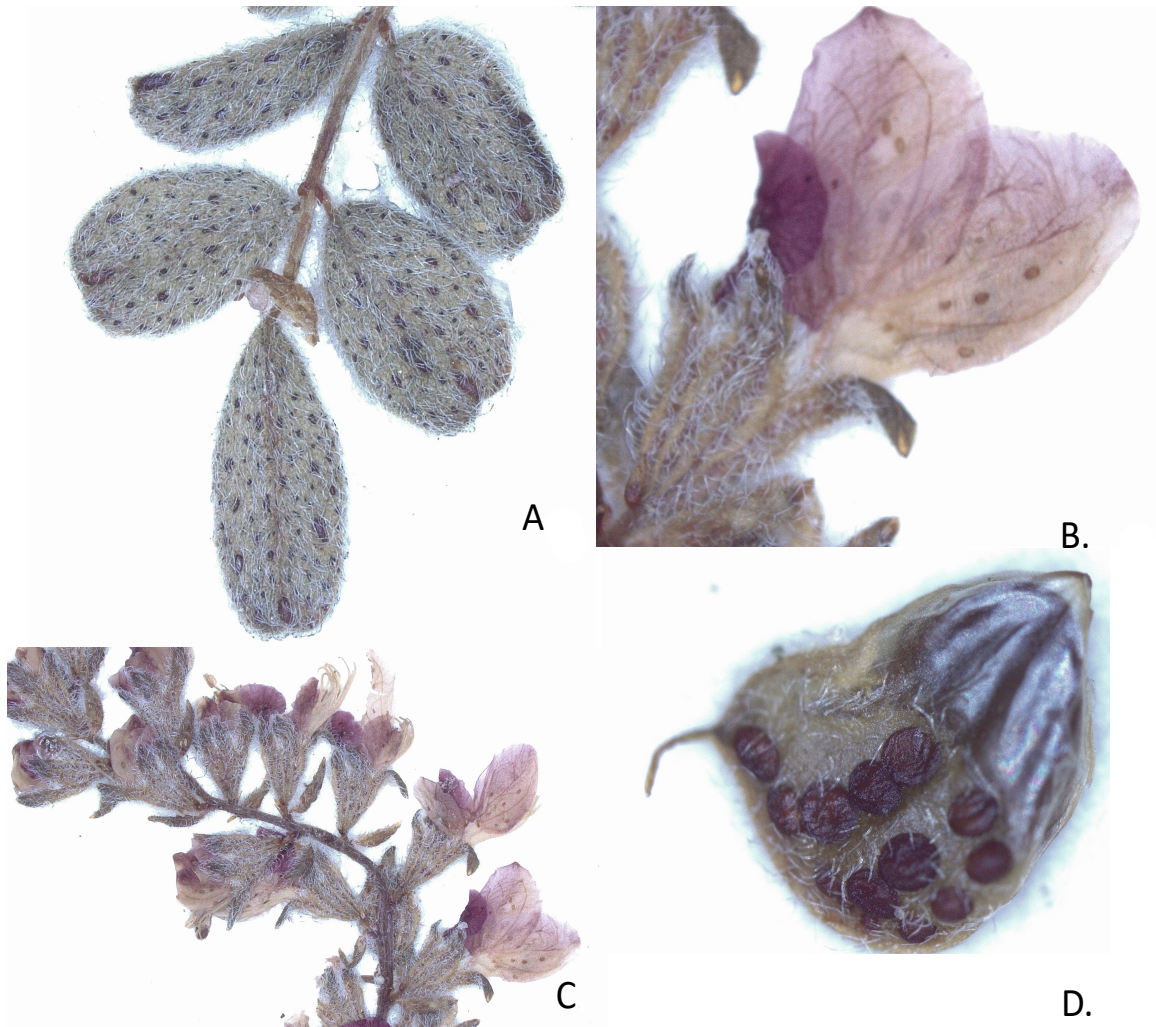


Figure 5: Diagnostic traits of *Marina arenaria* A. Pubescence and gland pattern on leaves; B. Corolla color and petal glands; C. Loose raceme and small floral bracts; D. Fruit gland pattern and pubescence.



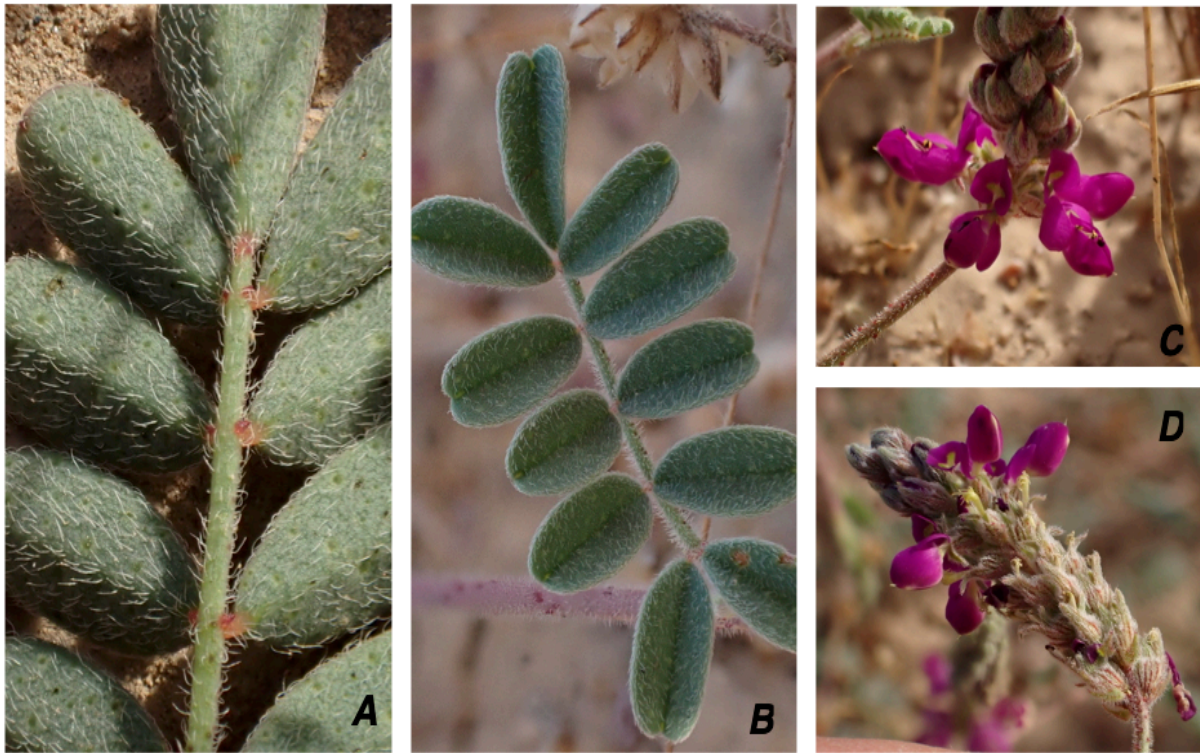


Figure 6: Diagnostic traits of *Marina peninsularis*. A. Incurved leaflet trichomes; B. Leaflet shape longer than that of *M. arenaria*; C. Bright corolla color and keel much larger than other petals; D. Dense raceme or spike and short floral bracts.

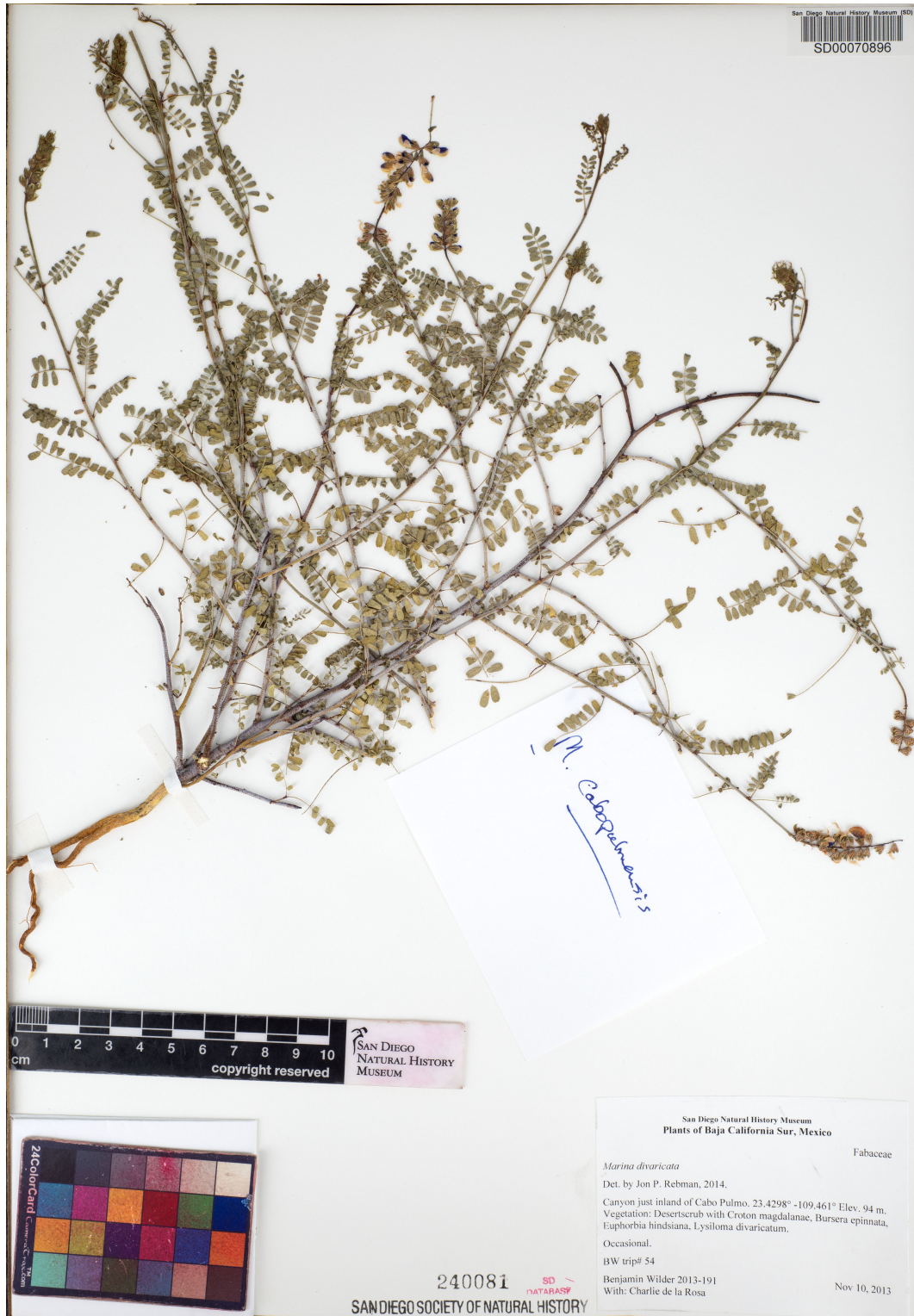


Figure 7: Holotype SD240081 *Marina cabopulmensis* S.E. Winitsky & J.P. Rebman. Benjamin Wilder 2013-191 with Charlie de la Rosa, 10 November 2013.



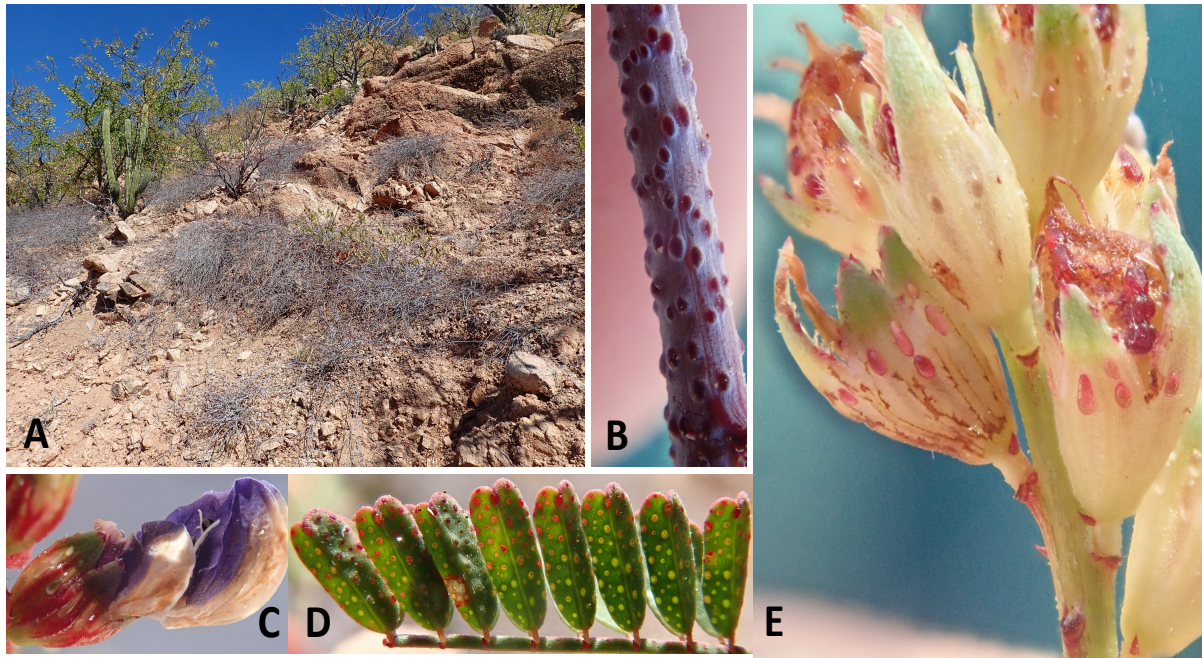


Figure 8: Diagnostic traits of *Marina cabopulmensis*. A. Prostate and drought deciduous on arroyo banks; B. Glaucus stem with large, protruding glands; C. Large, showy flowers; D. Large colorful glands on long leaflets; E. Glabrous calyces with 1-2 glands per rib interval.



Figure 9: Holotype SD228875 *Marina cacachilensis* S.E. Winitzky & J.P. Rebman. Rebman 25429 with John & Fran Reynolds, 21 January 2013.



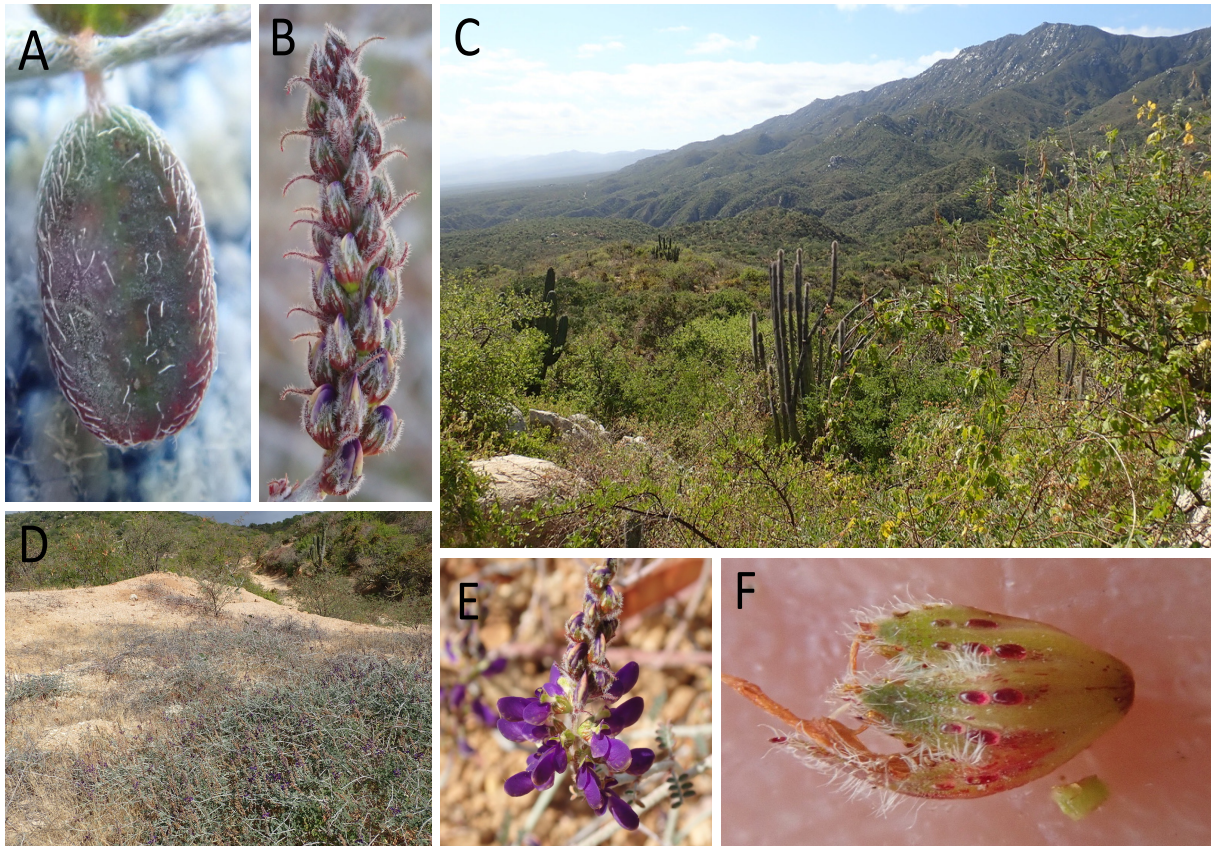


Figure 10: Diagnostic traits of *Marina cacachilensis*. A. Hairs along margins of leaflet; B. Long inflorescence bracts, dense racemes; C. Cacachilas Mountains, densely vegetated throughout most of the landscape; D. Break in vegetation invaded with *Marina cacachilensis*; E. Solidly purple flower; F. Pubescent calyx along ribs and orifice with 1-3 red glands down rib intervals.



Figure 11: Holotype: SD 260496 *Marina leondeluzii* S.E. Winitsky & J.P. Rebman. Jon Rebman 31140 with Michael Rebman, Kathleen Mitchell, & Scott Landis, 05 March 2016.



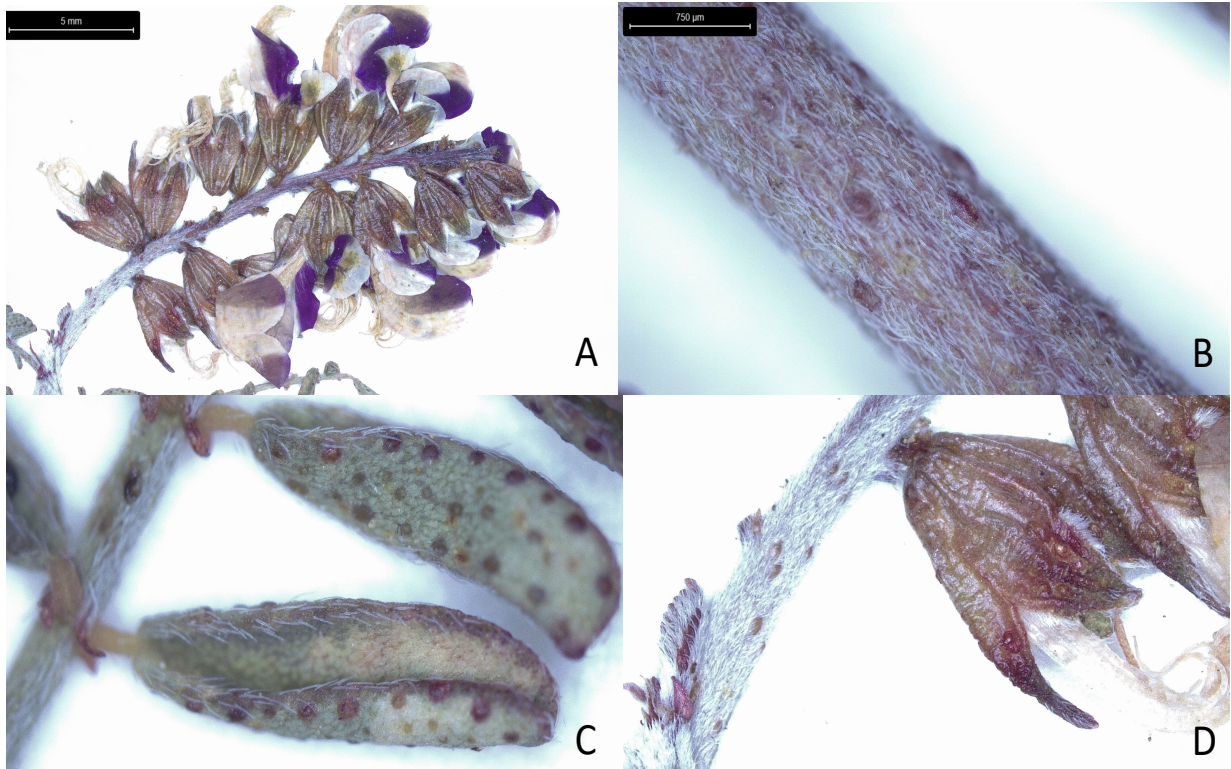


Fig 12: Diagnostic traits of *Marina leondelaluzii*. A. less flowers per inflorescence (18 maximum); B. strigose stems; C. Narrow, folded leaflets, covered in glands abaxially; D. Glabrous, dark colored calyces.



Figure 13: Holotype SD00040851 *Marina tomentosa* S.E. Winitzky & J.P. Rebman. Reymundo Domínguez Cadena 2362, 03 May 2001.



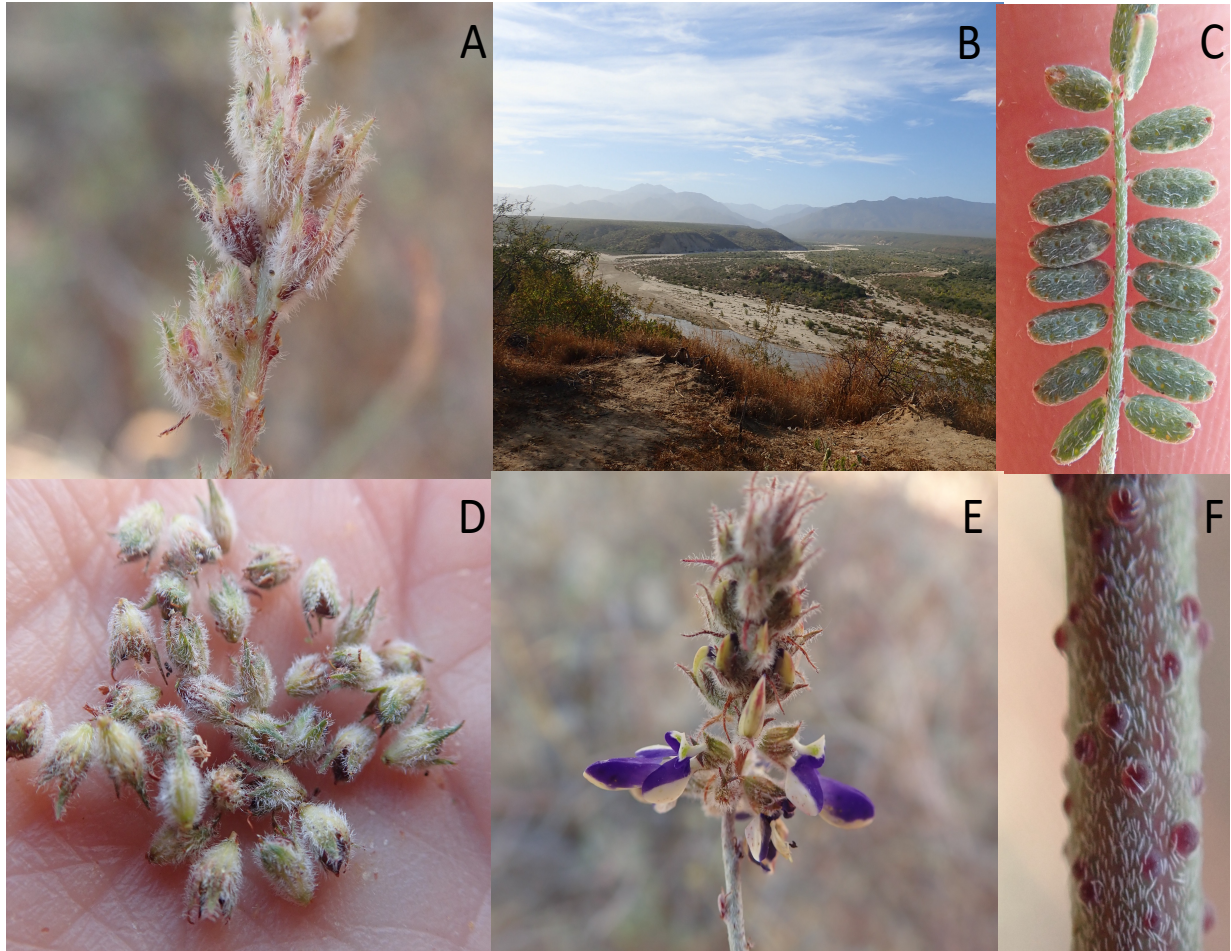


Figure 14: Diagnostic traits of *Marina tomentosa*. A. Long calyces with a single red gland per interval; B. habitat, shoulders of wide arroyo; C. Sparse, strigose hairs on leaflets; D. Calyces densely tomentose; E. Few flowered, loose raceme, long inflorescence bracts; F. Stem with short, sparse, strigose hairs.



Figure 15: Holotype SD00040852 *Marina rebmanii* S.E. Winitzky. Jon Rebman 27652 with Alfonso Medel Narvaez, Jose Luis Leon de la Luz, John LaGrange, 13 November 2013.



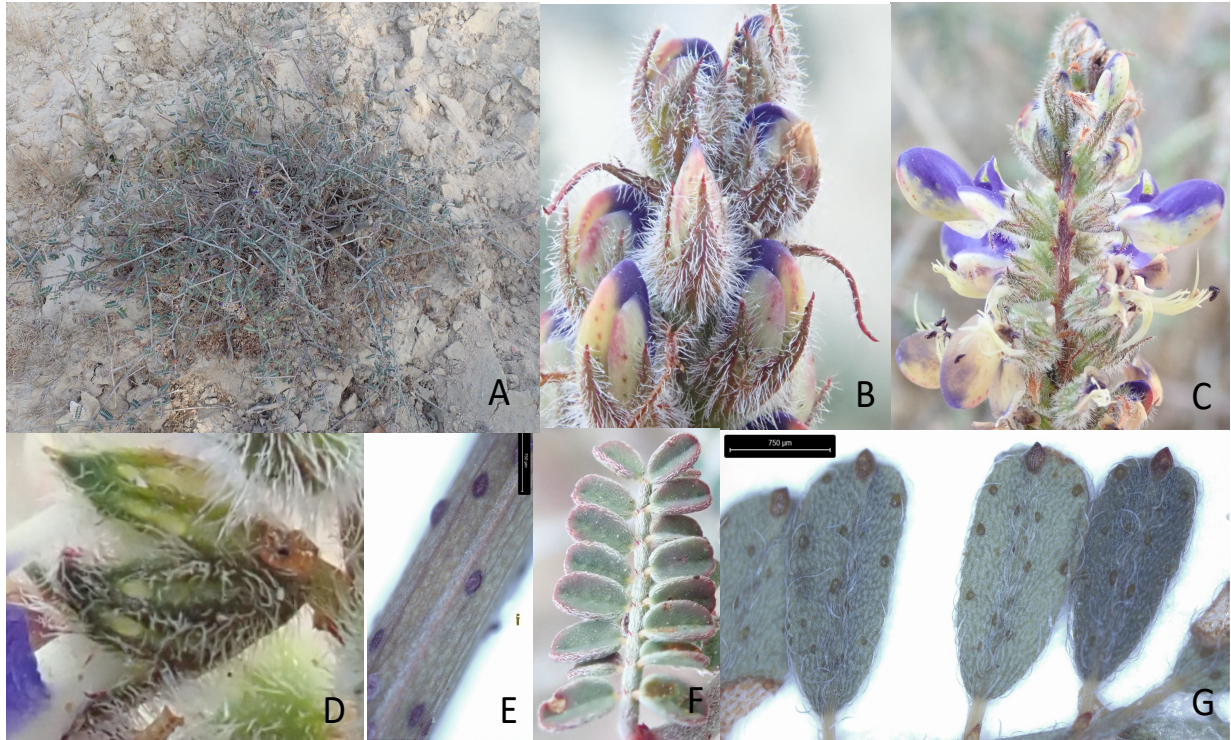


Figure 16: Diagnostic traits of *Marina rebmanii*. A. Habit- dichotomously forking, very stiff branches; B. Long calyx hairs, long, tapering floral bracts; C. Large inflorescence with many flowers per inflorescence; D. 4+ calyx glands per interval; E. Glabrous stem with smoothed glands; F. Short leaves with few leaflets; G. Leaflet gland pattern.

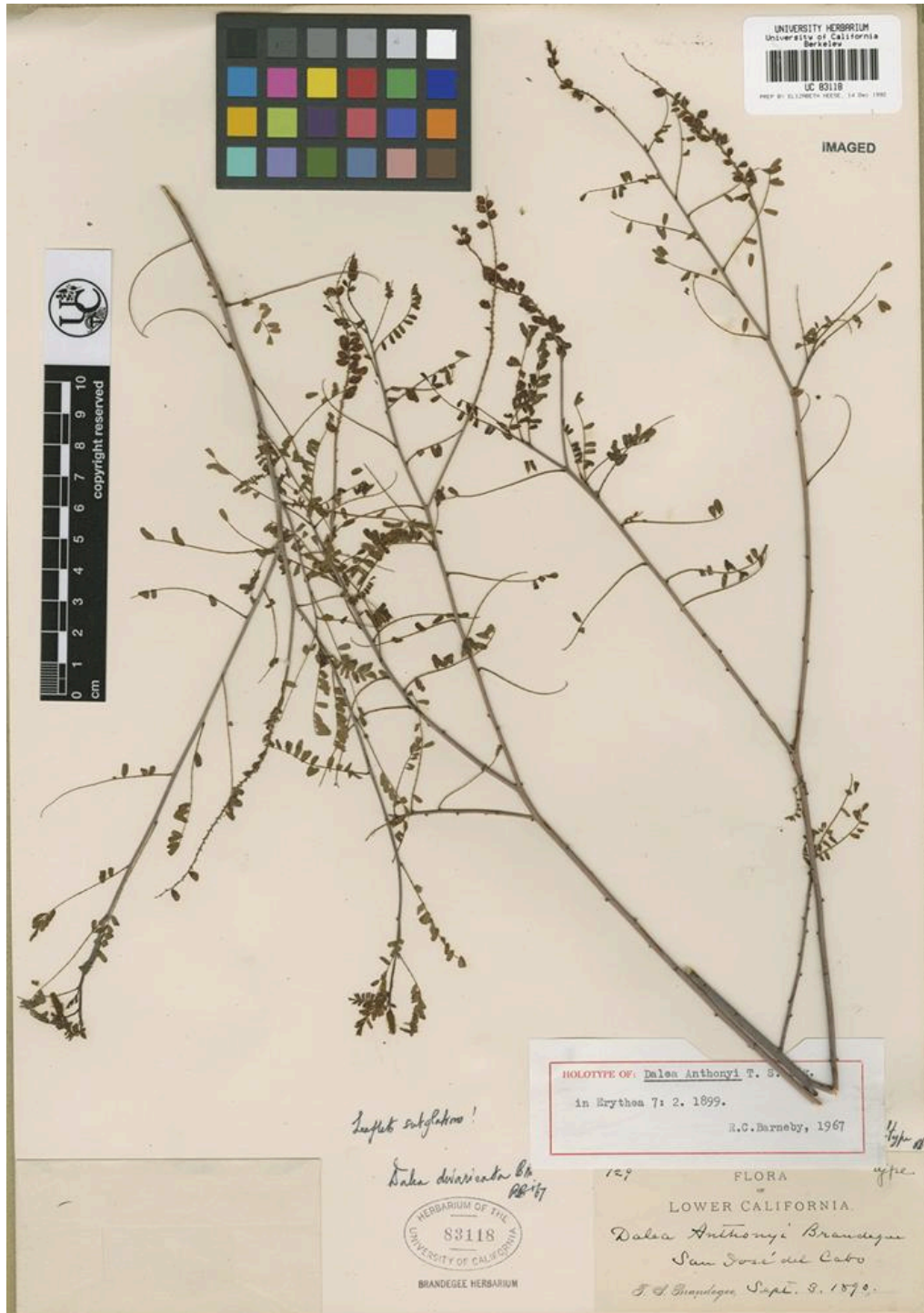


Figure 17: Holotype UC15153 *Marina anthonyi* T. S. Brandegee 129 San José del Cabo, 3 Sept 1890.



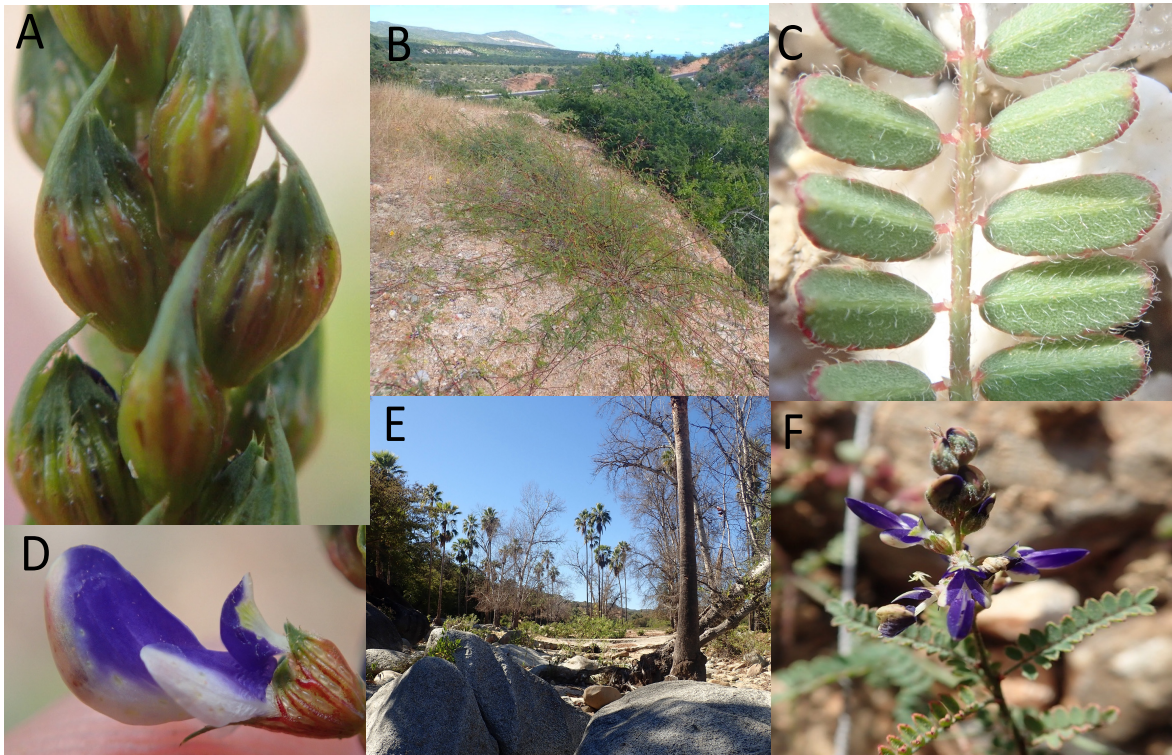


Figure 18: Diagnostic traits of *Marina anthonyi*. A. 2-5 glands per rib interval with a very long abaxial lobe; B. Prostrate growth form, can also be erect; C. Long, soft, hairy morph, with many leaflets per leaf; D. Glabrous calyx with showy flower; E. Often found in arroyos of the cape mountains; F. Few flowered, loose, raceme.

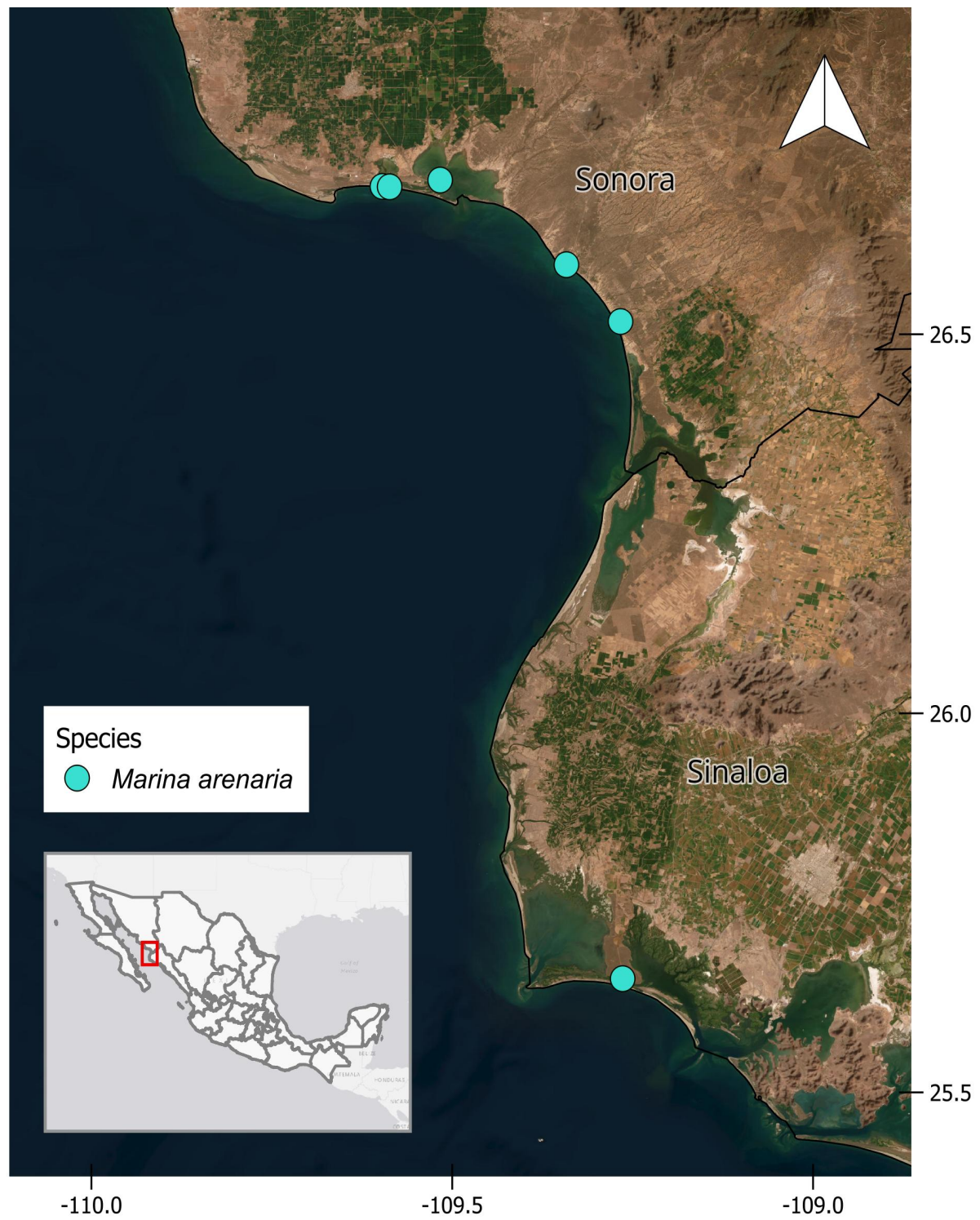


Figure 19: Map of currently known populations of *Marina arenaria* in Sonora and Sinaloa. Made with QGIS and an ESRI layer.



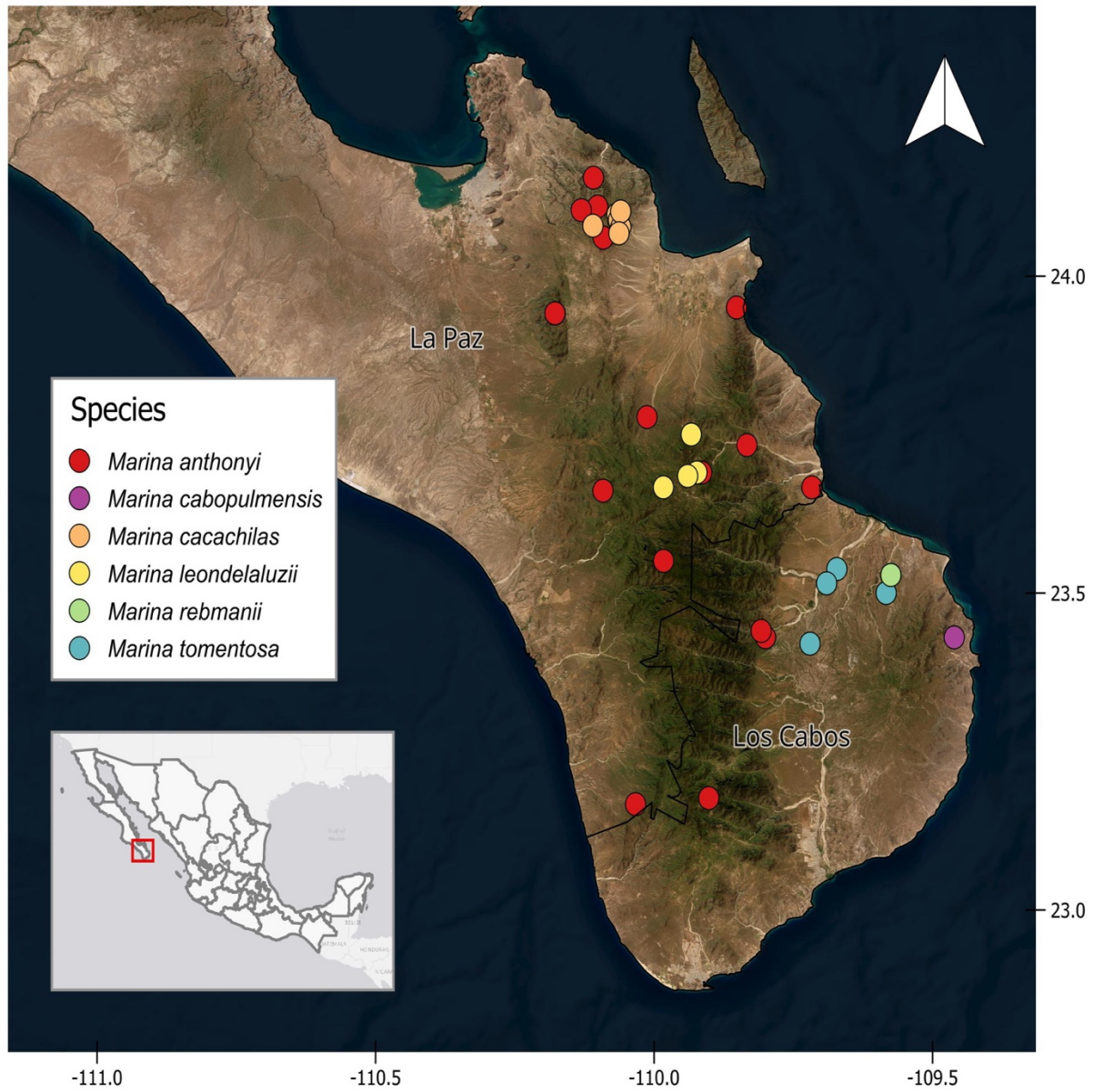


Figure 20: Map of currently known populations of the species described here from Baja California Sur. Made with QGIS and an ESRI layer.

LEAF ECOLOGY OF THE DALEOID AMORPHEAE (LEGUMINOSAE):  
THE REVELATION OF AN UNDESCRIBED LEAFLET  
TYPE ADAPTED TO HIGHLY SEASONAL LOWLAND ENVIRONMENTS

Abstract

Most nitrogen-fixing plant clades are not necessarily ecologically diverse, species rich or widespread. Yet, a high nitrogen metabolism imparted by nitrogen fixation provides a plant with increased photosynthetic capacity, which has evolutionary advantages. Plant adaptations to arid environments that are likely facilitated by high leaf nitrogen content include drought deciduousness, ephemeral leaflets, and opportunistic blooming, traits well developed in *Marina* and related daleoid legumes, the focal taxonomic group of our study centered in Mexico. We explore how leaflet traits derived from measures of carbon and nitrogen content (e.g., intrinsic water use efficiency), in addition to others such as leaflet number and texture, vary across precipitation and temperature regimes. We also explore leaflet traits in a phylogenetic context and how they vary among closely related species. We found that intrinsic water use efficiency ( $\delta wue$ ) estimates were best explained by precipitation during the wettest annual quarter. Low water use efficiency strongly relates to the presence of leaves each with many small wispy leaflets produced mainly by *Marina* species. A low level of phylogenetic signature of this model suggests a flexibility of *Marina* to independently evolve expendable leaflets, with low  $\delta wue$ , among closely related taxa, which collectively inhabit a diversity of hot and dry environments in Mexico. *Marina* plants can rapidly colonize an early serial stage environment or persist in a drought deciduous state in established vegetation. Such observations support the hypothesis that



a facultatively high nitrogen metabolism allows for the rapid production of leaves during a colonization or precipitation event and that *Marina* leaves quickly amortize their production costs so that *Marina* plants can persist in a drought deciduous phase. Such flexibility is an advantage for persistence in drought prone climates of seasonally dry tropical forests and woodlands and adjacent deserts.

### Introduction

Most plant groups that symbiotically fix nitrogen are either geographically restricted or are not species diverse, and this prompted McKey (1994) to review the idea that the ability of most legumes to symbiotically fix nitrogen is not directly responsible for the evolutionary success of the legume family. In contrast to other N-fixing angiosperm clades, legumes are incredibly diverse; ranking third as a family in species numbers and found globally across environments with ecologically varying traits and habits. This led Polhill et al. (1981) to designate legumes as a generalist family. Any evolutionary success of the legume family related to nitrogen fixation may be nothing more than another case among Losos' (2017) many examples of evolutionary one-offs.

Rather than a focus on symbiotic nitrogen fixation as a key innovation, McKey (1994) promoted the idea that a high nitrogen metabolism, which is shared by legumes (Sprent et al 1996) independent of whether it is facilitated by symbiotic nitrogen fixation, ectomycorrhizal associations, or other nitrogen acquisition methods, allowed for faster rates of photosynthesis, which could be advantageous for many reasons including rapid growth during colonization and amortizing costs of deciduous leaf production in highly seasonal environments. McKey follows up on the “evolutionary potential” hypothesis introduced by Rundel (1981) that legume success

may relate to a high nitrogen metabolism that allows for adaptation to local climatic conditions yet promotes flexibility to evolve across environments. McKey (1994) circumscribed the general environment where an elevated photosynthetic capacity related to a high nitrogen metabolism is advantageous. This includes where high ambient temperatures promote elevated metabolic rates (including potentially high rates of nitrogen fixation), where abundant light environments energize chloroplasts, and where ample water promotes open stomata so that high rates of CO<sub>2</sub> diffusion do not limit photosynthesis.

The “evolutionary potential” hypothesis could include the ability of many legumes to regulate their nitrogen fixation rates dependent on soil nitrogen availability (Mathesius 2022), thus allowing legumes to respond to different constraints within highly seasonal environments (Dorvat et al 2020). Studies since McKey’s (1994) have found that legumes not only have the potential for a high nitrogen lifestyle but are also able to express high variability of leaf nitrogen within legume species and across a nitrogen availability spectrum (Wolf et al 2017). Legumes are known for dominating the tropics as forest trees, but many of the most species-rich legume genera include many species of shrubs and herbs that inhabit highly seasonal environments, including *Acacia* sensu lato, *Astragalus*, *Crotalaria*, *Indigofera*, and *Mimosa* (Polhill et al 1981). Species of these genera often inhabit open and disturbed areas where light, in contrast to nitrogen, is not limiting. Regardless of tropical forest, woodland, or desert environment, a facultative nitrogen-fixation system found uniquely in legumes could be advantageous in diverse environments for down-regulating nitrogen fixation where available soil nitrogen is sufficient. Legume atmospheric nitrogen fixation may reflect soil nitrogen availability, but this does not always translate to leaf nitrogen content (Mathesius 2022), which can remain high across

legumes regardless of their nitrogen-fixation rates or nodulation potential (Sprent et al 1996). A high nitrogen metabolism also allows for diversification and specialization of defense mechanisms against herbivores (Polhill et al 1981), which allows for colonization of areas inaccessible without great investment in defenses typical of legumes, as well as temporal defenses against herbivores offered by leaf-flushing (Janzen 1981). In sum, facultative nitrogen fixation of legumes promotes adaptive responses in many directions and environments.

Here we focus on species of the legume genus *Marina*, a daleoid Amorpheae genus in the Papilionoideae (McMahon and Hufford 2005), which fundamentally inhabit McKey's (1994) generalized environment favoring a high nitrogen metabolism. *Marina* species could be more optimized than closely related legume genera for taking advantage of a high nitrogen metabolism and concomitant rapid leaf production. *Marina* species often colonize arid disturbed sites in early seral stages (e.g., riverbanks, roadsides, sites with low vegetation cover). *Marina* species also inhabit later successional environments where they leaf flush in response to a precipitation event, as in seasonally dry tropical forests and woodland (sensu Pennington et al. 2009). *Marina* species are most abundant in the warmer lower elevations and lower latitudes in Mexico, with a few taxa extending into adjacent Central America and southwestern USA. Analysis of collection localities of the five genera of daleoid Amorpheae (from Winitsky et al. Chapter 2), where *Marina* is divided into the Baja California and mainland clades (Winitsky et al. Chapter 1), reveals that Baja California *Marina* and *Psorothamnus* species collectively average the lowest elevation sites among the daleoid Amorpheae (Figure 1, top panel) but that both *Marina* clades and *Psorothamnus* species average the warmest sites (Figure 1, middle panel). Mainland *Marina* species average the highest precipitation sites, whereas Baja California *Marina* species average

the lower precipitation sites, but above those of *Psorodendron* and *Psorothamnus* (Figure 1, bottom panel). *Marina* species thus may be quintessential legumes, using McKey's (1994) argument, in having a flexibility to adapt to diverse arid environments but always where short-lived energetic leaves are produced during favorable wet periods and drought deciduous leaves allow survival in leafless condition during extended dry periods.

*Marina* species may allocate the least carbon to leaves and thus may have some of the most expendable short-lived leaves among tropical legumes. First, the effective leaf (i.e., leaflet) size of *Marina* species often ranges towards the smallest end for the entire legume family, which lies at about 2 mm long, the low end of effective leaf size reported for legumes by McKey (1994). Second, *Marina* leaflets are so thinly textured or chartaceous that when dry they readily disarticulate from the leaf rachis, which is manifested on the many herbarium sheets of *Marina* with disarticulated leaflets (*Marina* herbarium sheets are like those of the mimosoid genus *Desmanthus* in this regard). In addition, disarticulated leaflets of *Marina* species are prone to electrostatic charge such that sampling a *Marina* leaflet requires chasing it down with forceps. Bagging 25 wispy *Marina* leaflets requires something like 20-30 minutes whereas the same task for other legume leaflets including those of close relatives *Dalea* and *Camoufleur* takes less than a minute. Such observations of *Marina* leaves and leaflets suggest they represent minimal plant investments and therefore might have a carbon-nitrogen signature of this (i.e., relatively little carbon in such thinly textured wispy leaflets that maintain a high nitrogen metabolism expected of a legume). McKey's (1994) argument on the ecological importance of short-lived leaves in legumes could explain the wispy ephemeral leaflets of *Marina*.

Our goal has been to sample leaflet traits including those related to nitrogen metabolism from species of *Marina* and other daleoid Amorpheae and from across the temperature and precipitation regimes represented by the habitats of these legumes. We wanted to determine if any leaflet traits, including carbon and nitrogen content of leaflets, or variables derived from measurements of the isotopes of these two elements, vary with climate in a manner that would support the idea that the leaves and leaflets of *Marina* have evolved among environments so as to facilitate both rapid colonization in early serial stage arid environments and persistence in a drought deciduous phase in highly seasonal tropical woody environments.

### Materials and Methods

#### Response Variables

We wanted to explain variation in leaf or leaflet architecture and elemental composition as a function of environment because of the emphasis placed on leaves by McKey (1994). McKey's argument is that a high nitrogen metabolism in legume leaves is important ecologically and has resulted in the evolution of a great range in variation in size, structure, and longevity of legume leaves. We therefore explored which of the following leaf and leaflet traits might best serve as a response variable in a general model where leaf variation is explained by environment. Or how has a facultatively high nitrogen metabolism responded to the environment in terms of leaf trait variation. We also wanted to determine how leaf trait variation with environment varied among the main clades of daleoid Amorpheae. This focus derives from McKey's (1994) many predictions relating legume traits with a facultatively high nitrogen legume metabolism.

### Carbon-Nitrogen Related Leaflet Traits

We obtained carbon and nitrogen content, as well as  $^{13}\text{C}$  and  $^{15}\text{N}$  stable isotope abundances from leaflets representing 130 accessions and 38 species of daleoid Amorpheae (Figure 2; Supplemental Table 1). Leaflet samples came from herbarium specimens or silica-dried field collections, and these represented 28 *Marina*, eight *Dalea*, one *Psorothamnus*, and one *Psorodendron* species (Supplemental Table). We did not succeed in obtaining carbon-nitrogen data for four accessions of *Camoufleur*.

Leaflets were ground, weighed and placed in tins for analysis of carbon and nitrogen concentrations and stable isotope ratios at the Idaho State University Stable Isotope Laboratory where they underwent a Costech ECS 4010 elemental analyzer and a Thermo Delta V Advantage continuous flow isotope ratio mass spectrometer.

Variables derived from stable isotopes of carbon and nitrogen included the following (Supplemental Table):

The abbreviations "N" and "C" represent the percent of nitrogen and carbon found in the leaf and "CN" represents the ratio (C/N) of those elements.

The abbreviations "air $^{15}\text{N}$ " and "p $^{13}\text{C}$ " are the stable isotope signatures of  $^{13}\text{C}$  and  $^{15}\text{N}$  from the plant specimen. These natural stable isotope signatures are useful for investigating ecological processes because plant physiological processes discriminate against heavier isotopes, leading to informative variation in isotopic ratios (Dawson et al 2002).

The abbreviation "A $^{13}\text{C}$ " is the  $^{13}\text{C}$  signature of the atmosphere during the collection date, both year and month because there is seasonal variability as well as annual changes of  $^{13}\text{C}$ . Recorded quantities of  $^{13}\text{C}$  from La Jolla Scripps Institution of Oceanography were used because La Jolla is within our plant collection localities.

The abbreviation "Aco2" is the atmospheric CO<sub>2</sub> recorded at La Jolla (Scripps) at the time of date of collections, which also fluctuates seasonally, conversely to <sup>13</sup>C, and increases over time. We relied on herbarium label data to obtain localities and dates for retrieving quantities of "A13C" and "Aco2".

The abbreviation "delta" is the discrimination of <sup>13</sup>C and the preference for using the lighter isotope <sup>12</sup>C, which is calculated by  $(\text{atmospheric } ^{13}\text{C} - \text{leaf } ^{13}\text{C}) / (1 + \text{leaf } ^{13}\text{C} / 1000)$ .

The abbreviation "ci" is the leaf-level, intercellular CO<sub>2</sub> which is calculated by dividing the atmospheric CO<sub>2</sub> x discrimination of <sup>13</sup>C (delta) minus the atmospheric CO<sub>2</sub> fractionation due to diffusion (4.4) by the difference of the fractionation due to carboxylation (27) and fractionation due to diffusion (4.4). These isotopic fractionation constants are percentages that follow Farquhar, Ehleringer, & Hubick, 1989.

The abbreviation "ci\_ca" is the internal to atmospheric CO<sub>2</sub> ratio, calculated by dividing the difference of discrimination of <sup>13</sup>C (delta) and fractionation due to diffusion by the difference between fractionation due to carboxylation and diffusion.

The abbreviation "i\_wue" represents intrinsic water use efficiency (ppm) estimates, which can be calculated by multiplying the atmospheric CO<sub>2</sub> by (1 - internal/atmospheric CO<sub>2</sub> ratios) which is divided by 1.6 (the diffusivity of H<sub>2</sub>O is 1.6 times that of CO<sub>2</sub>). This estimate reflects the ratio of carbon obtained to water vapor lost through stomata (Dawson et al 2002). This method, contrasting with gas exchange measurements, captures the i\_wue across the time the leaf was being synthesized (Dawson et al 2002), rather than at a specific collection time. Estimates of i\_wue help us understand the relationships between nitrogen content of leaves and traits related to success in seasonally dry environments, which include drought deciduousness, highly ephemeral

leaflets, and opportunistic blooming. Legumes and other nitrogen-fixing plants specifically have a clear relationship between nitrogen content and  $\delta^{15}\text{N}$ , whereas non-nitrogen-fixing plants allocate more nitrogen to photosynthesis (Mathesius 2022). This makes sense in the context of *Marina* species, which tend to grow in environments without light limitation, but where water is seasonally highly limited.

### Physical Leaflet Traits

Physical measurements of leaflet traits were taken from 135 accessions of daleoid Amorpheae specimens. These included quantitative traits such as number of leaflets per leaf (lflt\_lf), weight (mean g per 25 leaflets), surface area (cm<sup>2</sup> per 25 leaflets), and specific leaf area (SLA or leaflet cm g<sup>-1</sup>). Leaflets per leaf vary greatly across Amorpheae taxa and an increase in leaflet number per leaf is hypothesized to be an adaptation to drought, allowing in theory leaves to discriminately shed leaflets depending on water availability (McKey 1994). A total of 25 leaflets per accession were weighed to obtain an average leaflet weight. ImageJ ([imagej.nih.gov/ij/download.html](http://imagej.nih.gov/ij/download.html)) was used to measure the average leaflet surface area from 25 leaflets of each specimen (Schneider et al 2012). SLA was calculated from the average weights and surface areas of 25 representative leaflets from each specimen to capture the investment needed to produce each leaflet (Wright et al 2004). Physical leaflet traits included qualitative traits such as electrostatic charge (yes/no), drought deciduous (present/absent), and life history (growth habit; Supplemental Table). Electrostatic charge was assigned “yes” when a leaflet levitated between open forceps when attempting to manipulate it. For scoring drought deciduousness, we followed Barneby’s (1977) assignments of daleoid Amorpheae species supplemented by field observations. As inferred from Barneby (1977), drought deciduousness is



the ability of a plant to be productive (e.g., maintain green stems or produce flowers or fruits) in leafless condition. Life history was categorized into annual herb, perennial herb, or shrub.

### Explanatory Variables

To determine how the above leaflet traits varied with the abiotic variables, we obtained 19 standard bioclimatic variables (O'Donnell and Ignizio 2012) for each of the 130 daleoid *Amorpheae* accessions represented by carbon-isotope data (Supplemental Table). Bioclimatic values were extracted from WorldClim v.2.0 model layers (WGS84 projection; Fick & Hijmans 2017) using the R program (R Core Team 2023) and the raster R package (Hijmans et al. 2023).

For all explorations of the above variables across different trait categories and among the main clades of daleoid *Amorpheae*, we used the R base packages for analysis of variance, a Tukey Honest Significant Differences tests for multistate trait categories (e.g., clades of daleoid *Amorpheae* and life history) and a Student's t-Test for binary categories (e.g., electrostatic charge and drought deciduousness).

### Model Selection Analysis Including BayesTraits Analyses

We analyzed carbon-nitrogen isotope-derived leaflet traits, physical leaflet traits, and bioclimatic variables separately. For each of these trait categories, we generated biplots from principal component analyses (R Core Team 2023), which permitted the identification of orthogonal sets of traits that had the greatest range of variation across the 130 accessions of daleoid *Amorpheae*. Candidate orthogonal sets of most-variable traits were further inspected with linear and phylogenetic regression analyses. Here, candidate response variables were further

considered if they were associated with consistently significant model coefficients and models with the highest R-squared values.

Exploratory linear regression analyses were conducted in R using base libraries. We made exploratory estimates of Lambda for single variables (e.g.,  $\rho_{wue}$ , N, and various bioclimatic variables) using BayesTraits version 4.0.1 (Pagel & Meade 2023) and the Random Walk (Model A) MCMC option for continuous data and samples of trait data.

Phylogenetic regression analyses were conducted with BayesTraits version 4.0.1 using the independent contrast regression option and samples of trait data (Pagel & Meade 2023). Competing models alternatively included different tree transformation variables, including Variable Rates and Lambda transformations. For some models we estimated Lambda and for other models we set Lambda to a minimum (0.001) or to a maximum value (1.0), where a Lambda of 1.0 suggests the phylogenetic tree has high phylogenetic signal and can accurately predict leaflet trait values among close relatives. Models invoking Variable Rates use a reversible jump Monte Carlo Markov Chain mechanism to stretch and compress branches throughout the tree during model inference, thereby accounting for shifting rates of evolution in leaflet trait values, assuming a Brownian motion model of trait evolution (Pagel & Meade 2023). These models work with a single tree in BayesTraits, so we opted for a maximum likelihood consensus tree derived from RAxML (Stamatakis 2014) on XSEDE, which was accessed using the CIPRES Science Gateway portal (Miller et al., 2010). Winitsky et al. (Chapter 1) present the details of this phylogenetic analysis.

The 38 terminal branches of the daleoid Amorpheae phylogeny (Winitsky et al. Chapter 1) were each associated with leaflet trait data. BayesTraits allows samples of trait data such that

each of the 38 terminal branches (or species) in the daleoid Amorpheae tree were represented by multiple accessions of linked data, which are traits sampled from the same accession (e.g.,  $\delta^{13}C_{leaf}$  estimated for one accession was linked with a bioclimatic variable obtained from the same accession). Multiple linked trait values of leaflets for each of the 38 terminal taxa were randomly subsampled every MCMC generation such that each terminal branch was represented by a different set of linked trait values each generation.

We ran MCMC chains for 130 million generations and sampled parameters every 100 thousand generations. A 30-million-generation burnin therefore yielded 1000 samples with stationary marginal likelihoods. We reran BayesTraits analyses on each model to ensure we achieved MCMC likelihood stationarity. We estimated marginal log likelihood scores using the steppingstone sampler in BayesTraits with 300 stones and each stone ran for 30000 iterations. Marginal log likelihood scores for each model were compared using log Bayes factors following the protocol described in the BayesTraits manual (Pagel & Meade 2023).

## Results

### Quantitative Physical Leaflet Traits Among Daleoid Amorpheae Accessions.

Of four quantitative physical leaflet traits, specific leaf area (SLA) was most variable among daleoid Amorpheae accessions. Among the main clades of daleoid Amorpheae, SLA did not differ because within-clade SLA variation was as much as among-clade SLA variation. Leaf area (mean cm<sup>2</sup> per 25 leaflets) was next most variable and generally orthogonal to SLA (with a Pearson correlation of 0.22). The only physical quantitative leaf trait with some notable variation among daleoid Amorpheae clades was leaflet number per leaf, which showed a weak tendency to

be high in both *Marina* clades especially compared to *Psorothamnus* (but not to *Dalea*; data not illustrated).

#### Quantitative Carbon-Nitrogen Leaflet Traits Among Daleoid Amorpheae Accessions

Of the 13 quantitative carbon-nitrogen leaflet traits,  $\delta^{15}\text{N}$  and  $\text{C:N}$  showed most variation among daleoid Amorpheae accessions and were generally orthogonal (Pearson correlation = -0.32). Estimates of  $\delta^{15}\text{N}$  showed the most significant differences among the main daleoid Amorpheae clades (Figure 3). Subsequent regression analyses demonstrated that models using  $\delta^{15}\text{N}$  as the response variable were consistently associated with significant variable coefficients and the highest R-squared values (e.g., Tables 1 and 2).

#### Qualitative Physical Traits Among Daleoid Amorpheae Accessions

Electrostatically charged leaflets reflect the small thinly textured chartaceous leaflets of many *Marina* species. Such leaflets are lighter in weight and have a smaller surface area than other daleoid Amorpheae leaflets, and they tend to be associated with leaves that have many leaflets per leaf (e.g., >12; Figure 4, top panel). Electrostatically charged leaflets were found in 34 of 37 mainland *Marina* accessions (92%) and 43 of 64 Baja California *Marina* accessions (67%). *Dalea* included 1 of 27 accessions (4%) with electrostatically charged leaflets and *Psorothamnus* accessions were not found to have such leaflets. Wispy electrostatically charged leaflets of mainly *Marina* species are produced where precipitation is greatest during the wettest quarter (Figure 4, middle panel), and they are associated with a lower  $\delta^{15}\text{N}$  (Figure 4, bottom panel). Models explaining  $\delta^{15}\text{N}$  therefore explain the presence of small wispy leaflets produced mainly by *Marina* species.

### Bioclimatic Variables

Of the 19 bioclimatic variables, those involving precipitation and precipitation seasonality consistently showed the greatest differences among the main clades of daleoid Amorpheae, especially between the Baja California and mainland *Marina* clades. These included precipitation during the wettest quarter (bioclimatic variable 16; Figure 5) and mean annual precipitation (bioclimatic variable 12). Subsequent regression analyses demonstrated that models using bioclimatic variable 16 or 12 as an explanatory variable, and  $\delta wue$  as the response variable, were consistently associated with significant variable coefficients and the highest R-squared values, with bioclimatic variable 16 performing slightly better in these regards (Tables 1 and 2).

### Linear Regression Analysis

The model  $\delta wue$  as a function of bioclimatic variable 16 plus daleoid Amorpheae clade reveals distinctions among the four main clades of daleoid Amorpheae (Table 1; Figure 6). Substituting bioclimatic variable 12 (mean annual precipitation) produced similar model coefficients and R-squared values (Table 2). Baja California *Marina* have leaves with the highest average  $\delta wue$  and inhabit environments with lower precipitation regimes, whereas mainland *Marina* have leaves averaging lower  $\delta wue$  and inhabit environments at the wetter end of the precipitation gradient (Figure 5). This daleoid Amorpheae moisture gradient is concentrated at the dry end of the tropical precipitation gradient given that >90% of daleoid Amorpheae occurrences occupy sites with a mean annual precipitation of less than 1000 mm (Figure 1; bottom panel). Wispy electrostatically charged leaflets, those most often associated with low  $\delta wue$ , are common to mainland *Marina* (Figure 4, bottom panel).

### Phylogenetic Regression Analysis

The phylogenetic regression analysis reveals that model  $\delta_{wue}$  as a function of precipitation during the wettest quarter (bioclimatic variable 16) was always associated with the most significant model coefficient estimates (pMCMC) and highest R-squared values (Table 3). Model selection also revealed that phylogeny is an unimportant model variable (Table 3) because we found that a Lambda set close to 0 (i.e., 0.001) was always associated with the highest log likelihood scores, sometimes significantly so. When models setting Lambda = 0.001 were not significantly better fitting than models that estimated Lambda, Lambda estimates were always low at about or less than 0.42 (Table 3). Models setting Lambda = 1.0 were always worse fitting (Table 3). Individual estimates of Lambda for most quantitative leaflet trait data were generally low (e.g., for leaflet N, estimates of Lambda  $\approx$  0.37) except for  $\delta_{wue}$  where for this leaflet trait estimates of Lambda  $\approx$  0.67.

### Discussion

The best fitting model of  $\delta_{wue}$  as a function of precipitation during the wettest quarter was associated with weak phylogenetic signature. This suggests that closely related samples of species do not covary with respect to  $\delta_{wue}$  as a function of climate. Leaflet traits related to  $\delta_{wue}$  are free to evolve depending on local climatic conditions. This finding is in line with the mixed results reported in earlier legume studies investigating leaf nitrogen content in a phylogenetic context. Some studies have found phylogenetic signal at a coarse level (Fyllas et al 2009), while others have found phylogeny irrelevant to nitrogen content (Bhaksar et al 2009). This may reflect the wide variation of nutrient acquisition strategies, life forms, and successional roles exhibited by legumes, which suggests that legumes, even among close relatives, are phylogenetically

unconstrained to evolve among functional groups. In *Marina* and other daleoid Amorpheae, this is exemplified by species or populations that are primary successional colonizers versus species or populations that are drought deciduous inhabitants of established arid vegetation.

We found great differences between the Baja California and mainland *Marina* clades (Figure 2; Winitsky et al. Chapter 1) with respect to precipitation regimes (Figures 1 - bottom panel, 3, and 6). Such precipitation variation lies entirely within arid environments because the entire daleoid Amorpheae clade inhabits environments with generally less than 1000 mm of annual precipitation (Figure 1, bottom panel; Winitsky et al. Chapter 2). This is well below the annual precipitation threshold of about 1200 mm that determines seasonally dry tropical forests and woodlands rich in arborescent succulent plants from other lowland tropical woody vegetation such as savannas and wet forests (e.g., Oliveira-Filho 2013; Ringelberg et al. 2020).

#### Leaves and Leaflets of Daleoid Amorpheae

Perhaps the wispy leaflets of many *Marina* species, which are associated with low  $\rho_{wue}$ , are optimized to take advantage of highly seasonal precipitation in the environments inhabited by *Marina* species. They may well be inexpensive to produce in terms of carbon input such that they amortize their cost during a brief wet period and are readily expendable during subsequent drought. In the arid environments inhabited by *Marina* species, it is at the wetter end of the seasonal precipitation gradient where the wispy leaflets of *Marina* are most commonly produced (Figure 4, middle panel). The production of wispy ephemeral leaflets of many *Marina* species where precipitation during the wettest quarter averages about 400 mm, and that are associated with low  $\rho_{wue}$ , suggests these leaves are highly optimized to be functional only during wet periods yet readily lost during the inevitable subsequent drought period, which can be extensive

if not erratic within and among years. This represents yet another option for dealing with highly seasonal precipitation of deserts and neotropical seasonally dry woodlands and forests. This and the non-universal production of wispy ephemeral leaflets among species and accessions of both the mainland and especially the Baja California *Marina* clades explains why phylogeny is an unimportant explanatory variable (i.e., wispy leaflets are prone to convergent evolution in *Marina*), and precipitation seasonality (bioclimatic variable 16) explains  $\delta^{13}C$  somewhat better than mean annual precipitation (bioclimatic variable 12; Table 3).

Wispy leaflets found commonly but non-universally in *Marina* may represent an apomorphic tendency (sensu Cantino 1982) that unites all species of the genus *Marina*. *Marina* perhaps uniquely can vary the most in producing non-wispy and high- $\delta^{13}C$  leaflets, or wispy low- $\delta^{13}C$  leaflets, depending on the degree of the seasonality and other environmental constraints. The evolution of distinctive wispy leaflets by *Marina* species represents another way in which legumes effectively produce deciduous leaves that rapidly amortize their carbon production costs and become readily expendable as drought inevitably ensues. Such an ability of legumes to readily evolve diverse leaf traits is what led McKey (1994) to conclude that the high nitrogen metabolism rather than biological nitrogen fixation of legumes is the cause of high levels of legume trait diversity and legume abundance and species richness in many environments especially in the lowland tropics.

We found that larger numbers of leaflets per leaf corresponded well with a wispy leaflet texture, in addition to a lower  $\delta^{13}C$  in daleoid Amorpheae (Figure 4, top and bottom panels). Although daleoid Amorpheae leaves vary greatly in leaflet number, from one to 29 leaflets per leaf, most of these species produce small sized leaflets (Figure 7) regardless of leaflet number



per leaf (Supplemental Table). Although mainly species of *Marina* produce leaves with many wispy leaflets, a few *Marina* species produce leaves with five or fewer leaflets and these tend to be larger, as exemplified by species of *Marina* series *Unifoliolatae* (Rydberg) Barneby. The correlation between leaflet number per leaf and average cm<sup>2</sup> of 25 leaflets is -0.34 (Supplemental Table). In general, *Marina* leaves with few leaflets tend to have a somewhat thicker texture and generally have longer lifespans, as inferred by the observation that they don't readily disarticulate from the leaf rachis on herbarium specimens. Such *Marina* leaves are produced by species in the wetter and less seasonal regions in southern Mexico, where they may not rely on leaf flushing following a precipitation event or drought deciduousness during dry periods.

The especially short-lived leaves and leaflets of mainly *Marina* species may provide at least a few ecological advantages, in addition to rapid growth during colonization or leaf flushing during a precipitation event (McKey 1994). For example, short-lived high-nitrogen leaves can function in the proliferation of mobile chemical defenses like alkaloids and isoflavonoids, which are known from tribe Amorpheae (Salem et al 2006, Belofsky et al 2013). McKey (1994) points out that non-mobile chemical defenses, such as tannins and fiber, are lost when leaves and leaflets are shed whereas mobile chemical defenses are not. Leaf-flushing of short-lived leaves can satiate herbivores such that an average leaf has a high probability of amortizing its cost before it is attacked, and simultaneously shedding infected leaves and subsequently persisting in leafless condition during extended drought may effectively rid a *Marina* population of important herbivores and offer the general opportunity of phenological escape from leaf predators.

Leaf and leaflet morphological variation now known to occur among daleoid Amorpheae exists in spite of a uniformity in seed morphology and mode of germination. Seed germination in

all of the legume tribe Amorpheae is epigeal, where the cotyledons quickly become leaf-like and photosynthetic (Smith 1983), a type of legume germination that is common throughout open environments (Duke and Polhill 1981). According to McKey (1994), epigeal germination, as found in Amorpheae, is predicted to be most common in legumes, including among nitrogen-fixing legumes, because photosynthetic leaf-like cotyledons promptly engage the legume seedling in a high nitrogen metabolism. Given that legumes are most abundant and diverse in warm, open, and nutrient-rich settings (the last perhaps in microsites), they often inhabit environments that are not resource limiting. The operation of a nitrogen-demanding strategy is thus likely early in seedling ontogeny in most legumes (McKey 1994), and thus in species of Amorpheae.

#### Nitrogen Content of Daleoid Amorpheae

Leaves of legumes are on average at the high end of nitrogen concentrations (McKey 1994), although nitrogen content has been found to be quite plastic within taxa, depending both on the sources of available nitrogen and the strategies of acquisition employed by the plant (Dovrat et al 2020, Bhaskar et al., 2016, Wolf et al., 2017). When comparing our dataset of carbon and nitrogen concentrations and their stable isotope ratios to legume leaves sampled across genera of the Brazilian cerrado (which contains no daleoid Amorpheae), daleoid legumes have consistently higher leaf nitrogen levels. The highest concentration from the Brazilian study was from *Indigofera*, reaching 2.68% nitrogen (Sprent et al 2006). Leaflets from our daleoid dataset (Supplemental Table) had many representatives with leaf nitrogen above the concentration found in *Indigofera*. The average leaf nitrogen of our dataset was 2.93%, suggesting that daleoid Amorpheae have a relatively high leaf nitrogen content. Although high

leaf nitrogen content was previously hypothesized to be correlated to high rates of nitrogen-fixation, additional surveys of non-nodulating legumes reveal that they also maintain high leaf nitrogen (Sprent et al 2006, McKey 1994). A study from seasonally dry tropical forests and woodlands of Mexico, where many daleoid Amorpheae, especially *Marina* species, are abundant and diverse, found that legumes varied more widely in nitrogen content than non-legumes (Bhaksar et al 2016). A glasshouse study of four herbaceous Mediterranean legumes that measured leaf nitrogen concentrations under differing soil nitrogen and inoculation scenarios found a range of 1-8% leaf nitrogen content (Wolf et al. 2017). This encompasses the entire range of nitrogen content known for plants, suggesting that a wide range of nitrogen content is possible within and among legume species. These Mediterranean species exemplify an extra-tropical legume growth habit of colonizers in early successional settings similar to *Marina*. Wolf et al. (2017) hypothesize that these findings of extreme plasticity in leaf nitrogen content have advantages among variable post disturbance settings. This is the same argument we are making for the diverse arid environments inhabited by *Marina* species and the ecological advantages they gain by having a high leaf nitrogen content, which may well facilitate a plasticity in  $\delta^{15}\text{N}$  estimates (Figure 3; Baja California versus mainland *Marina* clades).

#### Sources of Daleoid Amorpheae Leaf Nitrogen.

Hedin et al.'s (2009) leaky nitrostat hypothesis posits that biological nitrogen fixation by canopy epiphytes and shallow soil heterotrophs, in addition to atmospheric nitrogen deposition, input sufficient nitrogen into tropical wet forests to up-regulate the nitrogen cycle and offset losses due to leaching. The leaky nitrostat model could well apply to seasonally dry tropical forests and woodlands and adjacent deserts where arborescent succulent plants are common (e.g.,

Ringelberg et al. 2020) and where legumes are abundant and species rich (Pennington et al. 2009). In addition to epiphytes, soil heterotrophs, and atmospheric deposition inputting nitrogen, seasonally dry tropical woodlands and deserts regularly experience extensive and erratic drought. A precipitation event in such highly seasonal tropical environments likely releases soil nutrients, which derive from death and decay during the preceding drought. A high nitrogen metabolism may give legumes such as *Marina* a metabolic advantage in responding rapidly to a precipitation event not only by leaf flushing inexpensive leaves that quickly amortize their production costs before the next drought period, but also by promptly scavenging soil nutrients released by the precipitation event.

Although our study does not attempt to classify the sources of nitrogen in the leaves of daleoid Amorpheae, whether from fixation or from the soil, previous studies (Shearer et al 1983) have estimated that Papilionoideae of the Cataviña region, Baja California, fix 70 percent of their nitrogen from the atmosphere. To make these estimates determining the sources of nitrogen, it is necessary to obtain  $^{15}\text{N}$  ratios from non-nitrogen fixing plants in the same environment as well as measurements of soil  $^{15}\text{N}$  abundances. Since *Marina* often grows in legume dominated landscapes, natural abundances of nitrogen isotopes will be impacted from surrounding nitrogen fixers. Regardless, our goal at this point is to attempt to explain any leaflet trait variation that is related to carbon and nitrogen content (e.g.,  $\delta^{15}\text{N}$  as a function of environment and phylogeny.)

### Conclusion

Throughout seasonally dry neotropical woodlands and forests and adjacent deserts, where *Marina* and other daleoid Amorpheae are abundant and species diverse, the legume family is also abundant and species rich. Our study suggests that the advantage of the facultatively high

nitrogen metabolism of legumes in harsh environments where drought can be extensive and erratic, both within and among years, is likely related to an evolutionary flexibility imparted by such a metabolism. Among the many leaf, seed, and seedling traits enumerated by McKey (1994) and others that relate to the advantages of a facultatively high nitrogen legume metabolism, we think our study reveals yet another type of such a trait, which is found mainly among species of *Marina*. That is a legume leaflet that is designed to be especially short-lived because it is adapted to environments where wet periods span only short time intervals on average. A small wispy leaflet minimally invested in carbon yet rich in nitrogen content may represent one apex in the evolution of a legume leaf, as described by McKey (1994), where a leaf is optimally designed to amortize its production costs during a short-wet season, perhaps involving a colonization event, and before the next inevitable drought ensues. Then, a *Marina* plant can persist in a drought deciduous, or leafless condition. This small wispy leaflet revealed by our study, which is associated with low  $\delta^{15}N$  and prone to convergent evolution, represents just one of many legume traits that relate to the evolutionary advantages of a facultatively high nitrogen legume metabolism. This finding further underscores the flexibility and evolutionary potential imparted by such a metabolism.

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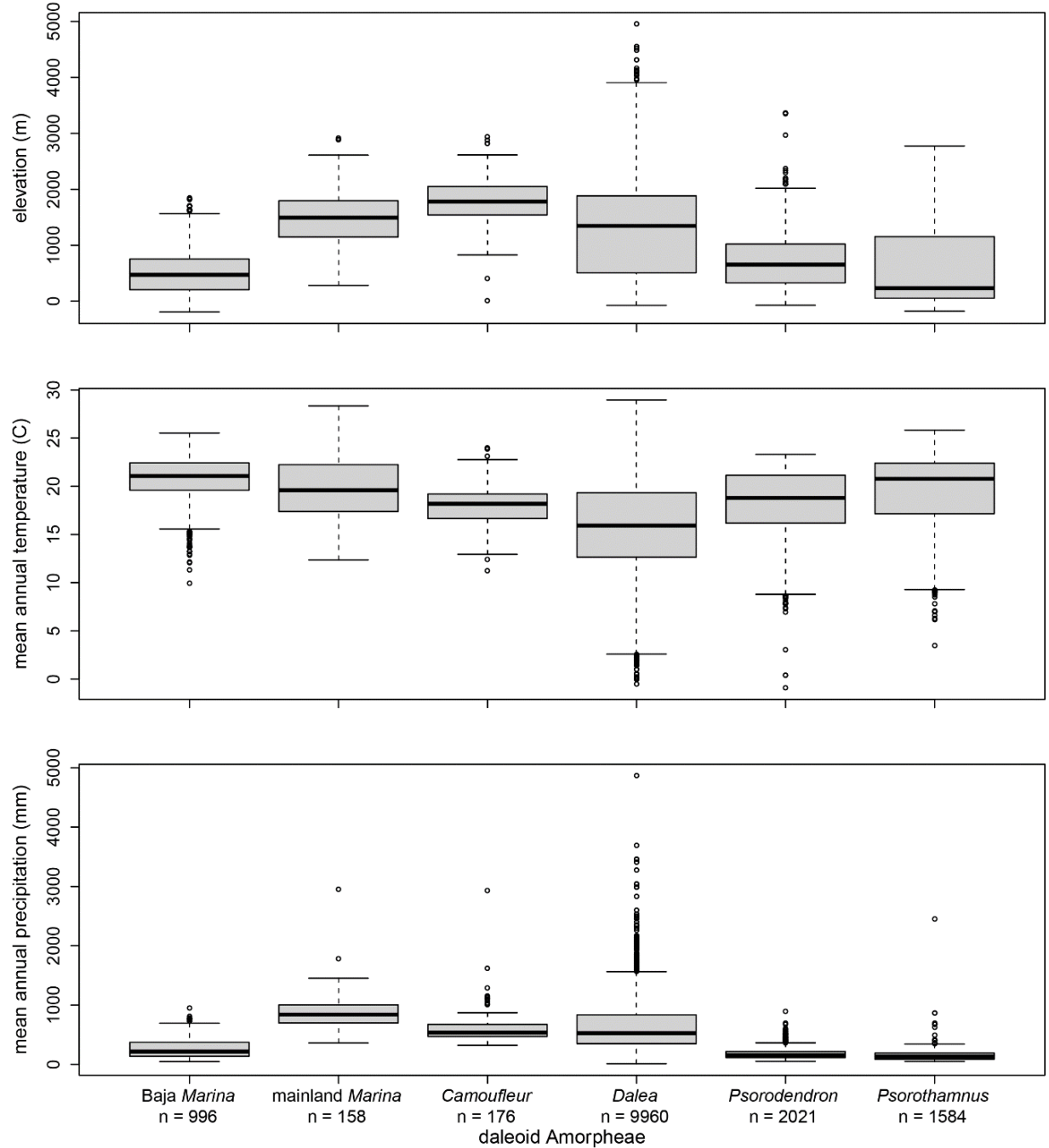


Figure 1. Elevation and climate differences among the daleoid Amorpheae. Top panel: elevation (m) where, according to Tukey's Honestly Significant Difference post-hoc test, Baja California Marina and *Psorothamnus* do not differ. Middle panel: mean annual temperature (degrees C) where the two *Marina* clades and *Psorothamnus* do not differ. Bottom panel: mean annual precipitation (mm) where mainland *Marina* averages the highest values and Baja California *Marina* averages lower values but above those of *Psorodendron* and *Psorothamnus*. Bioclimatic variables represent 14,865 herbarium collections of the five genera of daleoid Amorpheae (Winitsky et al. Chapter 2), where *Marina* is divided into its two principal subclades (Winitsky et

al. Chapter 1). In all boxplots, the thick horizontal line represents the median value, the box encompasses 50% of the data points, the whiskers 95% of the data, and points represent outliers.

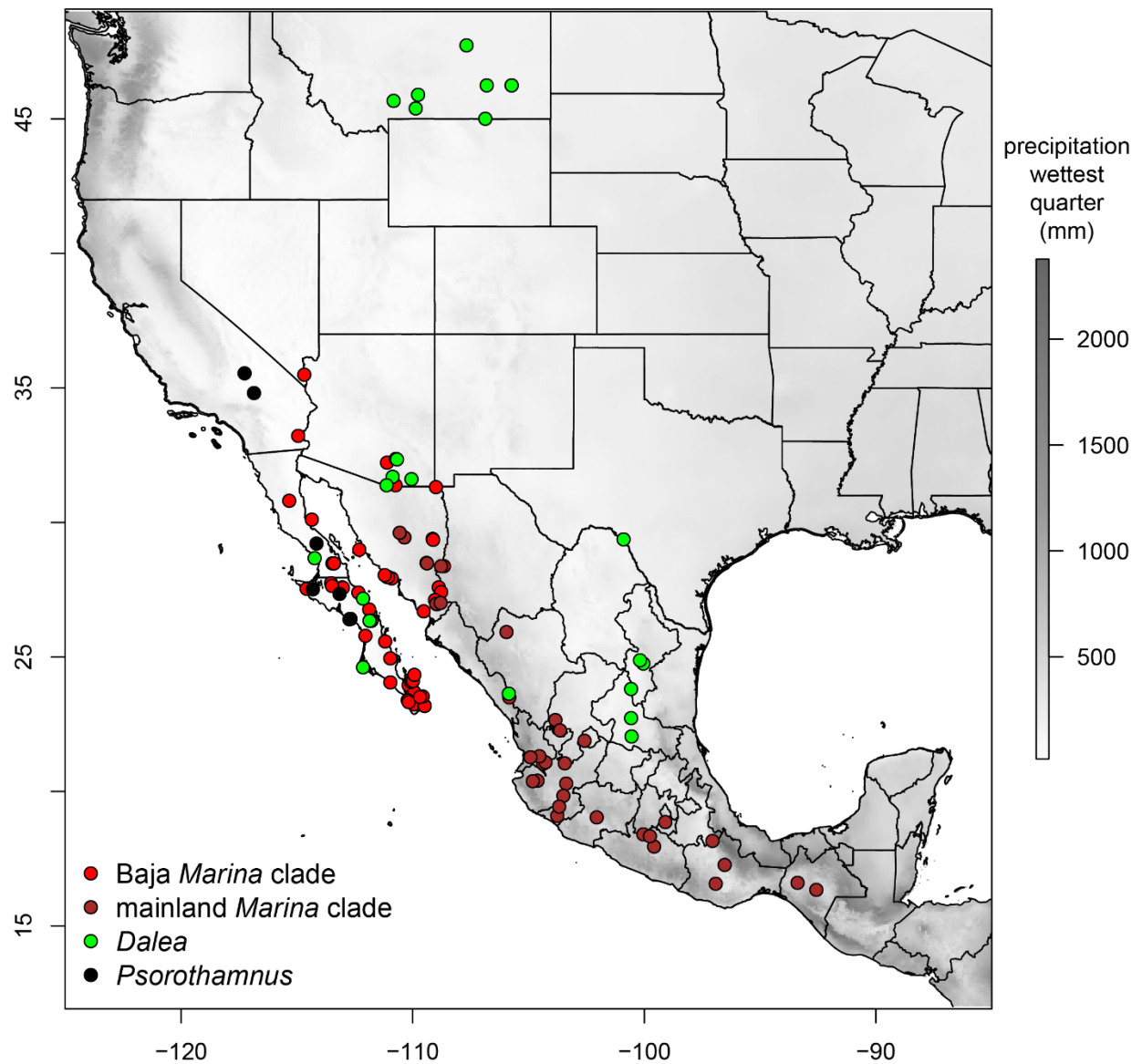


Figure 2. Geographic distribution of the 130 daleoid *Amorpheae* accessions sampled for carbon- and nitrogen-derived leaflet traits.

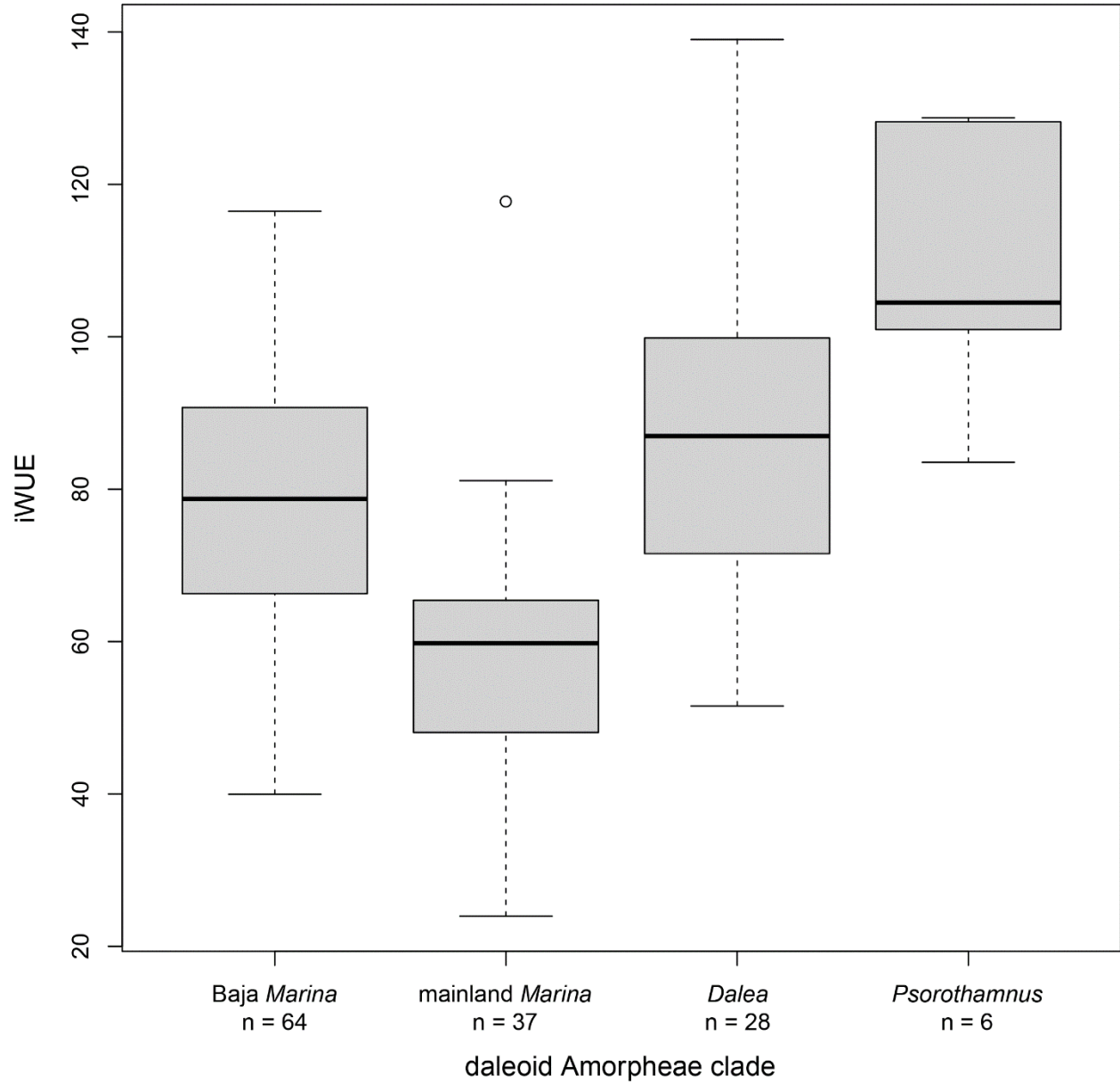


Figure 3. Water use efficiency (iWUE) as a function of the main clades of daleoid Amorpheae. Tukey's Honestly Significant Difference post-hoc test revealed significant differences for all pairwise comparisons except for the *Dalea*-*Psorothamnus* comparison ( $p = 0.11$ ).

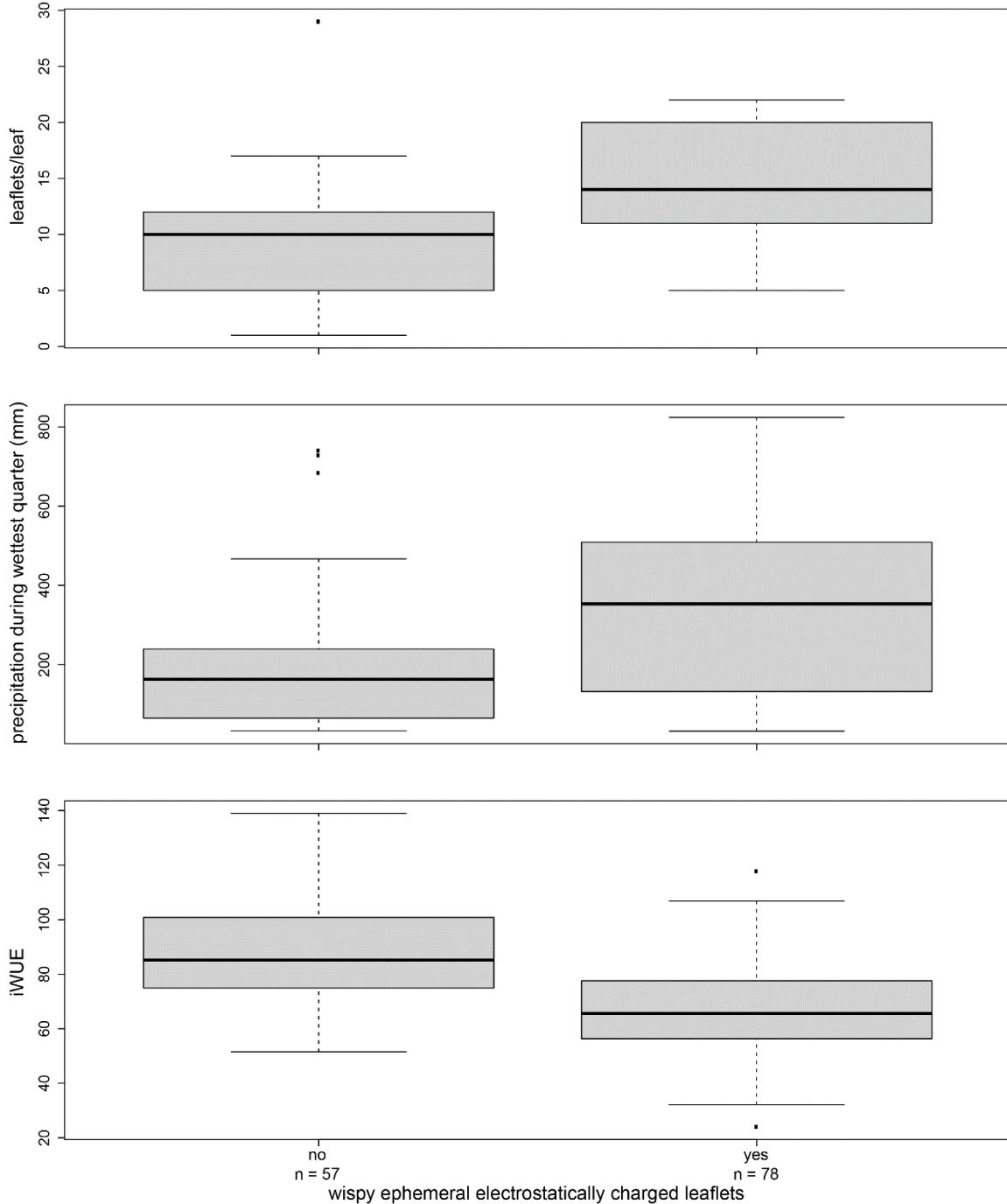


Figure 4. Wispy ephemeral small leaflets of mainly *Marina* species, which become electrostatically charged when dry. Top panel. Electrostatic leaflets associated with leaves having many leaflets (i.e., >12 leaflets per leaf). Middle panel. Electrostatic leaflets associated with greater precipitation during the wettest quarter. Bottom panel. Electrostatic leaflets associated with lower water use efficiency (iWUE). Student's t-Test reveals highly significant differences between the two groups of electrostatic charge (no/yes) for leaflets/leaf, precipitation, and iWUE.

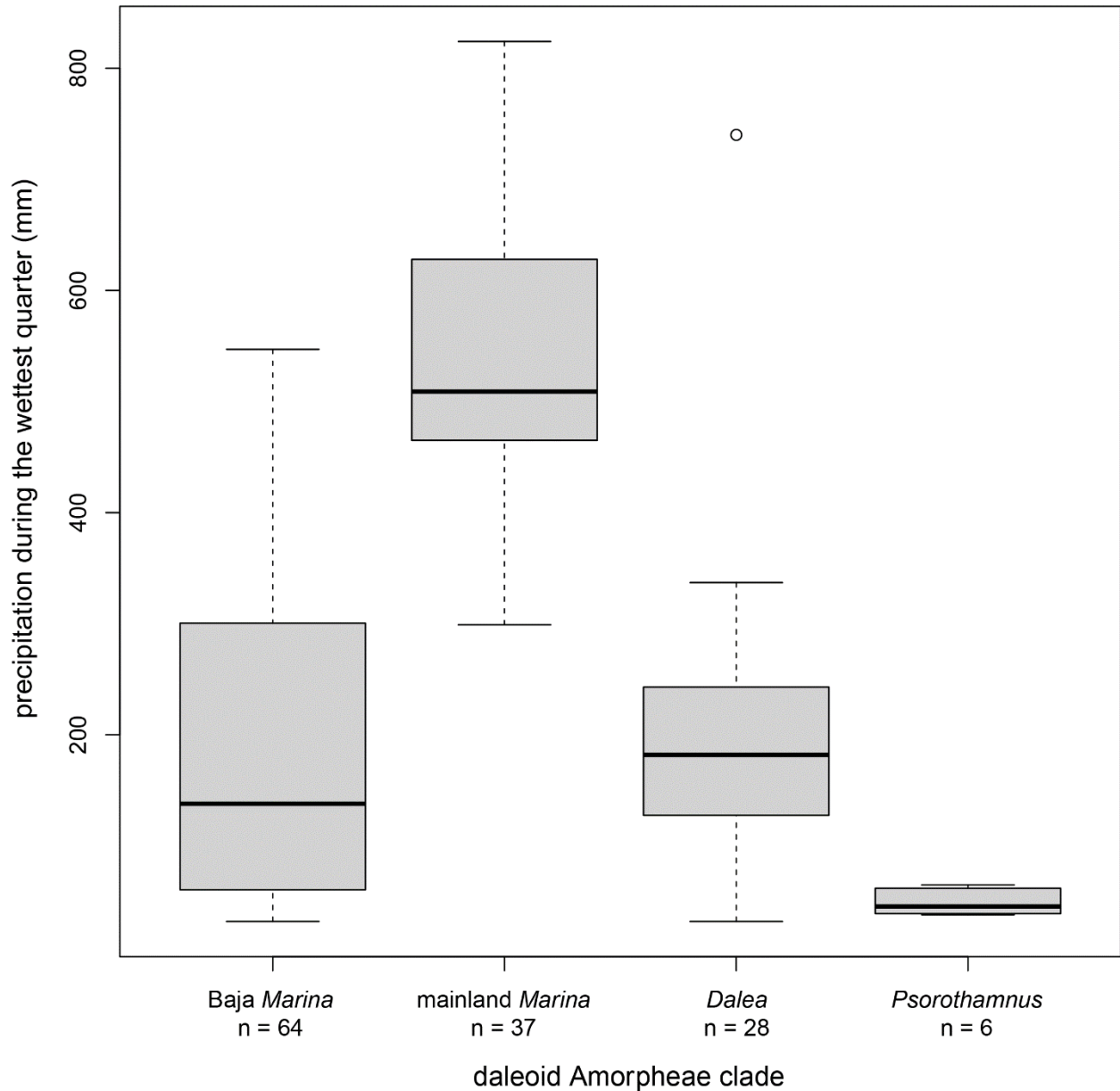


Figure 5. Precipitation during the wettest annual quarter (bioclimatic variable 16) as a function of the main clades of daleoid Amorpheae. Tukey's Honestly Significant Difference post-hoc test revealed significant differences for all pairwise comparisons except for the Baja California *Marina* clade and *Dalea* ( $p = 0.98$ ), the Baja California *Marina* clade and *Psorothamnus* ( $p = 0.10$ ), and the *Dalea* clade and *Psorothamnus* ( $p = 0.08$ ).

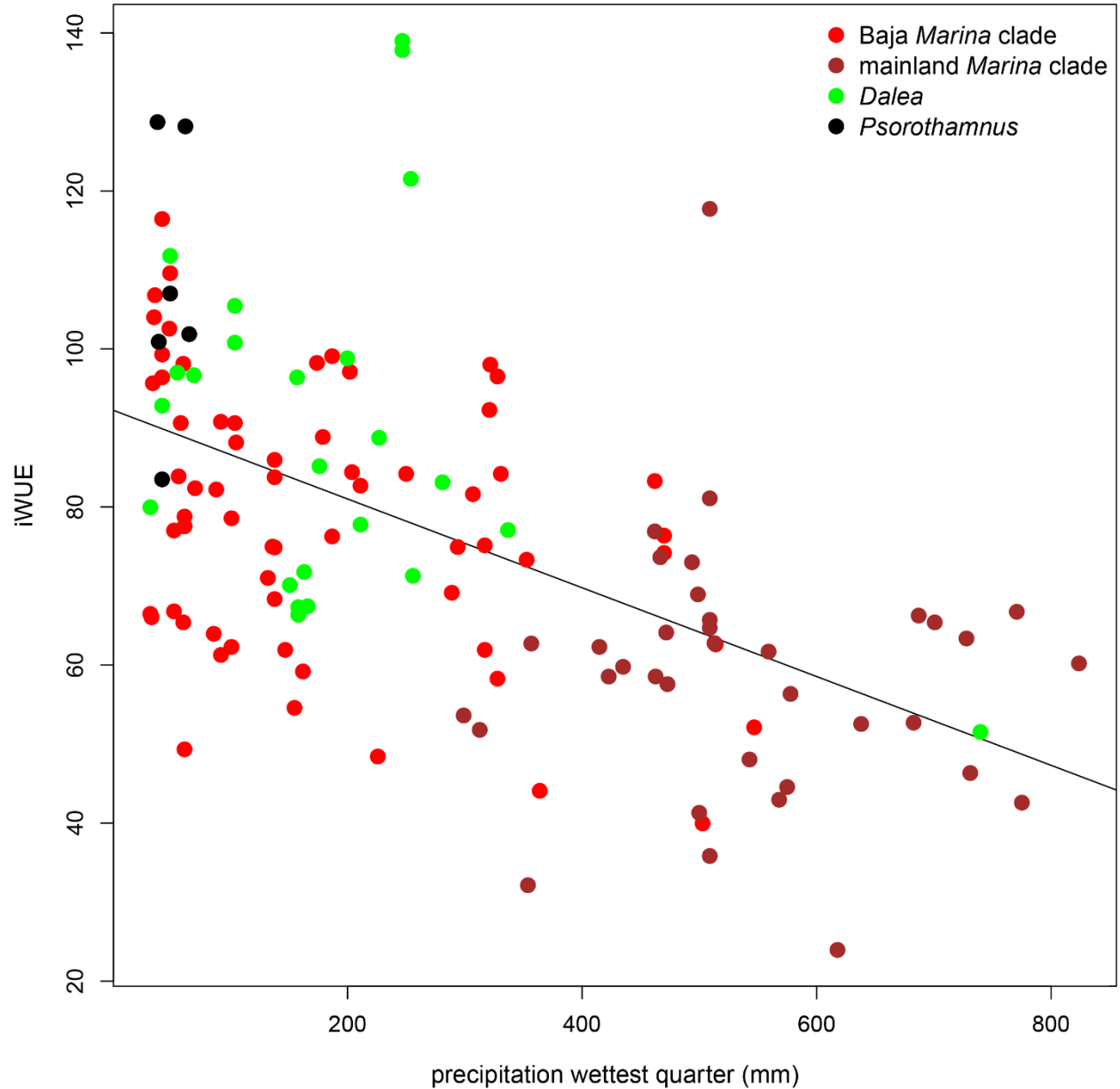


Figure 6. Intrinsic water use efficiency (iWUE) as a function of precipitation during the wettest annual quarter (bioclimatic variable 16). Adjusted R-squared = 0.3792 (Table 1). The main clades of the daleoid Amorpheae are indicated by color. The least squares regression line derives from all 130 data points (Figure 2).

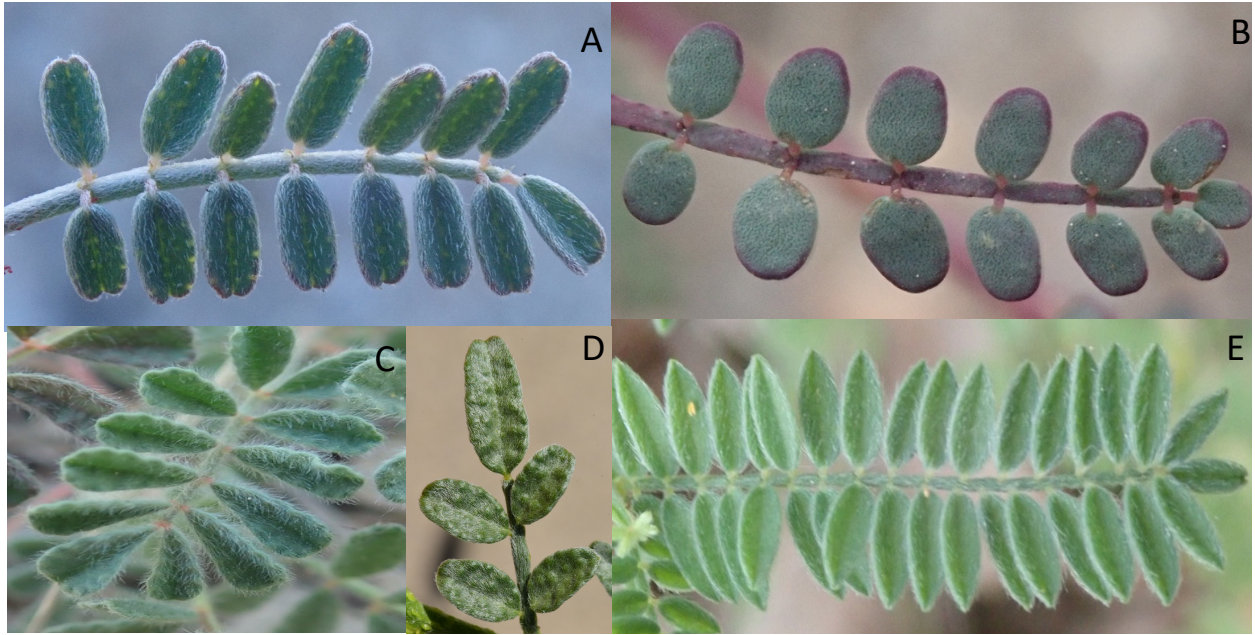


Figure 7: Leaflets of selected daleoid Amorpheae species. A. *Marina maritima* leaflets measure 1-4 mm long. B. *Camoufleur filiciformis* leaflets 1-3 mm long. C. *Dalea neomexicana* leaflets 2.5-8 mm long. D. *Psoralea kingii* leaflets 5-23 mm long (photo by Joey Santore). E. *Dalea albiflora* leaflets 2-7 mm long.



Table 1. Linear regression in R: Intrinsic water use efficiency (iWUE) as a function of precipitation during the wettest annual quarter (bioclimatic variable 16) plus clades of daleoid Amorpheae (Figure 6).

iWUE ~ precipitation wettest quarter + daleoid Amorpheae clade

| Coefficients:           | Estimate | Std. Error | t value | Pr(> t ) |
|-------------------------|----------|------------|---------|----------|
| Intercept               | 84.95522 | 2.98054    | 28.503  | < 2e-16  |
| Bioclimatic variable 16 | -0.03358 | 0.01126    | -2.981  | 0.00345  |
| mainland Marina clade   | -7.98786 | 5.40031    | -1.479  | 0.14162  |
| Dalea clade             | 11.30809 | 4.12951    | 2.738   | 0.00708  |
| Psorothamnus clade      | 25.09502 | 7.51624    | 3.339   | 0.00111  |

Residual standard error: 17.25 on 125 degrees of freedom

Adjusted R-squared: 0.3792

F-statistic: 20.7 on 4 and 125 DF, p-value: 4.159e-13

Table 2. Linear regression in R: Intrinsic water use efficiency (iWUE) as a function of mean annual precipitation (bioclimatic variable 12) plus clades of daleoid Amorpheae.

iWUE ~ mean annual precipitation + daleoid Amorpheae clade

| Coefficients:           | Estimate  | Std. Error | t value | Pr(> t ) |
|-------------------------|-----------|------------|---------|----------|
| Intercept               | 84.801701 | 2.985844   | 28.401  | < 2e-16  |
| Bioclimatic variable 12 | -0.020722 | 0.007142   | -2.902  | 0.004389 |
| mainland Marina clade   | -8.508853 | 5.353503   | -1.589  | 0.114496 |
| Dalea clade             | 13.186379 | 4.201953   | 3.138   | 0.002121 |
| Psorothamnus clade      | 25.904571 | 7.485079   | 3.461   | 0.000737 |

Residual standard error: 17.28 on 125 degrees of freedom

Adjusted R-squared: 0.377

F-statistic: 20.51 on 4 and 125 DF, p-value: 5.154e-13

Table 3. Phylogenetic regression in BayesTraits. Models with the highest marginal likelihoods. Model: Water use efficiency (iWUE) as a function of precipitation during the wettest quarter (bioclimatic variable 16), or mean annual precipitation (bioclimatic variable 12), plus the phylogeny of daleoid Amorpheae. Lambda = Lambda estimated, whereas Lambda 0.001 and Lambda 1.0 signifies Lambda set at 0.001 or 1.0, respectively. VR = variable rates, LL=estimated marginal log likelihood derived from the steppingstone sampler. Pagel & Meade (2023) log Bayes factors = 2(log marginal likelihood better fitting model – log marginal likelihood worse fitting model). For Models 1 and 2, log Bayes factors = 0.8 (weak evidence that Model 1 is a better fitting than Model 2). For Models 1 and 3, log Bayes factors = 3.4 (positive evidence that Model 1 is a better fitting than Model 3). For Models 1 and 4, log Bayes factors = 5.6 (strong evidence that Model 1 is a better fitting than Model 4). Numbers in parentheses behind the bio12/bio16 coefficient estimates are pMCMC (the proportion of 1000 MCMC Bayesian samples where a negative coefficient was estimated as positive). The Lambda column indicates where fixed at 0.001 or 1.000, where estimated, or where not applicable (NA) because variable rates were estimated.

Model 1: iWUE ~ bio16 + Lambda 0.001

Model 2: iWUE ~ bio16 + Lambda

Model 3: iWUE ~ bio12 + Lambda

Model 4: iWUE ~ bio16 + VR

Model 5: iWUE ~ bio16 + Lambda 1.000

| Model | coefficient           | R-squared | Lambda  | LL      |
|-------|-----------------------|-----------|---------|---------|
| 1     | bio16 -0.0635 (0.000) | 0.43      | 0.001   | -169.49 |
| 2     | bio16 -0.0558 (0.001) | 0.31      | 0.389   | -169.89 |
| 3     | bio12 -0.0319 (0.006) | 0.25      | 0.424   | -171.19 |
| 4     | bio16 -0.0464 (0.019) | 0.26      | NA (VR) | -172.27 |
| 5     | bio16 -0.0560 (0.034) | 0.25      | 1.000   | -175.5  |

Supplemental Table 1: Carbon, Nitrogen and Specific Leaf Area data. Variables discussed in-depth within text.

| <b>Specimen</b> | <b>SLA</b> | <b>lflt_lf</b> | <b>air15N</b> | <b>p13C</b> | <b>N</b> | <b>C</b> | <b>CN</b> | <b>A13c</b> | <b>Aco2</b> | <b>wue</b> | <b>delta</b> | <b>ci_ca</b> | <b>ci</b> |
|-----------------|------------|----------------|---------------|-------------|----------|----------|-----------|-------------|-------------|------------|--------------|--------------|-----------|
| Winitsky 1611   | 118.54     | 17             | -2.01         | -28.20      | 2.71     | 43.05    | 15.89     | -8.48       | 415.75      | 77.12      | 20.29        | 0.70         | 292.35    |
| Winitsky 1615   | 84.86      | 17             | -1.00         | -23.40      | 1.81     | 43.21    | 23.87     | -8.78       | 414.25      | 137.81     | 14.97        | 0.47         | 193.75    |
| Winitsky 1615   | 84.86      | 17             | -0.87         | -23.30      | 1.98     | 48.37    | 24.43     | -8.78       | 414.25      | 139.00     | 14.87        | 0.46         | 191.85    |
| Breedlove59349  | 103.98     | 10             | -0.66         | -26.50      | 3.24     | 42.15    | 13.01     | -7.59       | 340.59      | 71.30      | 19.43        | 0.67         | 226.50    |
| Winitsky 1717   | 59.04      | 10             | -0.71         | -27.20      | 3.16     | 47.04    | 14.89     | -9.00       | 423.14      | 97.02      | 18.71        | 0.63         | 267.91    |
| Winitsky 1559   | 72.16      | 8              | 1.01          | -28.20      | 3.24     | 47.47    | 14.65     | -8.75       | 414.06      | 79.99      | 20.01        | 0.69         | 286.08    |
| Brink 1057      | 97.33      | 4              | -2.33         | -26.00      | 2.70     | 42.72    | 15.82     | -7.28       | 333.63      | 71.78      | 19.22        | 0.66         | 218.77    |
| Lavin sn        | 69.57      | 4              | -1.59         | -26.40      | 2.88     | 42.85    | 14.88     | -8.08       | 376.27      | 85.18      | 18.81        | 0.64         | 239.97    |
| Lavin sn        | 75.74      | 4              | -0.97         | -26.40      | 2.20     | 36.16    | 16.44     | -8.28       | 415.75      | 96.45      | 18.61        | 0.63         | 261.43    |
| Harvey sn       | 305.71     | 11             | -0.88         | -26.50      | 2.42     | 41.62    | 17.20     | -7.51       | 338.58      | 70.14      | 19.51        | 0.67         | 226.35    |
| Rumely sn       | 28.76      | 6              | 1.69          | -26.20      | 2.46     | 45.77    | 18.61     | -7.73       | 350.24      | 77.81      | 18.97        | 0.64         | 225.75    |

|                     |        |    |       |        |      |       |       |       |        |        |       |      |        |
|---------------------|--------|----|-------|--------|------|-------|-------|-------|--------|--------|-------|------|--------|
| Winitsky 1567       | 87.39  | 6  | -1.65 | -26.90 | 3.38 | 43.32 | 12.82 | -8.84 | 414.25 | 96.70  | 18.56 | 0.63 | 259.53 |
| Winitsky 1715       | 62.50  | 6  | -1.09 | -26.89 | 4.40 | 47.68 | 10.84 | -9.00 | 423.14 | 100.82 | 18.38 | 0.62 | 261.83 |
| Winitsky 1732       | 71.32  | 6  | -2.21 | -26.51 | 2.47 | 44.44 | 17.99 | -9.00 | 423.14 | 105.47 | 17.99 | 0.60 | 254.39 |
| Winitsky 1736       | 44.13  | 6  | -2.63 | -27.54 | 3.07 | 46.25 | 15.07 | -9.00 | 423.14 | 92.85  | 19.07 | 0.65 | 274.57 |
| Winitsky 1757       | 55.88  | 6  | 2.42  | -25.99 | 2.20 | 44.25 | 20.11 | -9.00 | 423.14 | 111.83 | 17.44 | 0.58 | 244.21 |
| Jones sn            | 37.72  | 3  | 0.30  | -25.24 | 2.89 | 43.50 | 15.05 | -6.72 | 305.00 | 67.48  | 19.00 | 0.65 | 197.03 |
| Winitsky 1614       | 80.82  | 3  | -0.61 | -24.80 | 2.32 | 46.22 | 19.92 | -8.78 | 415.75 | 121.56 | 16.43 | 0.53 | 221.26 |
| Welker sn           | 50.16  | 5  | 3.46  | -26.80 | 2.62 | 40.55 | 15.48 | -7.53 | 338.22 | 67.37  | 19.80 | 0.68 | 230.43 |
| Lavin sn            | 76.88  | 5  | -1.67 | -26.70 | 1.83 | 39.20 | 21.42 | -8.31 | 395.83 | 88.76  | 18.89 | 0.64 | 253.81 |
| Lavin sn            | 110.62 | 5  | -1.90 | -26.20 | 1.53 | 39.76 | 25.99 | -8.28 | 415.75 | 98.85  | 18.40 | 0.62 | 257.58 |
| Welker sn           | 50.16  | 3  | 3.40  | -26.90 | 2.51 | 39.80 | 15.86 | -7.53 | 338.22 | 66.39  | 19.90 | 0.69 | 232.00 |
| Sanders 4956        | 62.07  | 17 | -1.52 | -28.56 | 2.02 | 51.35 | 25.42 | -7.62 | 342.63 | 51.54  | 21.56 | 0.76 | 260.16 |
| Winitsky 1612       | 69.64  | 17 | -0.86 | -27.70 | 2.43 | 42.09 | 17.32 | -8.48 | 415.75 | 83.16  | 19.77 | 0.68 | 282.70 |
| Reina 2009-<br>1020 | 106.84 | 12 | 2.73  | -27.52 | 3.96 | 43.69 | 11.03 | -8.01 | 382.20 | 73.33  | 20.06 | 0.69 | 264.87 |

|                         |        |    |       |        |      |       |       |       |        |       |       |      |        |
|-------------------------|--------|----|-------|--------|------|-------|-------|-------|--------|-------|-------|------|--------|
| Sanders 13270           | 74.77  | 12 | -1.51 | -27.10 | 2.68 | 45.42 | 16.95 | -8.08 | 360.28 | 74.23 | 19.55 | 0.67 | 241.51 |
| Van Devender<br>90-649  | 143.59 | 12 | -2.15 | -29.90 | 2.01 | 40.67 | 20.23 | -7.70 | 351.30 | 39.96 | 22.89 | 0.82 | 287.36 |
| Van Devender<br>97-1250 | 80.00  | 12 | -1.18 | -28.81 | 2.50 | 43.45 | 17.38 | -7.70 | 358.07 | 52.12 | 21.74 | 0.77 | 274.67 |
| Winitsky 1749           | 95.00  | 14 | -1.94 | -30.35 | 3.08 | 44.02 | 14.29 | -9.00 | 423.14 | 58.30 | 22.02 | 0.78 | 329.87 |
| Winitsky 1743           | NA     | 11 | 0.46  | -28.10 | 1.84 | 48.13 | 26.16 | -9.00 | 423.14 | 85.98 | 19.65 | 0.67 | 285.57 |
| Reina 2010-548          | 19.35  | 12 | -1.41 | -27.48 | 3.32 | 43.57 | 13.12 | -8.59 | 394.94 | 82.75 | 19.42 | 0.66 | 262.54 |
| Winitsky 1604           | 36.20  | 12 | -1.99 | -27.80 | 1.82 | 42.55 | 23.38 | -8.48 | 414.25 | 81.65 | 19.87 | 0.68 | 283.60 |
| Rebman 30796            | 64.52  | 18 | 2.31  | -29.36 | 2.78 | 32.64 | 11.74 | -8.51 | 401.43 | 61.27 | 21.48 | 0.76 | 303.39 |
| Winitsky 1563           | 77.86  | 18 | -0.54 | -27.30 | 3.21 | 46.18 | 14.39 | -8.75 | 414.06 | 90.80 | 19.07 | 0.65 | 268.78 |
| Rebman 30948            | 70.02  | 12 | -0.84 | -28.00 | 2.90 | 47.50 | 16.38 | -8.32 | 402.74 | 75.19 | 20.25 | 0.70 | 282.43 |
| Winitsky 1564           | 60.00  | 12 | -1.55 | -29.10 | 1.47 | 34.11 | 23.20 | -8.75 | 414.06 | 69.16 | 20.96 | 0.73 | 303.40 |
| Winitsky 1566           | 35.29  | 12 | -0.74 | -28.60 | 2.60 | 46.05 | 17.71 | -8.84 | 414.25 | 76.28 | 20.34 | 0.71 | 292.21 |
| Winitsky 1737           | 73.78  | 12 | -0.32 | -27.25 | 2.40 | 47.27 | 19.70 | -9.00 | 423.14 | 96.41 | 18.76 | 0.64 | 268.89 |

|                     |        |    |       |        |      |       |       |       |        |        |       |      |        |
|---------------------|--------|----|-------|--------|------|-------|-------|-------|--------|--------|-------|------|--------|
| Winitsky 1750       | 72.50  | 12 | -0.88 | -27.24 | 2.36 | 44.70 | 18.94 | -9.00 | 423.14 | 96.53  | 18.75 | 0.63 | 268.69 |
| Winitsky 1562       | 94.86  | 12 | -1.00 | -29.70 | 2.17 | 43.97 | 20.26 | -8.75 | 414.06 | 61.93  | 21.59 | 0.76 | 314.97 |
| Fishbein 1913       | 77.42  | 14 | -1.63 | -30.22 | 2.73 | 46.68 | 17.10 | -7.60 | 352.87 | 35.86  | 23.32 | 0.84 | 295.49 |
| Sanders 13486       | 8.80   | 14 | -1.74 | -26.44 | 2.64 | 52.48 | 19.88 | -8.08 | 360.28 | 81.12  | 18.86 | 0.64 | 230.49 |
| Steinmann 94-38     | 19.35  | 14 | 5.67  | -23.09 | 3.19 | 47.86 | 15.00 | -8.17 | 363.05 | 117.74 | 15.27 | 0.48 | 174.66 |
| Condit sn           | 38.00  | 14 | -2.23 | -26.80 | 1.61 | 35.93 | 22.32 | -6.87 | 312.50 | 56.36  | 20.48 | 0.71 | 222.33 |
| Leon de la Luz 8773 | 104.62 | 14 | -0.99 | -26.89 | 2.90 | 53.00 | 18.28 | -8.04 | 364.58 | 76.92  | 19.37 | 0.66 | 241.51 |
| Johnson 471-73      | 78.26  | 14 | -0.67 | -26.40 | 3.14 | 45.49 | 14.49 | -7.28 | 327.90 | 66.75  | 19.64 | 0.67 | 221.09 |
| Joyal 1827          | 88.24  | 14 | -0.89 | -28.01 | 3.90 | 45.21 | 11.59 | -8.00 | 353.95 | 62.78  | 20.59 | 0.72 | 253.51 |
| McVaugh 386         | 66.67  | 14 | -0.63 | -26.78 | 4.03 | 46.92 | 11.64 | -6.96 | 319.20 | 58.57  | 20.37 | 0.71 | 225.49 |
| Rinehart 7334       | NA     | 14 | -2.01 | -26.97 | 2.31 | 42.95 | 18.59 | -7.07 | 323.50 | 58.58  | 20.45 | 0.71 | 229.76 |
| Sanders 12948       | 193.55 | 14 | 0.05  | -27.50 | 3.01 | 43.57 | 14.48 | -7.77 | 354.18 | 65.74  | 20.29 | 0.70 | 248.99 |
| Rebman 29189        | 53.76  | 14 | -0.58 | -26.06 | 3.42 | 71.96 | 21.04 | -8.42 | 398.88 | 98.04  | 18.11 | 0.61 | 242.01 |

|                          |        |    |       |        |      |       |       |       |        |        |       |      |        |
|--------------------------|--------|----|-------|--------|------|-------|-------|-------|--------|--------|-------|------|--------|
| Rebman 31140             | 36.52  | 14 | -1.20 | -27.65 | 3.58 | 52.63 | 14.70 | -8.68 | 406.54 | 84.21  | 19.51 | 0.67 | 271.80 |
| Winitsky 1751            | 128.07 | 14 | 3.01  | -26.40 | 2.19 | 41.74 | 19.06 | -9.00 | 423.14 | 106.82 | 17.87 | 0.60 | 252.23 |
| Gentry 4699              | 174.65 | 6  | -0.76 | -26.83 | 3.11 | 55.81 | 17.95 | -6.77 | 309.00 | 54.58  | 20.61 | 0.72 | 221.67 |
| Rebman 25119             | 332.36 | 6  | -1.25 | -27.55 | 3.06 | 42.19 | 13.79 | -8.26 | 397.78 | 78.84  | 19.83 | 0.68 | 271.64 |
| Rebman 25119             | 332.36 | 6  | -1.31 | -27.66 | 3.23 | 45.57 | 14.11 | -8.26 | 397.78 | 77.57  | 19.95 | 0.69 | 273.67 |
| Sanders 2510             | 54.55  | 6  | -1.55 | -26.47 | 2.05 | 32.96 | 16.08 | -7.82 | 345.38 | 74.91  | 19.16 | 0.65 | 225.52 |
| Martinez 14298           | 120.00 | 5  | -0.54 | -28.52 | 2.90 | 45.58 | 15.72 | -7.65 | 344.56 | 52.57  | 21.48 | 0.76 | 260.44 |
| Reina 97-107             | 31.64  | 15 | -0.04 | -26.46 | 3.52 | 33.54 | 9.53  | -8.18 | 366.26 | 83.29  | 18.78 | 0.64 | 232.99 |
| Van Devender<br>95-313   | 40.22  | 15 | -1.28 | -28.39 | 2.26 | 35.01 | 15.49 | -8.19 | 364.86 | 62.66  | 20.79 | 0.73 | 264.61 |
| Vandevender<br>2009-1123 | 387.10 | 15 | -0.55 | -30.15 | 2.66 | 42.49 | 15.97 | -8.01 | 382.20 | 44.09  | 22.83 | 0.82 | 311.65 |
| Jenkins 96-146           | 142.50 | 6  | -1.08 | -28.35 | 2.59 | 46.32 | 17.88 | -8.06 | 364.69 | 61.70  | 20.88 | 0.73 | 265.97 |
| Magallanes<br>3437       | 124.21 | 10 | 3.21  | -27.28 | 4.33 | 44.50 | 10.28 | -7.82 | 342.64 | 66.28  | 20.01 | 0.69 | 236.60 |



|                    |        |    |       |        |      |       |       |       |        |       |       |      |        |
|--------------------|--------|----|-------|--------|------|-------|-------|-------|--------|-------|-------|------|--------|
| Mexia 1550         | 79.50  | 10 | -1.67 | -30.17 | 2.24 | 25.71 | 11.48 | -6.74 | 304.80 | 23.95 | 24.16 | 0.87 | 266.48 |
| Breedlove<br>60038 | 175.45 | 1  | -2.36 | -26.37 | 2.40 | 36.77 | 15.32 | -7.61 | 344.60 | 73.68 | 19.27 | 0.66 | 226.71 |
| Sanders 14323      | 50.00  | 7  | -1.13 | -26.27 | 3.28 | 46.32 | 14.12 | -8.17 | 363.05 | 84.45 | 18.59 | 0.63 | 227.92 |
| Rebman 25429       | 86.02  | 11 | -1.07 | -26.30 | 3.37 | 46.52 | 13.80 | -8.27 | 393.44 | 92.30 | 18.52 | 0.62 | 245.76 |
| Rebman 28911       | 79.23  | 11 | 0.20  | -28.06 | 1.94 | 45.49 | 23.45 | -8.42 | 398.88 | 74.93 | 20.21 | 0.70 | 278.99 |
| Rebman 30821       | 64.52  | 11 | 6.08  | -29.13 | 2.73 | 43.36 | 15.88 | -8.51 | 401.43 | 63.96 | 21.24 | 0.75 | 299.10 |
| Winitsky 1560      | 104.42 | 11 | 0.87  | -28.00 | 3.22 | 40.19 | 12.48 | -8.75 | 414.06 | 82.39 | 19.80 | 0.68 | 282.23 |
| Winitsky 1565      | 81.80  | 11 | -0.93 | -26.70 | 3.07 | 42.59 | 13.87 | -8.84 | 414.25 | 99.10 | 18.35 | 0.62 | 255.70 |
| Winitsky 1739      | 105.71 | 11 | -1.15 | -28.28 | 2.47 | 43.27 | 17.52 | -9.00 | 423.14 | 83.77 | 19.84 | 0.68 | 289.10 |
| Ripley 14649       | 64.00  | 7  | -1.40 | -28.70 | 2.54 | 47.41 | 18.67 | -7.02 | 319.30 | 41.32 | 22.32 | 0.79 | 253.19 |
| Ripley 14905       | 185.71 | 7  | -2.31 | -28.09 | 1.89 | 39.76 | 21.04 | -7.07 | 323.50 | 48.06 | 21.63 | 0.76 | 246.60 |
| Sanders 11754      | 414.75 | 8  | -1.03 | -29.96 | 2.70 | 50.95 | 18.87 | -8.00 | 356.49 | 43.00 | 22.64 | 0.81 | 287.69 |
| Breedlove<br>58870 | 157.00 | 20 | -1.61 | -29.40 | 3.20 | 43.02 | 13.44 | -7.59 | 340.59 | 42.61 | 22.48 | 0.80 | 272.41 |

|                    |        |    |       |        |      |       |       |       |        |       |       |      |        |
|--------------------|--------|----|-------|--------|------|-------|-------|-------|--------|-------|-------|------|--------|
| Breedlove<br>58972 | 19.12  | 20 | -1.75 | -27.41 | 3.75 | 48.98 | 13.06 | -7.59 | 340.59 | 62.32 | 20.38 | 0.71 | 240.88 |
| Breedlove<br>18912 | 516.13 | 20 | -1.94 | -26.26 | 4.05 | 56.14 | 13.86 | -7.01 | 327.14 | 65.42 | 19.77 | 0.68 | 222.47 |
| Feddema 2476       | 210.02 | 20 | -1.65 | -29.61 | 3.09 | 50.89 | 16.47 | -6.97 | 316.80 | 32.15 | 23.33 | 0.84 | 265.37 |
| Gentry 19633       | 32.26  | 20 | -1.85 | -26.60 | 2.01 | 30.72 | 15.28 | -6.96 | 319.20 | 60.23 | 20.18 | 0.70 | 222.83 |
| Moore 994          | 92.31  | 20 | -1.18 | -27.69 | 3.90 | 46.03 | 11.80 | -7.07 | 323.50 | 51.82 | 21.21 | 0.74 | 240.58 |
| Tenorio 9887       | 218.78 | 20 | -1.65 | -27.13 | 3.64 | 47.54 | 13.06 | -7.33 | 341.33 | 62.75 | 20.35 | 0.71 | 240.93 |
| Moran 9456         | 153.33 | 20 | -1.35 | -27.86 | 1.96 | 45.43 | 23.18 | -6.99 | 316.80 | 48.47 | 21.47 | 0.76 | 239.26 |
| Moran 23879        | 45.83  | 12 | 1.43  | -25.34 | 1.92 | 30.80 | 16.04 | -7.32 | 333.92 | 78.60 | 18.49 | 0.62 | 208.16 |
| Rebman 31726       | 64.52  | 12 | -1.77 | -27.67 | 1.95 | 39.55 | 20.28 | -8.70 | 406.66 | 84.24 | 19.51 | 0.67 | 271.88 |
| Rebman 4351        | 58.44  | 12 | -0.79 | -28.04 | 3.86 | 45.30 | 11.74 | -7.85 | 361.74 | 62.30 | 20.77 | 0.72 | 262.06 |
| Rebman 6426        | 40.18  | 12 | -0.30 | -25.63 | 3.49 | 44.51 | 12.75 | -8.34 | 373.75 | 95.66 | 17.74 | 0.59 | 220.69 |
| Sanders 13349      | 121.90 | 11 | 2.16  | -26.89 | 3.94 | 45.02 | 11.43 | -8.08 | 360.28 | 76.42 | 19.33 | 0.66 | 238.00 |
| Sanders 9153       | 60.21  | 11 | 0.00  | -26.67 | 3.34 | 49.34 | 14.77 | -7.58 | 347.83 | 71.06 | 19.61 | 0.67 | 234.14 |

|                       |        |    |       |        |      |       |       |       |        |        |       |      |        |
|-----------------------|--------|----|-------|--------|------|-------|-------|-------|--------|--------|-------|------|--------|
| Rebman 25013          | 125.24 | 11 | 0.83  | -30.10 | 3.53 | 43.76 | 12.40 | -8.26 | 397.78 | 49.34  | 22.51 | 0.80 | 318.83 |
| Sanders 434355        | 58.18  | 11 | -1.93 | -26.21 | 2.68 | 45.50 | 16.98 | -8.79 | 412.97 | 104.05 | 17.89 | 0.60 | 246.48 |
| Winitsky 1568         | 111.43 | 11 | -0.65 | -29.50 | 4.34 | 45.53 | 10.49 | -8.84 | 414.25 | 65.44  | 21.29 | 0.75 | 309.55 |
| Winitsky 1610         | 40.74  | 11 | 1.86  | -27.20 | 2.50 | 42.51 | 17.00 | -8.48 | 414.25 | 88.86  | 19.24 | 0.66 | 272.07 |
| Winitsky 1613         | 57.46  | 11 | -0.13 | =29.40 | 2.75 | 37.82 | 13.75 | -8.78 | 417.69 | 66.48  | 21.24 | 0.75 | 311.32 |
| Winitsky 1728         | 57.50  | 11 | 2.30  | -27.11 | 4.93 | 45.39 | 9.21  | -9.00 | 423.14 | 98.12  | 18.61 | 0.63 | 266.14 |
| Winitsky 1730         | 71.67  | 11 | -1.44 | -27.72 | 3.59 | 44.38 | 12.36 | -9.00 | 423.14 | 90.65  | 19.25 | 0.66 | 278.11 |
| Winitsky 1734         | 69.09  | 11 | -1.71 | -27.01 | 3.03 | 42.60 | 14.06 | -9.00 | 423.14 | 99.35  | 18.51 | 0.62 | 264.18 |
| Winitsky 1758         | 100.53 | 11 | -0.45 | -27.72 | 4.68 | 44.39 | 9.49  | -9.00 | 423.14 | 90.65  | 19.25 | 0.66 | 278.11 |
| Leon de la Luz<br>510 | 76.97  | 10 | -1.27 | -28.48 | 3.09 | 42.32 | 13.70 | -8.22 | 388.82 | 66.09  | 20.85 | 0.73 | 283.08 |
| DeGroot 4863          | 103.69 | 10 | -0.79 | -25.37 | 3.66 | 48.25 | 13.18 | -8.48 | 383.70 | 102.61 | 17.33 | 0.57 | 219.52 |
| Winitsky 1725         | 140.00 | 10 | -1.41 | 28.27  | 3.46 | 52.27 | 15.11 | -9.00 | 423.14 | 83.90  | 19.83 | 0.68 | 288.91 |
| Winitsky 1735         | 205.71 | 10 | -1.41 | 25.61  | 3.98 | 48.11 | 12.09 | -9.00 | 423.14 | 116.47 | 17.05 | 0.56 | 236.78 |
| Winitsky 1754         | 108.57 | 10 | -1.22 | 26.17  | 3.51 | 47.74 | 13.60 | -9.00 | 423.14 | 109.63 | 17.63 | 0.59 | 247.73 |

|                               |        |    |       |       |      |       |       |       |        |       |       |      |        |
|-------------------------------|--------|----|-------|-------|------|-------|-------|-------|--------|-------|-------|------|--------|
| Laughlin 1640                 | 129.03 | 10 | -1.33 | 28.16 | 2.67 | 45.14 | 16.91 | -7.02 | 319.30 | 46.34 | 21.75 | 0.77 | 245.16 |
| Lavin 5048                    | 72.58  | 10 | -2.41 | 27.59 | 2.29 | 42.04 | 18.36 | -7.51 | 340.41 | 59.78 | 20.65 | 0.72 | 244.76 |
| Lavin 5158                    | 118.43 | 5  | 0.90  | 28.00 | 2.57 | 43.15 | 16.79 | -7.65 | 343.58 | 57.62 | 20.94 | 0.73 | 251.39 |
| Winitsky 1748                 | 190.00 | 14 | -1.43 | 27.10 | 3.14 | 45.61 | 14.53 | -9.00 | 423.14 | 98.25 | 18.60 | 0.63 | 265.94 |
| Cuevas 1142                   | 37.22  | 20 | -1.00 | 28.47 | 4.11 | 46.58 | 11.33 | -7.63 | 349.68 | 53.66 | 21.45 | 0.75 | 263.82 |
| Breedlove<br>59839            | 77.42  | 20 | -1.16 | 29.28 | 2.40 | 53.49 | 22.29 | -7.61 | 344.60 | 44.57 | 22.32 | 0.79 | 273.30 |
| Mendez 8610                   | 138.25 | 20 | -2.64 | 29.92 | 3.24 | 46.39 | 14.32 | -7.74 | 347.04 | 39.69 | 22.86 | 0.82 | 283.53 |
| Steinmann 93-<br>433          | 111.76 | 20 | 0.49  | 27.77 | 2.34 | 44.29 | 18.93 | -7.85 | 359.59 | 64.75 | 20.49 | 0.71 | 255.99 |
| Steinmann &<br>Ramirez A 6932 | 120.97 | 20 | -1.11 | 28.09 | 3.90 | 45.43 | 11.65 | -8.43 | 389.85 | 73.01 | 20.23 | 0.70 | 273.04 |
| Van Devender<br>94-160        | 87.35  | 20 | 3.61  | 27.21 | 3.29 | 42.67 | 12.97 | -7.76 | 356.01 | 68.98 | 19.99 | 0.69 | 245.64 |
| Martinez 4831                 | 150.45 | 1  | -1.41 | 27.30 | 2.30 | 38.12 | 16.57 | -7.59 | 340.59 | 63.41 | 20.27 | 0.70 | 239.14 |
| Iltis 3022                    | 100.00 | 1  | -1.20 | 28.33 | 3.20 | 43.30 | 13.53 | -7.58 | 337.89 | 52.75 | 21.35 | 0.75 | 253.49 |

|               |        |    |       |       |      |       |       |       |        |        |       |      |        |
|---------------|--------|----|-------|-------|------|-------|-------|-------|--------|--------|-------|------|--------|
| Vazquez 1447  | 55.32  | 8  | -1.68 | 27.88 | 2.86 | 41.13 | 14.38 | -8.00 | 353.95 | 64.11  | 20.45 | 0.71 | 251.37 |
| Winitsky 1747 | 93.91  | 11 | -0.20 | 27.19 | 2.55 | 47.34 | 18.56 | -9.00 | 423.14 | 97.14  | 18.70 | 0.63 | 267.71 |
| Rebman 25073  | 87.26  | 22 | 3.26  | 27.60 | 3.35 | 40.70 | 12.15 | -8.26 | 391.52 | 77.03  | 19.89 | 0.69 | 268.27 |
| Rebman 25073  | 109.92 | 22 | -1.01 | 28.59 | 3.00 | 43.90 | 14.63 | -8.26 | 397.78 | 66.83  | 20.93 | 0.73 | 290.86 |
| Rebman 31020  | 71.25  | 22 | -0.70 | 29.30 | 1.84 | 40.54 | 22.03 | -8.32 | 397.73 | 59.23  | 21.62 | 0.76 | 302.97 |
| Sanders 2623  | 14.89  | 22 | 3.32  | 27.19 | 4.25 | 44.48 | 10.47 | -7.88 | 345.84 | 68.39  | 19.85 | 0.68 | 236.42 |
| Winitsky 1731 | 320.00 | 22 | -0.82 | 27.92 | 3.35 | 43.18 | 12.89 | -9.00 | 423.14 | 88.19  | 19.46 | 0.67 | 282.03 |
| Winitsky 1558 | 89.01  | 22 | 0.21  | 29.70 | 3.57 | 40.84 | 11.44 | -8.75 | 414.06 | 61.93  | 21.59 | 0.76 | 314.97 |
| Wilder 06-380 | NA     | 22 | 1.96  | 27.00 | 3.85 | 43.33 | 11.25 | -8.28 | 383.27 | 82.26  | 19.24 | 0.66 | 251.66 |
| Felger 95-272 | 69.09  | 22 | -1.43 | 27.17 | 2.34 | 34.14 | 14.59 | -8.17 | 363.13 | 75.01  | 19.53 | 0.67 | 243.11 |
| Winitsky 1618 | 15.14  | 7  | 3.56  | 24.48 | 2.73 | 43.71 | 16.01 | -8.93 | 420.92 | 128.74 | 15.94 | 0.51 | 214.93 |
| Winitsky 1619 | 4.19   | 7  | 1.21  | 24.43 | 2.40 | 47.70 | 19.88 | -8.89 | 418.74 | 128.20 | 15.93 | 0.51 | 213.62 |
| Winitsky 1716 | 27.72  | 4  | 13.90 | 26.80 | 3.88 | 45.43 | 11.71 | -9.00 | 423.14 | 101.92 | 18.29 | 0.61 | 260.07 |
| Winitsky 1726 | 47.50  | 4  | 4.65  | 26.88 | 4.52 | 46.78 | 10.35 | -9.00 | 423.14 | 100.94 | 18.37 | 0.62 | 261.63 |
| Winitsky 1738 | 79.17  | 4  | -1.27 | 28.30 | 2.20 | 44.48 | 20.22 | -9.00 | 423.14 | 83.53  | 19.86 | 0.68 | 289.50 |

|               |        |   |      |       |      |       |       |       |        |        |       |      |        |
|---------------|--------|---|------|-------|------|-------|-------|-------|--------|--------|-------|------|--------|
| Winitzky 1753 | 143.07 | 4 | 0.32 | 26.38 | 3.52 | 44.87 | 12.75 | -9.00 | 423.14 | 107.06 | 17.85 | 0.60 | 251.84 |
|---------------|--------|---|------|-------|------|-------|-------|-------|--------|--------|-------|------|--------|

## CONCLUSIONS AND FUTURE WORK

The combination of morphological study, phylogenomic analyses and targeted fieldwork have resolved the evolutionary groups within *Marina*, including the illumination of cryptic taxa and a monotypic sister genus. We have revised species complexes and genera so that species represent monophyletic groups. Although we still have fragmentary knowledge on some of the rare *Marina* species, we have a taxonomic framework from which to proceed. We have a better understanding of *Marina*'s flexibility in regards its water use efficiency, allowing it to adapt readily across a spectrum of precipitation regimes.

In the near future, I plan to formally publish these dissertation chapters. To support the new descriptions, I plan to survey the narrow endemic *Marina* species of Baja California Sur to generate more ecological and geographic data with which to inform land use decisions moving forward. There are several taxonomic implications of the phylogenomic analyses that were not addressed in this thesis. This includes understanding variation within *Camoufleur filiciformis*, particularly across a north south gradient and on and off gypsum, which will require more conspecific sampling. Cryptic taxa within the mainland section of *Marina* are suspected based on the inferred phylogenies and geographic disjunctions, but are in of need further investigation, including intensive museum study and field work to historic localities.

During this time of accelerated biodiversity loss, the interdisciplinary data available through herbaria are invaluable and diversity of results acquired from specimens in this research emphasizes the importance of maintaining these collections. The future for many unprotected taxa, including *Marina*, relies on the collaboration of field biologists, museum curators, teachers, and principal investigators to prioritize the biodiversity crisis in research

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