

## SUCCULENT PLANT DIVERSITY OF THE SONORAN ISLANDS, GULF OF CALIFORNIA, MEXICO

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**Abstract:** Succulent life forms are a prominent feature of the Sonoran Gulf of California islands (Alcatraz, Cholludo, Dátil, Patos, San Esteban, San Pedro Mártir, San Pedro Nolasco, and Tiburón). Among a total flora of 378 species of vascular plants, there are 62 succulent taxa (16%) in 16 families and 33 genera, which we place in three categories: xerophytic succulents (32), semisucculents (22), and halophytic succulents (8). Succulent plant distribution on each island is unique and reflects the shaping climatic, biotic (including herbivores), soil, and topographical features of each of these microcosms. Cactaceae is the most diverse family (25 taxa), with six endemic species, all small cacti, found on Islas San Esteban, San Pedro Nolasco, Dátil, and Cholludo. The smaller islands in the region have a significantly higher percentage of succulent species. Here we present a discussion of the different succulent categories and a detailed floristic listing for all succulent species, which represents the first specimen-based flora of succulents from Gulf of California islands.

**Resumen:** Las formas de vida de las plantas suculentas son una notable característica de las islas Sonorenses del Golfo de California (Alcatraz, Cholludo, Dátil, Patos, San Esteban, San Pedro Mártir, San Pedro Nolasco, y Tiburón). Existen 62 taxa de plantas suculentas en una flora total de 378 especies de plantas vasculares (16%). A estas las que dividimos en tres categorías: suculentas xerófitas (32), semisuculentas (22), y suculentas halófitas (8). La distribución de suculentas en cada una de las islas es única y refleja la influencia de los rasgos climáticos, bióticos (incluyendo a los herbívoros), tierra, y topográficos de cada uno de estos microcosmos. Las Cactáceas son la familia más diversa (25 taxa). Tienen seis especies endémicas que se distribuyen en Islas San Esteban, San Pedro Nolasco, Dátil, y Choyudo. Las islas pequeñas poseen un porcentaje significativamente más alto de especies de suculentas. En este artículo presentamos la primera flora de islas del Golfo de California basada en colecta de especímenes de suculentas. Además del listado detallado, presentamos una discusión de las diferentes categorías de suculentas de estas islas.

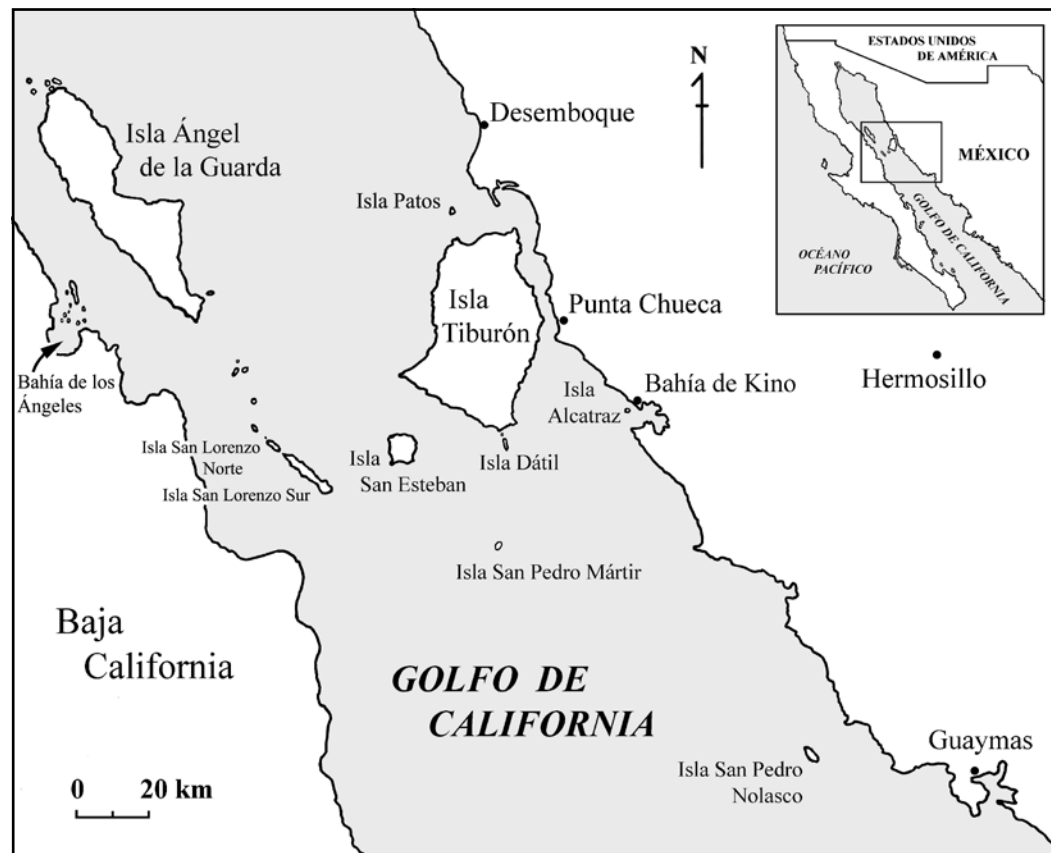
**Key words:** Gulf of California, island biogeography, endemic cacti, succulent plants

### Introduction

From complete dominance to endemism, the eight islands on the Sonoran side of the Gulf of California contain considerable diversity of succulent life forms. The Central Gulf Coast subdivision of the Sonoran Desert has been termed a “sarcocaulous desert” due to the common occurrence of succulent and semisucculent trees and shrubs

with exaggerated stem (trunk and limb) diameters (Shreve 1951) and is the vegetation type on all Gulf of California islands. Yet the biotic and abiotic factors of each island are fundamentally unique, and the vegetation of each island is correspondingly distinctive. Succulence is a critical adaptation to the arid environment of the Central Gulf Coast of the Sonoran Desert, analysis of which yields many insights to the flora of these islands.

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**Figure 1.** Sonoran and Baja Californian islands in the Midriff section of the Gulf of California, Mexico. Map by Cathy Moser Marlett.

The insular succulent flora falls into three categories: *xerophytic succulents*, *semisucculents*, and *halophytic succulents*. An agreed-upon definition of succulence states that a succulent is any plant containing succulent tissue, defined as “a living tissue that, besides possible other tasks, serves and guarantees an at least temporary storage of utilizable water, which makes the plant... temporarily independent from external water supply” (Dimmitt and others 2005; from Von Willert and others 1992). The category of *xerophytic succulent* includes those species that absorb and store water after even light rains, and utilize this stored water to maintain significant levels of photosynthesis and other metabolic processes when there is essentially no available soil moisture (Dimmitt and others 2005). *Semisucculent* is a non-specific term used for plants that are not entirely composed of succulent tissue, but store water in some fashion in part of their living tissue, be it in stems, caudices (persistent base of a perennial), or other organs. *Halophytic succu-*

*lents* have succulent tissues and grow in saline environments, in our case on beaches and in tidal wetlands.

We propose that the above classification of the succulent habit can be applied to the warm desert regions of North America, and may be applicable in other regions as well. However, this definition of succulence often does not work in tropical regions, where many species are in part succulent or fleshy, but whose adaptations may be different from those seen in arid environments. The goals of this paper are to provide a detailed treatment of a principal component of the insular Gulf of California flora, to investigate the ecological and biogeographical patterns within its succulent flora, and to standardize the use of succulent terms.

### Study Area

The eight Sonoran islands of the Gulf of California range greatly in size, topography, and degree of isolation (Fig 1). Tiburón, with an area of over 1200 km, is the

largest island in Mexico and harbors more than 350 plant species. This island has the greatest topographical heterogeneity of any gulf island and has two major north-south-trending mountain ranges. The larger, Sierra Kunkaak, lies on the east side of the island and reaches about 900 m (ca. 3000 ft), with areas of dense thornscrub-like vegetation and numerous disjunct relict plant populations at its higher elevations (Wilder and others 2008). Sierra Menor, running along the west flank of the island, houses quite arid desert scrub throughout. Between the two ranges is an expansive central valley. Tiburón and the smaller islands Alcatraz (1.45 km<sup>2</sup>, 55 plant species), Dátil (1.25 km<sup>2</sup>, 102 plant species), Patos (0.45 km<sup>2</sup>, 13 plant species), and Cholludo (0.2 km<sup>2</sup>, 28 plant species) are geologically related to the mainland of Sonora. These islands occur in shallow water and were connected to the mainland during the last ice age. San Esteban (41 km<sup>2</sup>, 122 plant species), San Pedro Mártir (2.7 km<sup>2</sup>, 24 plant species), and San Pedro Nolasco (3.45 km<sup>2</sup>, 57 plant species) are of volcanic origin and occur in deep water, having been isolated throughout their existence. Isla San Esteban is 11 km off the southwest tip of Tiburón, 58 km from the closest point in Sonora, and 50 km from the nearest locality in Baja California. Nolasco is 15 km off the Sonora mainland northwest of Guaymas.

### Xerophytic Succulents

The xerophytic succulents comprise the most diverse succulent group on the Sonoran islands, with 32 taxa (Table 1). The main component of this group is cacti, which are conspicuous on all vegetated islands in the Gulf of California and contain the greatest diversity of insular endemics (11 species, 26%) for any plant family represented (Rebman 2002), six of which occur on the islands treated here. The Sonoran islands support a diversity of small cacti (*Echinocereus* with three species, two of them endemics, and *Mammillaria* with five species, four endemic). Their plasticity is evident and indicative of adaptations to different topographies of the islands, a favorable climate for succulents, relatively limited dispersal mechanisms (Rebman 2002), a lack of herbivores, and insular isolation. In fact, six of the seven endemics on these islands are small cacti.

The endemic giant rainbow cactus (*Echinocereus grandis*) occurs on San Esteban and the Baja California islands of San Lorenzo and Las Animas. *Echinocereus grandis* on San Esteban has relatively drab, pale, cream-colored flowers (Fig 2a), while on San Lorenzo and Las Animas the flowers are bright pink (Fig 2b; Thomas Bowen and Jon Rebman, personal communication 2006). On Isla Tiburón, the Sonoran rainbow cactus (*E. scopulorum*), the likely sister species or “progenitor” to the endemic *E. grandis*, has showy flowers, which are considerably brighter and larger than those of *E. grandis* on San Esteban and San Lorenzo. The endemic *E. websterianus* on San Pedro Nolasco likewise has smaller and paler flowers and shows a similar relationship with the mainland *E. scopulorum* (Taylor 1985). The reduced size and brightness of the island endemics may be related to reduced need to advertise for pollinators. This *Echinocereus* complex is a fascinating example of the plasticity and continued radiation of cacti on Gulf islands.

Xerophytic succulents are the dominant succulent form on Islas San Esteban, San Pedro Mártir, and Cholludo. On San Esteban, one of the most arid Sonoran islands, a community of 11 xerophytic succulents occurs throughout the island. Eight are cacti and one is an endemic agave. This succulent community is a striking aspect of the island’s vegetation, especially in contrast to neighboring islands (Fig 3). The dome-shaped island of San Pedro Mártir is covered by a forest of cardón cacti (*Pachycereus pringlei*) striking in its extent and density (Fig 4). Isla Cholludo, off the southern tip of Tiburón, is dominated by a formidable and scarcely penetrable cactus forest unique in the region (Fig 5). Principal elements in this succulent landscape are *Pachycereus pringlei* and *Stenocereus thurberi*, interlaced with an understory of *Cylindropuntia fulgida*. Cholludo’s dense succulent vegetation is due to compounding factors. The island likely receives summer rains that are more significant than in adjacent areas (Felger and Lowe 1976). This reflects the orographic effects of the mountains in the southwestern part of Tiburón and that island’s large size. The surrounding sea also contributes to a relatively high humidity and considerable amelioration of temperature extremes. These factors, combined with the north-facing aspect, or slope, of the island, nitrogen deposits from roosting sea birds, and the absence of herbivory by rodents and other mammals help explain

Table 1. Succulent flora of the Sonoran islands, Gulf of California.

Family	Species	Succulence <sup>1</sup>	TIB <sup>2</sup>	EST <sup>2</sup>	NOL <sup>2</sup>	MAR <sup>2</sup>	ALC <sup>2</sup>	DAT <sup>2</sup>	PAT <sup>2</sup>	CHO <sup>2</sup>
Agavaceae	† <i>Agave cerulata</i> ssp. <i>denizens</i>	XS		EST						
	<i>Agave chrysglossa</i>	XS	TIB		NOL					
Aizoaceae	<i>Agave subimplex</i>	XS	TIB					DAT		CHO
	<i>Sesuvium portulacastrum</i>	HS	TIB				ALC			
Amaranthaceae	<i>Trianthema portulacastrum</i>	SS	TIB				ALC		PAT	
	<i>Allenrofea occidentalis</i>	HS	TIB				ALC			
	<i>Chenopodium murale</i>	HS	TIB				ALC			PAT
	<i>Salicornia bigelovii</i>	HS	TIB				ALC			
	<i>Salicornia subterminalis</i>	HS	TIB				ALC			
	<i>Suaeda esteroa</i>	HS	TIB	EST			ALC		PAT	
	<i>Suaeda nigra</i>	HS	TIB	EST			ALC	DAT		
	<i>Asclepias albicans</i>	SS	TIB	EST						
	<i>Asclepias subulata</i>	SS	TIB	EST				DAT		CHO
	<i>Bajacalia crassifolia</i>	SS	TIB	EST				DAT		
Bataceae	<i>Hofmeisteria fasciculata</i> var. <i>fasciculata</i>	XS			NOL					
	<i>Hofmeisteria crassifolia</i>	XS								
Boraginaceae	<i>Batis maritima</i>	HS	TIB				ALC			
	<i>Heliotropium curassavicum</i>	SS	TIB				ALC			
Bursaceae	<i>Bursera fagaroides</i> var. <i>elongata</i>	SS	TIB							
	<i>Bursera hindiana</i>	SS	TIB	EST				DAT		CHO
	<i>Bursera laxiflora</i>	SS	TIB							
	<i>Bursera microphylla</i>	SS	TIB	EST	NOL		ALC	DAT		
	<i>Carnegia gigantea</i>	XS	TIB	EST		MAR	ALC		PAT	CHO
Cactaceae	<i>Cylindropuntia alcabes</i> var. <i>alcabes</i>	XS	TIB	EST			ALC	DAT		
	<i>Cylindropuntia bigelovii</i>	XS	TIB	EST			ALC	DAT		
	<i>Cylindropuntia cholla</i>	XS				MAR				
	<i>Cylindropuntia fulgida</i> var. <i>fulgida</i>	XS	TIB		NOL		ALC			
	<i>Cylindropuntia fulgida</i> var. <i>mamillata</i>	XS	TIB	EST?	NOL		ALC	DAT	PAT	CHO
	<i>Cylindropuntia leptocaulis</i>	XS	TIB					DAT		
	<i>Cylindropuntia versicolor</i>	XS	TIB					DAT		
	† <i>Echinocereus grandis</i>	XS		EST						
	<i>Echinocereus scopulorum</i>	XS	TIB							
	† <i>Echinocereus websterianus</i>	XS			NOL					
<i>Ferocactus emoryi</i>	XS					ALC				

Family	Species	Succulence <sup>1</sup>	TIB <sup>2</sup>	EST <sup>2</sup>	NOL <sup>2</sup>	MAR <sup>2</sup>	ALC <sup>2</sup>	DAT <sup>2</sup>	PAT <sup>2</sup>	CHO <sup>2</sup>
Euphorbiaceae	<i>Ferocactus tiburonensis</i>	XS	TIB							
	<i>Lophocereus schottii</i> var. <i>schottii</i>	XS	TIB				ALC	DAT	PAT	CHO
	† <i>Mammillaria estebanensis</i>	XS		EST						
	<i>Mammillaria grabamii</i> ssp. <i>sheldoni</i>	XS	TIB				ALC			
	† <i>Mammillaria multidigitata</i>	XS			NOL					
	† <i>Mammillaria tayloriorum</i>	XS			NOL					
	† <i>Mammillaria</i> sp.	XS					ALC	DAT		CHO
	<i>Opuntia engelmannii</i> var. <i>engelmannii</i>	XS			NOL					
	<i>Opuntia</i> sp.	XS								
	<i>Pachycereus pringlei</i>	XS	TIB	EST	NOL	MAR	ALC	DAT	PAT	CHO
Fouquieriaceae	<i>Peniocereus striatus</i>	XS	TIB					DAT		
	<i>Stenocereus gummosus</i>	XS	TIB	EST				DAT	PAT	CHO
	<i>Stenocereus thurberi</i>	XS	TIB	EST	NOL		ALC	DAT	DAT	CHO
	<i>Cnidoscolus palmeri</i>	SS	TIB					DAT		
	<i>Euphorbia lomelii</i>	SS			NOL					
	<i>Euphorbia misera</i>	SS	TIB	EST				DAT		
	<i>Euphorbia xanti</i>	SS	TIB							
	<i>Jatropha cinerea</i>	SS	TIB							
	<i>Jatropha cuneata</i>	XS	TIB	EST	NOL			DAT		
	<i>Fouquieria diguetii</i>	SS		EST?	NOL					
Loasaceae	<i>Euchide rupestris</i>	SS	TIB	EST	NOL			DAT		
	<i>Ficus palmeri</i>	SS	TIB	EST	NOL			DAT		
Nyctaginaceae	<i>Abronia maritima</i> ssp. <i>maritima</i>	XS	TIB	EST	NOL	MAR	ALC	DAT		CHO
	<i>Portulaca halimoides</i>	SS	TIB				ALC			
Portulacaceae	<i>Portulaca oleracea</i>	SS	TIB							
	<i>Portulaca umbraticola</i> ssp. <i>lancoolata</i>	SS	TIB							
Rusaceae	<i>Talinum paniculatum</i>	SS	TIB							
	<i>Dasylirion gentryi</i>	SS	TIB							
Totals			TIB	EST	NOL	MAR	ALC	DAT	PAT	CHO
16 families		XS: 32	18	11	11	3	11	13	5	9
33 genera		SS: 22	20	8	5	1	4	8	1	2
		HS: 8	8	1	0	0	6	0	2	0
		Total: 62	46	20	16	4	21	21	8	11

<sup>1</sup> Succulent categories: XS = xerophytic succulent, SS = semisucculent, HS = halophytic succulent.<sup>2</sup> Island abbreviations: TIB = Tiburón, EST = San Esteban, NOL = San Pedro Nolasco, MAR = San Pedro Mártir, ALC = Alcatraz, DAT = Dátil,

PAT = Patos, and CHO = Cholludo. Islands are listed in order of decreasing size.

† Insular endemic.

the succulent forest of Cholludo. Similar dense succulent communities are seen on other small Gulf of California islands, including some of the islands in Guaymas bay (Turner and others 2003).

Agaves are also principal xerophytic succulents of the Sonoran islands. Three species are present, including one endemic (*A. cerulata* ssp. *dentiens*). *Agave chrysoglossa* on Tiburón is common from 350 m to the peak of Sierra Kunkaak, where it inhabits a thornscrub-like vegetation (Fig 6a). This agave is also common on San Pedro Nolasco on all but the south-facing slopes and much of the west side of the island. The smaller *A. subsimplex* occurs on Tiburón, where it is common on rocky talus slopes at the north end and scattered localities elsewhere on the island. It is notably abundant on Dátil and Cholludo as well (Fig 6b). The single-island endemic *A. cerulata* ssp. *dentiens* is widespread and abundant on San Esteban. Within *A. cerulata* ssp. *dentiens* two clonal forms are apparent (Fig 6c). Plants at lower elevations tend to have grayer leaves and numerous marginal spines, while those occurring on the mountain slopes at higher elevations tend to have noticeably greener leaves with reduced spines or even spineless margins (Felger and Moser 1985). The higher elevations of San Esteban are often enshrouded in sea fog (Fig 3). This added moisture may underlie the observed morphological distinctions. For example, the occurrence of large numbers of succulent rosette species has been correlated with fog in the mountains of Mexico and arid environments (Martorell and Ezcurra 2002). The role of sea fog is likely a significant factor in the development and distribution of xerophytic succulents not just on San Esteban, but on other islands and the peaks of the Sierra Kunkaak of Tiburón as well.

**Table 2. Flora sizes and percent succulent species for the Sonoran Gulf of California islands (listed in decreasing order of size).**

Island	Total flora size	% Succulent species
Tiburón	348+	13%
San Esteban	122	16%
San Pedro Nolasco	57	28%
San Pedro Mártir	24	17%
Alcatraz	55	38%
Dátil	102	21%
Patos	13	62%
Cholludo	28	39%

### Semisucculents

Many species exhibit succulence as defined by Von Willert and others (1992) in some but not all of their structures, and others have succulent tissue thinly dispersed among other anatomical structures, disguising their succulent nature. Here we follow the lead of Dimmitt and others (2005) as well as proposing other semisucculent species not covered in their study region. We are not including various species that have tuberous roots in this category (for instance, *Tumamoca macdougalii* (Cucurbitaceae), *Proboscidea altheifolia* (Martyniaceae), *Amoreuxia palmatifida* (Bixaceae)), or those species with borderline semisucculent leaves, such as *Atriplex barclayana* (Amaranthaceae), *Maytenus phyllanthoides* (Celastraceae), and *Rhizophora mangle* (Rhizophoraceae). There is no fine line separating the semisucculent from the nonsucculent, but plants that skirt that boundary do offer intriguing distributional patterns that elucidate larger biogeographical trends.

The majority of Sonoran island semisucculents occur on Tiburón, which harbors 20 of the 22 such species described here (Table 1)—probably a consequence of the island's large size and the diversity of niche opportunities available compared with smaller islands of lower relief. This pattern is best exemplified by the four *Bursera* species on Tiburón. The genus has two distinct sections: *Bullockia* and *Bursera*, each represented on the island by a pair of sister species: one of drier, desert conditions and the other of more southerly thornscrub or tropical deciduous forest (TDF) affinities (Cody and others 2002). The *Bullockia* section contains *Bursera hindisiana* (desert affinity) and *B. laxiflora* (thornscrub/TDF affinity) and the *Bursera* section contains *B. microphylla* (desert affinity) and *B. fagaroides* (thornscrub/TDF affinity). A two-species *Bursera* system is prevalent through most of the Gulf of California islands, with one species per site from each section, their identities varying with habitat—desert or thornscrub (Cody and others 2002). Tiburón is the only Gulf island where both species pairs are sympatric. This pattern is indicative of the topographic complexity of the island. Tiburón is about 120 km north and 160 km west of the interfaces of the Sonoran Desert and

tropical thornscrub habitats (Búrquez and others 1999). The massive Sierra Kunkaak and a maritime climate support numerous species of tropical affinity, creating a thornscrub component of the flora not expected due to its disjunction from more tropical areas (Wilder and others 2007).

*Euphorbia xanti* is another interesting semisucculent record for Tiburón. Cody and others (1983) proposed that this species migrated from the Baja California peninsula to the Sonoran mainland via the Midriff islands. There are a number of species that, while widespread on the Baja California peninsula, have limited distributions on the Sonoran mainland and are indicative of ice-age migrations (Van Devender and others 1994; Clark-Tapia and Molina-Freaner 2003). *Euphorbia xanti* occurs in a limited range along the Gulf Coast of Sonora within desertscrub vegetation (Steinmann and Felger 1997). Despite its prominent Baja California distribution, with limited occurrence in Sonora, its closest relatives are on the mainland rather than the Baja California peninsula (Ramírez 1996; Wilder and others 2007).

### Halophytic Succulents

The eight halophytic succulents (Table 1) on the Sonoran islands are mostly confined to coastal areas, including tidal wetlands, and where there is at least a modest beach area. Most of the Sonoran islands lack these conditions; they have, instead, extensive cliff faces that plunge dramatically into the sea, evidence of their uplift ca. three million years ago with the creation of the modern Gulf of California (Carreño and Helenes 2002). San Esteban, San Pedro Nolasco, San Pedro Mártir, Dátil, Patos, and Cholludo are almost entirely without halophytic succulents, except the minor occurrences of *Suaeda nigra* on San Esteban and Patos and *Chenopodium murale* on Patos. Halophytic succulents, however, form a significant component of the Gulf of California coastal wetland vegetation, which is critically important to the rich maritime ecosystems (Felger 2004; Whitmore and others 2005). The majority of Sonoran island halophytic succulents occur along the eastern shore of Tiburón on the Canal del Infiernillo (Fig 7), primarily at the three mangrove *esteros* (tidal wetlands). The majority of the succulent halophytes are wide ranging, including *Salicornia bigelovii* and *Sesuvium portulacastrum*, which are cosmopolitan in distribution. By tapping into a dependable,

although saline, source of water, halophytic succulents represent a very different adaptation to that seen in xerophytic or semisucculent species, and demonstrate another fashion in which succulence is a successful adaptation.

### Analysis

All endemic plant taxa on the Sonoran islands (six cacti and one agave) are succulent, with the exception of *Coreocarpus sanpedroensis* (Asteraceae) of San Pedro Nolasco, illustrating the importance of succulents to the floristic diversity of the islands of the Gulf of California. San Pedro Nolasco, diverse for its small size (57 species, 3.5 km<sup>2</sup>), shares the title for highest single-island plant endemism in the Gulf of California, along with Isla Ángel de la Guarda, with four species (Rebman 2002). San Esteban has three endemics. The sixty-two succulent taxa of the Sonoran islands (16% of the total flora, 12% of which are endemic) form the most characteristic component of the island vegetation and display fascinating adaptations to this arid region.

When the succulent flora of the islands is analyzed it is seen that the smaller islands in the region have a significantly higher percentage of succulent species than the larger islands (Fig 8; Table 2). A significant factor for vegetation of the small islands is the general lack of herbivores (notably mammals), which increases the survivability of plant species, especially succulents. Another potential factor is the moisture-laden maritime air, which often settles over the smaller islands of lower relief. Soil condition is another factor; many of these smaller islands are home to large concentrations of sea birds (Alcatraz, Cholludo, Mártir, and Patos), whose guano adds considerable nitrogen to the soil (Polis and others 2002). It has been documented that the large accumulation of guano on these desert islands is strongly correlated with species-poor floras (Anderson and Wait 2001). However, it has also been shown that these guano rich islands in the Gulf of California actually support higher productivity than islands without guano, even in dry years (Polis and others 1997; Wait and others 2005). It is likely that some succulent species can better tolerate the high nitrogen and phosphorus concentrations and translate these nutrients into relatively high productivity (Anderson and Polis 1999). Too much guano, however, is toxic to plants. The relatively high percentage of succulent species on

smaller islands is counter to the usual species–area relationship. However, this result can be explained by the subsidized island biogeography theory of Anderson and Wait (2001). This supplement to the equilibrium theory of island biogeography of MacArthur and Wilson (1967) suggests that the relationship between subsidies, island size, and diversity depends on where a taxonomic or trophic group falls on the standard unimodal (or quadratic) hypothesized curve for the relationship between productivity and diversity. In our case the succulent flora of the Sonoran islands falls on the ascending side of the productivity–diversity curve, where richness increases with an increase in productivity. This will decrease the slope of the species–area curve for those islands relative to the usual hypothesized line, resulting in increased diversity, as we have observed (see Anderson and Wait 2001).

### Succulent Flora

The succulent plants of the Sonoran islands of the Gulf of California are presented below. We document a total of 62 succulent taxa in 16 families and 33 genera. The most diverse family is Cactaceae, with 24 species and one variety in 10 genera. The next most diverse families are the Amaranthaceae, with six species in four genera, and the Euphorbiaceae, with six species in three genera. We believe this listing is complete, except for a few additional succulent species that may be found in the rugged mountains at the higher elevations on Isla Tiburón. Our knowledge of the island floras is based on previous floristic work (Watson 1889; Johnston 1924; Gentry 1949; Felger and Lowe 1976; Felger and Moser 1985; Moran 1983; Moran and Rebman 2002; Rebman and others 2002) and our own extensive experience in the region.

The plants in this annotated checklist are listed alphabetically by family, genus, and species. Plant families follow the APG II format (Angiosperm Phylogeny Group). Selected synonyms of scientific names are in italics. Common names are given in the following order if known: Cmiique Iitom (Seri, in Roman font); local Spanish (*italics*); and English (Roman). The Comcáac (Seri) names are based largely on the works of Felger and

Moser (1985), Moser and Marlett (2005), and Humberto Romero's knowledge. Representative herbarium specimens or records are cited for each of the eight islands in which the plants occur. Bibliographic information is provided for taxa described from the Sonoran islands. For locality descriptions see Wilder and others (2007), Moser and Marlett (2005), and Felger and Moser (1985). "Geographic Range" is the general distribution in addition to the Sonoran islands.

All specimens cited are at the University of Arizona Herbarium (ARIZ), unless otherwise indicated. Many of the duplicate specimens of our collections are variously deposited at MEXU, SD, and USON, as well as other herbaria in Mexico and the United States. We cite some specimens from Isla Alcatraz from the herbarium of the Prescott College Field Station at Bahía de Kino; photos of these specimens are at ARIZ and tabased in SEINet. More detailed information for specimens at ARIZ can be accessed electronically via *Southwest Environmental Information Network* database (SEINet: <http://seinet.asu.edu>), and data for specimens at USON can be found at *Plantas Silvestres de Sonora: Un Herbario Electrónico en Línea, Catálogo de Especies* (<http://herbario.uson.mx/BasedeDatos.htm>).

This is mostly a specimen-based flora, and all specimens cited have been seen by Felger and/or Wilder unless otherwise noted. Some records are verified by observation, photo documentation, or published report. Islands are listed in order of decreasing size. The name of the collector and the collection number are given. In cases where more than one collector is listed on a label, generally only the first collector's name is given. If no collection number is provided on the herbarium label, then the specimen is identified by the date of collection, for example, *Scott 11 Apr 1978*. When the date of collection is significant, such as collections of historic interest or type collections, both the collection number and date are provided. In a few cases the herbarium accession number follows the herbarium abbreviation in order to avoid confusion in the case of multiple specimens, especially type collections. Spellings of locations and the like generally follow the original herbarium label.

### Species Accounts

#### AGAVACEAE (Agave Family)

The three agaves of the Gulf of California islands are xerophytic succulents and are the most prominent leaf succulents in the flora.

#### *Agave cerulata* TRELEASE ssp *dentiens* (TRELEASE) GENTRY

*Cal Acad Sci Occ Pap* 130: 43, 1978

*A. dentiens* TRELEASE, *Missouri Bot Gard Rep* 22: 51, 1912

Heme, xiica istj caaitic; *maguey*; San Esteban century plant

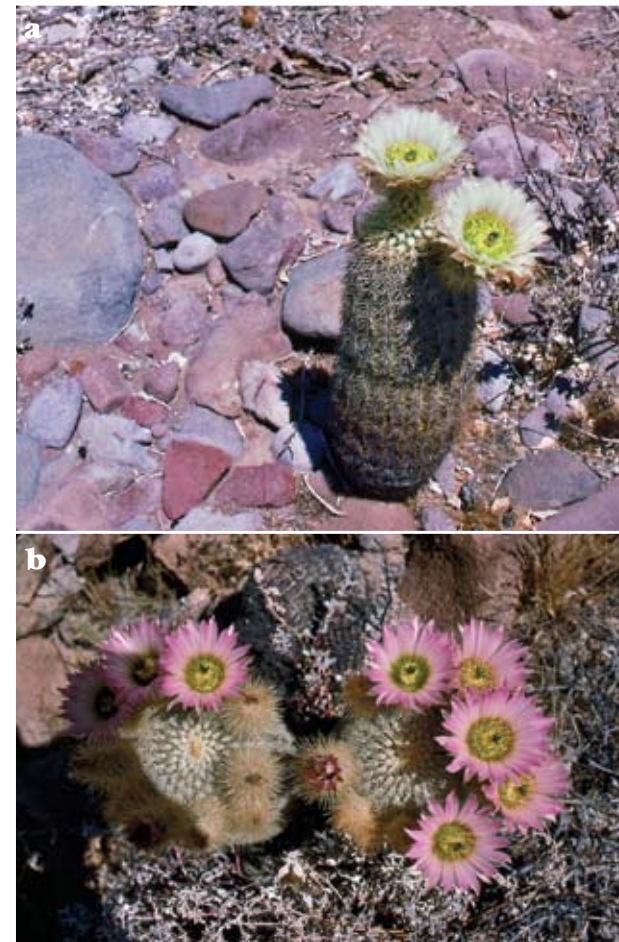
"This medium-sized century plant is considerably larger and more massive than *A. subsimplex*... It forms expansive colonies on the coarse rocky slopes of San Esteban, and is one of the major landscape elements of the island" (Felger and Moser 1985: 222). Across most of the island the plants have markedly gray- to bluish-glaucous leaves. Green leaved clones, however, are common on the heights of the island, where fog and clouds are more frequent. Green and grayish clones occur intermixed (Fig 6c).

"This highly variable subspecies is endemic to San Esteban Island, and is the only agave occurring on that island.... Unlike all other agaves in the Seri region, edible plants of this species could be found throughout the year. However, they are most flavorful during the latter part of January" (Felger and Moser 1985: 222). Perhaps development of the flowering stalk (plants

that are starting to become reproductive—the usual situation for agaves to be suitable for harvest because of accumulation of carbohydrates) becomes arrested due to drought, and such plants might be suitable for harvesting and eating all year. This is an intriguing adaptation.

"It is possible that the agaves on Angel de la Guarda Island should be aligned with *A. cerulata dentiens*" (Gentry 1982: 369). Tom Bowen (personal communication, 2006) tells us that superficially the Ángel de la Guarda agaves appear indistinguishable from those on San Esteban. Agaves are not widespread on Ángel and at low elevation are seen only in a limited area on the west side of the island. Gentry recognized three other subspecies, all in the central part of the Baja California peninsula. A recent investigation into the *A. deserti* complex to which *A. cerulata* ssp *dentiens* belongs provides evidence for a lack of genetic differentiation among various populations of *A. cerulata* (Navarro-Quezada and others 2003). However, based upon morphological features and the need for more genetic studies, the treatment of *A. cerulata* ssp *dentiens* as a single-island endemic remains valid for now (Francisco Molina-Freaner, personal communication 2007).

**San Esteban:** "Lower California,



**Figure 2.** *Echinocereus grandis*. **a.** Isla San Esteban, note the pale cream-colored flowers. **b.** Isla San Lorenzo Sur, note the bright pink flowers. Photos by Thomas Bowen.

San Esteban,” 13 Apr 1911, *Rose 16819* (Holotype, US, images). Mountain slope, ca. 120 m, *Felger 7048*. Arroyo Limantour, *Felger 77–11*. E side of island, large colonies common on hillside and in arroyo, *Moran 21748b*.

***Agave chrysoglossa* I. M. JOHNSTON**

*Proc Calif Acad Sci IV, 12: 998, 1924*

Hasot; amole

Medium-sized agaves forming clusters of mostly several rosettes. Leaves rather narrow and firm, thick, bright to dull green, the margins entire. Flower stalks 2–3 m tall, spike-like and densely flowered. Flowers yellow; late spring. **Tiburón:** Common and widespread at higher elevations of Sierra Kunkaak, on cliffs and rock slopes (Fig 6a); the lowest record is 350 m. The plants are heavily grazed by bighorn sheep, introduced on the island in the 1970s. Its absence from other local islands is presumably due to lack of suitable high-elevation habitat. **San Pedro Nolasco:** Widespread, especially abundant on east-facing slopes on the east side of the island. **Geographic Range:** W-central Sonora, mostly in coastal ranges.

**Tiburón:** Sierra Kunkaak, 354 m, *Wilder 06–28*; ca. 385 m, *Wilder 06–504*; *Scott 11 Apr 1978* (UNM, two sheets). **Nolasco:** *Johnston 3123* (Holotype, CAS). *Stinson & Robinson 29 Apr 1974* (SD). *Moran 4042* (SD).

***Agave subsimplex* TRELEASE**

*Missouri Bot Gard Rep 22: 60, 1912*

Maamjö, ahmo; maguey, mezcäl

Generally a small agave; quite variable in size. **Tiburón:** Widely scattered through the island, mostly on rocky slopes. **Dátil:** Canyon bottoms to peak elevations, generally not on south facing slopes. The name Dátil, usually applied to yuccas and the date palm, was given to this island because of the prevalence of this agave (Fig 6b). **Cholludo:** Primarily on the NE slope. **Geographic Range:** W Sonora in coastal mountains.

**Tiburón:** El Sauz, *Moran 8786* (SD). Sierra Caracol, *Knight 1050* (UNM). Tecomate, *Whiting 9047*. NW side, *Wilder 07–454*. **Dátil:** *Felger 2781, 13431*. *Moran 13022* (SD). *Wilder*

**Figure 3.** Arroyo Limantour on Isla San Esteban. Note remnant fog on the high peak. Photo by Richard Felger.



**Figure 4.** Cardón forest on Isla San Pedro Mártir. Photo by Benjamin Wilder.

*07–103, 07–183*. **Cholludo:** Lower California, Seal Island, 13 Apr 1911, *Rose 16811* (Holotype, US; Isotype, MO; images). *Felger 2721, 13425*.

**AIZOACEAE (Aizoon or Mesemb Family)**

***Sesuvium portulacastrum* L.**

Sea purslane

Halophytic succulent perennials, forming spreading mats. **Tiburón:** Wet, saline soils bordering the inland margins of mangrove and other esteros, upper beaches including low dunes; often tidally inundated. **Alcatraz:** On low sandy flats. **Geographic Range:** Tropical and subtropical shores in many regions of the world.

**Tiburón:** Ensenada Blanca, *Felger 14978*. N of Estero San Miguel, *Wilder 06–6*. Palo Fierro, *Felger 6320*. Tecomate, *Wilder 07–248*. **Alcatraz:** E side, sand beach, *Felger 14927*. E side, flat, *Wilder 07–388*.

***Trianthema portulacastrum* L.**

Comáacöl; verdolaga de cochí; horse purslane

Hot-weather annuals, often semisucculent. **Tiburón:** Widespread in the lowlands. **Alcatraz:** Sandy flats. **Patos:** Seasonally widespread; found on the island for the first time in 2007. **Geographic Range:** Widespread and often weedy; worldwide.

**Tiburón:** Corralitos, *Felger 15366*. Haap Hill, *Felger T74–22*. Palo Fierro, *Felger 8929*. **Alcatraz:** E side, sandy soil, *Felger 14925*. E side, flat, *Wilder 07–389*. **Patos:** Mountain peak, ca. 20 m, *Felger 07–56*.

**AMARANTHACEAE (Amaranth Family)**

The six amaranth species represented on these islands, with the exception of *Chenopodium murale*, are halophytic succulents.

***Allenrolfea occidentalis* (S. WATSON) KUNTZE**

Tacs; chamizo verde, chamizo de agua; iodine bush

Small shrub. Fleshy tissue on *Allenrolfea* and *Salicornia* stems is derived from reduced, modified leaf bases, one per node for *Allenrolfea* and two for *Salicornia*. **Tiburón, Alcatraz:** Common on low-lying saline soils near the shore, often on ground slightly higher and drier than the mangrove/tidal mud zone where salicornias thrive. **Geographic Range:** Coastal deserts and inland alkali sinks; Oregon to Texas to Baja California Sur, NW Sinaloa, and the Chihuahuan Desert in Mexico.

**Tiburón:** Ensenada Blanca, *Felger 7138*. Ensenada de la Cruz, *Felger 12770*. Ensenada del Perro, *Wilder 07-161*. Palo Fierro, *Felger 10328*. Tecomate, *Whiting 9029*. **Alcatraz:** *Felger 12718*. E flat, dominant, *Wilder 07-395*.

***Chenopodium murale* L.**

Ziim Xat; chual; net-leaf goosefoot

Winter–spring annual, the herbage often becoming reddish and semisucculent, sometimes functioning as a halophytic succulent. **Tiburón:** Locally common at scattered sites mostly near the shore and at old Comcáac campsites. In April 2007 we saw unusually large, robust plants to ca. 1 m tall behind the beach at Ensenada del Perro. **Alcatraz:** Seasonally common on the E face of the mountain. **Patos:** Common on the small mountain where it was found for the first time on the island in 2007. **Geographic Range:** Long established and widespread in the Sonoran Desert. Native to the Old World and adventive from Canada to Guatemala.

**Tiburón:** Ensenada del Perro, behind beach, *Wilder 07-164*. **Alcatraz:** Abundant through much of island, especially near top of island on E-facing slopes, *Felger 12714*. E-facing slope of mountain, *Wilder 07-415*. **Patos:** Mountain peak, *Felger 07-55*.

Figure 5. Isla Cholludo. The dense cactus forest is dominated by cardóns (*Pachycereus pringlei*) and organ pipes (*Stenocereus thurberi*). Photo by Benjamin Wilder.

***Salicornia bigelovii* TORREY**

*S. europea* L., *S. pacifica* STANDLEY

Xnaa caaa; pickle weed, glasswort

Annual, extremely succulent. **Tiburón:** E side, margins of mangroves, often partially to fully submerged at high tide. **Geographic Range:** Shores of the Gulf of California and N on the Pacific Coast to southern California.

**Tiburón:** Palo Fierro, *Felger 12560*. Estero San Miguel, *Wilder 06-279*.

***Salicornia subterminalis* PARISH**

*Arthrocnemum subterminale* (PARISH) STANDLEY

Moundlike, low shrub. **Tiburón** and **Alcatraz:** Coastal, mostly at the inland margins of halophytic scrub and mangroves. **Geographic Range:** Shores of the Gulf of California to Sinaloa, Pacific coast of Baja California, and salt marshes and inland areas of California.

**Tiburón:** Coralitos, just above high tide zone, *Felger 15379*. Zozni Cmiipla, *Wilder 06-364*. **Alcatraz:** *Jiménez 42* (Prescott College Collection). E flat, *Wilder 07-398*.

***Suaeda esteroa* FERREN & S. A. WHITMORE**

Sipjö yanéaax; estuary seablite

The Gulf of California plants are annuals and perhaps a different taxon from those on the Pacific Coast, which are generally perennial. **Tiburón:** Documented from the margins of mangroves at the E side of the island. **Geographic Range:** Mangrove and saltscrub esteros, Gulf of California and Pacific coast of Baja California Sur to S California.

**Tiburón:** Margin of a mangrove estero at Zozni Cmiipla, within tidal zone, *Wilder 06-362*.

***Suaeda nigra* (RAFINESQUE) J. F. MACBRIDE**

*S. moquinii* (TORREY) GREENE

*S. ramosissima* (STANDLEY) I. M. JOHNSTON

*S. torreyana* S. WATSON

Sosa; sea blite

Shrubby perennial; herbage, inflorescences, and calyces succulent. **Tiburón, San Esteban, Alcatraz:** along the shores. **Patos:** Several shrubs were found for the first time on the island in 2007. **Geographic Range:** Canada to N and central Mexico.

**Tiburón:** Ensenada Blanca, *Felger 14934*. Ensenada de la Cruz, *Felger 9210*. Palo Fierro, *Felger 6421*. Bahía Agua Dulce, *Felger 6847*. **San Esteban:** *Felger 9199, 15462*. **Alcatraz:** *Felger 12711*. **Patos:** S shore, *Felger 07-54*.

**APOCYNACEAE (Dogbane Family)*****Asclepias albicans* S. WATSON**

Najcáazjc; yamate, candelilla; white-stem milkweed, wax milkweed

Stems semisucculent, reaching 2–2.5 m tall, mostly few, reedlike, white-waxy (Fig 9). **Tiburón:** Occasional on the dry W and S sides to slopes on the E part of the Sierra Kunkaak. **San Esteban:** Widespread and common, primarily on rocky outcrops. **Dátil:** Widely scattered. **Geographic Range:** SE California, both Baja California states, W Arizona, NW Sonora.

**Tiburón:** Ensenada Blanca, *Felger 14976*. Arroyo Sauzal, *Felger 9988*. Ensenada del Perro, *Wilder 07-163*. Punta Perla, *Felger 74-15*. Bahía Agua Dulce, *Moran 12998* (SD). Hast Coop, large volcanic hill S of Pazj Hax waterhole, *Wilder 07-381*. **San Esteban:** E-central side, *Felger 12760*. Main floodplain, *Felger 466*. Canyon at N side, *Felger 17555*. SW corner, *Hastings 71-52*. **Dátil:** NW side, *Felger 15350*. E side below ridge crest, *Wilder 07-137*.

***Asclepias subulata* DECAISNE**

Najcáazjc; jumete, mata candalilla; reed-stem milkweed

Dense clump of many semisucculent, erect stems usually to ca. 1 m. **Tiburón:** Widely scattered in lowland sites. **Geographic Range:** Sinaloa and W Sonora to W Arizona and S Nevada; Cape Region of Baja California Sur to SE California.

**Tiburón:** Arroyo Sauzal, 31 Jan 1965, *Felger*, observation. Punta San Miguel, *Wilder 07-187*. SW part of Central Valley, *Felger 12361*.



**Figure 6.** The Sonoran island agaves: **a.** *Agave chrysoglossa*, Sierra Kunkaak, Isla Tiburón; **b.** *A. subsimplex*, Isla Dátil; and **c.** *A. cerulata* ssp. *dentiens*, Isla San Esteban, with a characteristic higher-elevation green-leaved clone in the foreground and a characteristic low-elevation grayish-leaved clone common in the background.

#### ASTERACEAE (Aster Family)

***Bajacalia crassifolia* (S. WATSON) LOOCKERMAN, B. L. TURNER & R. K. JANSEN**

*Porophyllum crassifolium* S. WATSON

*P. tridentatum* var. *crassifolium* (S. WATSON) I. M. JOHNSTON

Low growing, highly aromatic subshrub; leaves semisucculent, linear to narrowly elliptic, 0.5–2.5 cm long. **Tiburón:** Common especially near the shore on rocky slopes, upper beaches and arroyos, along the S, W, and N margins of the island and locally in the Sierra Kunkaak. **San Esteban, Dátil:** Rocky shores and slopes to the peaks, arroyos and canyons. **Geographic Range:** Gulf coast of Baja California Sur, Isla Angel de la Guarda, and three Sonoran islands; not on the Sonora mainland. *Bajacalia*, a segregate of *Porophyllum*, consists of three distinctive Baja Californian/Gulf of California endemics with succulent leaves and yellow flowers: *B. crassifolia*, *P. moranii* B. L. TURNER, and *B. tridentata* (BENTHAM) LOOCKERMAN ET AL. (Loockerman and others 2003).

**Tiburón:** Ensenada Blanca, *Felger 15735*. Sauzal waterhole, *Felger 10088*. Carrizo Canyon, *Knight 1100 & 1105* (UNM). Near shore, NW side of island, *Wilder 07–431*. **San Esteban:** Arroyo Limantour, *Van Devender 92–488*. San Pedro, *Felger 16669*. S-central peak, *Felger 17543*. Near SE corner, *Moran 8836*. **Dátil:** SE side, *Felger 17515*.

***Hofmeisteria crassifolia* S. WATSON**

Xerophytic succulents. Mound-shaped perennials with succulent stems and leaves. **Nolasco:** Cliffs and canyon walls, especially N-facing. **Geographic Range:** Guaymas region of coastal Sonora.

**Nolasco:** *Felger 11433*.

#### ***Hofmeisteria fasciculata* (BENTHAM) WALPERS var. *fasciculata*** **Taca imas**

Xerophytic succulent; small, globose perennial with succulent stems and leaves. **Tiburón, San Esteban, Dátil, Cholludo:** Widespread on sea cliffs, canyon cliffs, and rock slopes. **Geographic Range:** Coastal Sonora from the Sierra Bacha southwards to mountains N of Bahía Kino, the Midriff islands, and the Gulf Coast of Baja California and Baja California Sur. Two other varieties occur in Baja California Sur.

**Tiburón:** Ensenada Blanca, *Felger 15738*. N of Punta Willard, *Perrill 5111*. Arroyo Sauzal, *Felger 10100*. El Monumento, *Felger 15562*. Sierra Kunkaak, *Wilder 06–468*. W of Tecomate, 980 ft, *Felger 6270*. NE side of island, sea cliff, *Felger 07–60*. **San Esteban:** SW corner, *Felger 17632*. Arroyo Limantour, *Wilder 07–56*. Cascajal, *Felger 9198*. S-central peak, *Felger 17547A*. San Pedro, *Felger 16667*. NW side, *Wilder 07–457*. **Dátil:** NE side, *Felger 9132*. NW side, *Felger 15351*. Ridge-crest, *Felger 13460*. SE side, *Felger 17506*. **Cholludo:** Steep rocky slopes, *Felger 17700*.

#### BATACEAE (Saltwort Family)

***Batis maritima* L.**

Pajóocsim, xpajóocsim, xpacóocsim; *dedito*; saltwort

Highly succulent halophyte, perennial, mostly forming dense mats of trailing and scrambling stems that often root at the nodes. The Comcáac used the roots to sweeten coffee before they had ready access to sugar (Felger and Moser 1985). **Tiburón:** Upper reaches of tidal wetlands including mangrove margins to saline, wet-but-seldom-inundated sandy or muddy soils. **Alcatraz:** Common among halophytic vegetation. **Geographic Range:** Pacific and Atlantic coasts of tropical and subtropical Americas including the Gulf of California region, Galapagos Islands, and Hawaii.

**Tiburón:** Ensenada de la Cruz, *Felger 12771*. N of Estero San Miguel, *Wilder 06–7*. Bahía Agua Dulce, *Felger 6819*. Tecomate, *Wilder 07–247*. **Alcatraz:** 27 May 2002, *Gracida 77* (Prescott College Collection). In *Allenrolfea* flat, *Wilder 07–406*.

#### BORAGINACEAE (Borage Family)

***Heliotropium curassavicum* L.**

Hant otópl, potács camoz; *hierba del sapo*; alkali heliotrope

Semisucculent perennial herb and often facultative annual. Stems and leaves semisucculent. Growing and flowering in response to warm or hot weather any time of year. **Tiburón:** Widely scattered in low-lying saline to alkaline soils, including upper beaches, arroyos and washes, waterholes, and brackish water of estero margins. **Alcatraz:** Rare on the E flat. **Geographic Range:** Warm regions of the western Hemisphere.

**Tiburón:** Ensenada de la Cruz, *Felger 9071*. Sauzal waterhole, *Felger 2766*. Palo Fierro, *Wilder 06–149*. **Alcatraz:** In *Allenrolfea* flat, *Wilder 07–420*.

#### BURSERACEAE (Bursera Family)

The four *Bursera* species have semisucculent trunks and limbs.

***Bursera fagaroides* (KUNTH) ENGLER var. *elongata* McVAUGH & RZEDOWSKI**

*Torote amarillo*, *torote de venado*; *fragrant elephant-tree*

Small tree to 4 (5) m tall, with a well-developed trunk; bark papery and exfoliating during the dry seasons. Similar to *B. microphylla*, but the trees, leaves and leaflets are larger, and it is in leaf only during the summer rainy period. Flowering and leafing out June through July. **Tiburón:** Sierra Kunkaak, mostly above mid-elevations and rocky slopes, canyons, and arroyos. *Bursera fagaroides* and *B. microphylla* sometimes grow intermixed, but *B. fagaroides* generally reaches higher densities in habitats slightly less xeric and of higher elevations than does *B. microphylla*. **Geographic Range:** Nayarit to SW Chihuahua and Sonora, and a small, disjunct population in S Arizona.

**Tiburón:** Siimen Haax, *Romero 07–4*. Cerro Kunkaak, 800 m, *Scott 11 Apr 1978* (UNM). Cerro San Miguel, *Quijada 91T016*. Top of Sierra Kunkaak Segundo, ca. 490 m, *Wilder 06–492*.



***Bursera hindsiana* (BENTHAM) ENGLER****Xopín; torote prieto, copalquín, copal; red elephant tree**

Mostly shrubs (small trees on the mainland). Bark smooth, not peeling; dark reddish brown on smaller branches. Leaves highly variable and produced at various seasons depending on soil moisture, to 5 cm, with (1) 3 (5) leaflets, the leafstalk often winged. Flowers on slender stalks 1–5 (–8) cm long. Fruits globose, red and green, resembling a miniature apple. August–October. **Tiburón, San Esteban, Dátil, and Cholludo:** Widely scattered but not the principal *Bursera* species on any island. **Geographic Range:** Through much of Baja California and the coast of Sonora from Puerto Lobos southward to the vicinity of San Carlos.

**Tiburón:** Ensenada Blanca, *Felger 14970*. Arroyo Sauzal, ca. 0.5 mi from shore, many have been heavily damaged by deer, *Wilder 06–92*. El Monumento, *Felger 15522*. Palo Fierro, *Felger 10320*. Cliff face of canyon at N base of Sierra Kunkaak, 415 m, *Wilder 06–402*. Valle de Águila, *Wilder 07–234*. NE side of island, *Felger 07–67*. **San Esteban:** N side of island, canyon, *Felger 17595*. Canyon at SE corner, *Felger 17624*. **Dátil:** NE side, not common, canyons and steep rocky slopes, *Felger 13461*. NW side of island, *Felger 15325*. **Cholludo:** Near center of island near N shore, rare, *Felger 9160*.

***Bursera laxiflora* S. WATSON****Xoop caacöl; torote prieto; fern-leaf bursera**

Large shrubs or small trees; all parts of the plants aromatic when crushed. Bark reddish brown, not peeling. Twigs slender. Leaves fernlike, produced at almost any season and drought deciduous. Flowering June–August (summer rainy season). **Tiburón:** Around the base and interior of mountains of Sierra Kunkaak, from the upper bajada to the high elevations. **Geographic Range:** Most of the S two-thirds of Sonora and also Sinaloa, SW Chihuahua, and Baja California Sur.

**Tiburón:** Haap Hill, *Felger T74–8*. Foothills, E side of Sierra Kunkaak, *Felger 6967*. Hast

Figure 7. Halophytic succulent community at Estero San Miguel, east shore of Isla Tiburón.

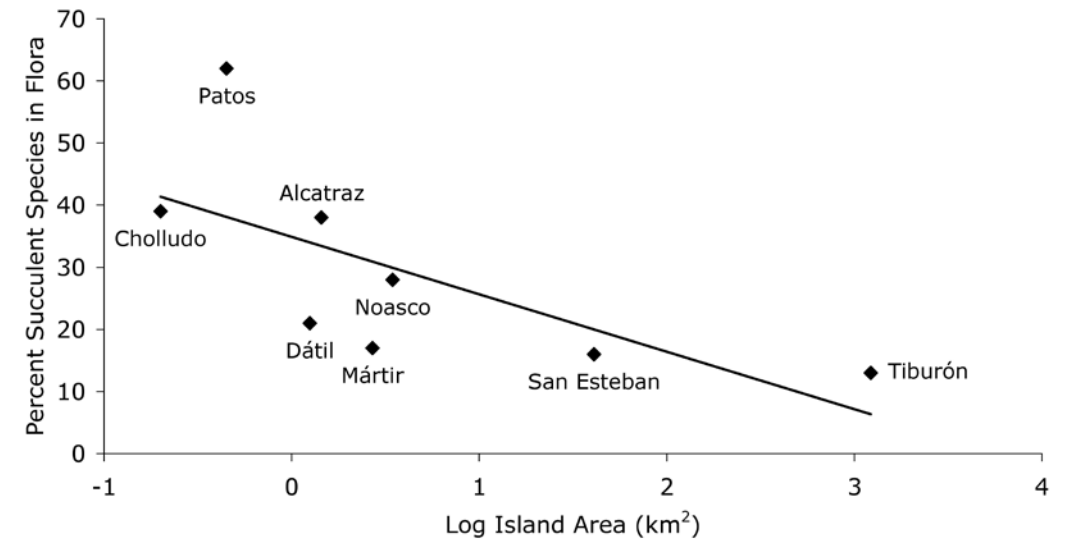


Figure 8. Relationship between the log of island area and percent succulent species in the floras of the Sonoran Gulf of California Islands. The smaller islands are relatively richer in succulent species than larger islands. The only island not fitting this pattern is Dátil, which has an unusually rich flora and high topographic heterogeneity. Patos, Cholludo, Alcatraz, and Mártir are “bird” islands, having high concentrations of guano. Regression analysis performed on the arcsin square root of the proportion of succulent species.  $y = -9.2525x + 34.893$ ;  $R^2 = 0.5012$ ;  $p\text{-value} = 0.04942$ .

Coopol, large volcanic hill S of Pazj Hax waterhole, *Wilder 07–373*. Sierra Kunkaak, ca. 3 km E of Siimen Haax waterhole, *Wilder 06–499*. Sierra Kunkaak Mayor, *Romero 06–3*.

***Bursera microphylla* A. GRAY.****Xoop, xoop hayéen ipáii; torote blanco, torote colorado, torote prieto, copal; elephant tree**

Small tree or large shrub (generally larger on Tiburón than on San Esteban). Limbs and trunk fat and semisucculent, the wood soft and pithy. Bark papery and exfoliating during the dry seasons. Herbage highly aromatic; leaves produced at various seasons following rains. *Xoop* is an important medicinal and ritual plant in Comcáac culture (Felger and Moser 1985). **Tiburón, San Esteban, San Pedro Nolasco, and Dátil:** Widespread and abundant, being the most prolific *Bursera* of these islands. It was rare on Alcatraz in the 1960s and was no longer present in 2007. **Geographic Range:** W Sonora to SW Arizona, Gulf islands, and most of Baja California to SE California.

**Tiburón:** Haap Hill, *Felger T74–32*. Palo Fierro, *Felger 11085*. Foothills of Sierra Kunkaak, *Wilder 05–18*. San Miguel Peak, 1000 ft, *Knight 921* (UNM). Tecomate, *Whiting 9035*. **San Esteban:** Limantour, *Felger 16608*. Near center of island, *Felger 469*. **Nolasco:** NE side of island, near ridgecrest, *Felger 06–111*. **Alcatraz:** Only one individual found on island, near beach at S side of flat terrain of E side of island, 8 Oct 1966, *Felger 14920*. **Dátil:** NE side, abundant, *Felger 9088*. NW end, *Felger 2772*.

**CACTACEAE (Cactus Family)**

There are 25 taxa of cacti in 10 genera on the Sonoran islands, ranging from plants about 10 centimeters tall to tree-sized columnar cacti. All are xerophytic succulents. The cactus flora of the state of Sonora includes about 100 species (Paredes and others 2000; Felger 2000), while the Sonoran Desert as a whole includes about 140 species, or about 6% of the total native flora (Felger and Zimmerman 2000). Cacti represent about 5% of the flora of the islands in the study area.

The columnar cacti in the region produce edible fruits and were significant food and wine resources for the Comcáac and continue to be harvested for delicious fruits and medicinal purposes (for instance, Felger and Moser 1985; Paredes and others 2000; Felger 2000).

***Carnegiea gigantea* (ENGELMANN) BRITTON & ROSE**

Mojépe; saguaro, sabuaro; saguaro

Giant columnar cactus, unbranched to several mostly erect branches. Saguaros tend to initiate branches higher off the ground than *cardons* (*Pachycereus pringlei*) and the mature saguaro stems are green rather than glaucous. Young plants are difficult to distinguish. **Tiburón:** Widespread; the densest concentrations occur in the Sierra Kunkaak and the E side of the Central Valley on the bajada coming off the Sierra Kunkaak, and the Tecomate region. **Alcatraz:** Felger (1966: 139) reports that “Of the two columnar species of arborescent columnar cacti on the island, *Carnegiea* is poorly established... Fruiting individuals of *Carnegiea* are present but most of the population consists of immature individuals.” In 2007 only a few taller (ca 7 m) individuals were present. There is no record of saguaro on Dátil. **Patos:** One or more saguaros were cut down in the 1946 when the vegetation was cleared by a Mexican guano mining company (Bowen 2000; Felger 1966; Gentry 1949). Ivan Johnston (1924: 1108) discovered saguaro on Patos in 1921: “The single plant on Patos Island is over 12 m high and has a single large branch.” “Another saguaro is evident in one of Osario Tafal’s 1946 photographs. It was an unbranched plant about 3 to 4 m high and grew below the low rock ledge at the southeast shore... The species no longer exists on the island” (Felger 1966: 358). None were seen on the island in 2007. **Cholludo:** A few juvenile saguaros were seen at the margin of the cactus forest. **Geographic Range:** SW Sonora to Arizona, and barely entering California near the Colorado River.

**Tiburón:** Arroyo Sauzal, 31 Jan 1965, Felger, observation (Felger 1966: 221). Rocky hill W of Palo Fierro, Felger 10025. **Alcatraz:** E base of mountain, 16 Sep 2007, Wilder 07-423 (photo). **Patos:** SE shore, 1946, Osario Tafal (photo; Felger 1966: 353). **Cholludo:** Felger (1966: 309).

***Cylindropuntia alcabes* (F. A. C. WEBER) F. M. KNUTH var *alcabes****Opuntia alcabes* F. A. C. WEBER var *alcabes*

Heem icös cmasl; choya; Baja California cholla

Chollas often 1–1.5 m tall. Flowers yellow, fruits fleshy, yellow. **San Esteban:** Common from low elevation arroyo benches to ridge crests of the peaks. **San Pedro Mártir:** Infrequent to locally common at higher elevations on the island. Often growing intermixed with *C. cholla*. **Geographic Range:** This species with four intergrading varieties occurs throughout most of the Baja California peninsula and adjacent Gulf islands.

**San Esteban:** Lindsay 3004 (SD). Arroyo Limantour, Felger 12732. **Mártir:** 18 Apr 1921, Johnston, observation (cited by Johnston 1924: 1115). Top of island, occasional, 8 dm tall, stem to 5 cm diameter, Moran 8815 (SD). Small canyon at base of SE-facing slope that leads to island summit, Felger 07-18 (USON).

***Cylindropuntia bigelovii* (ENGELMANN) F. M. KNUTH***Opuntia bigelovii* ENGELMANN

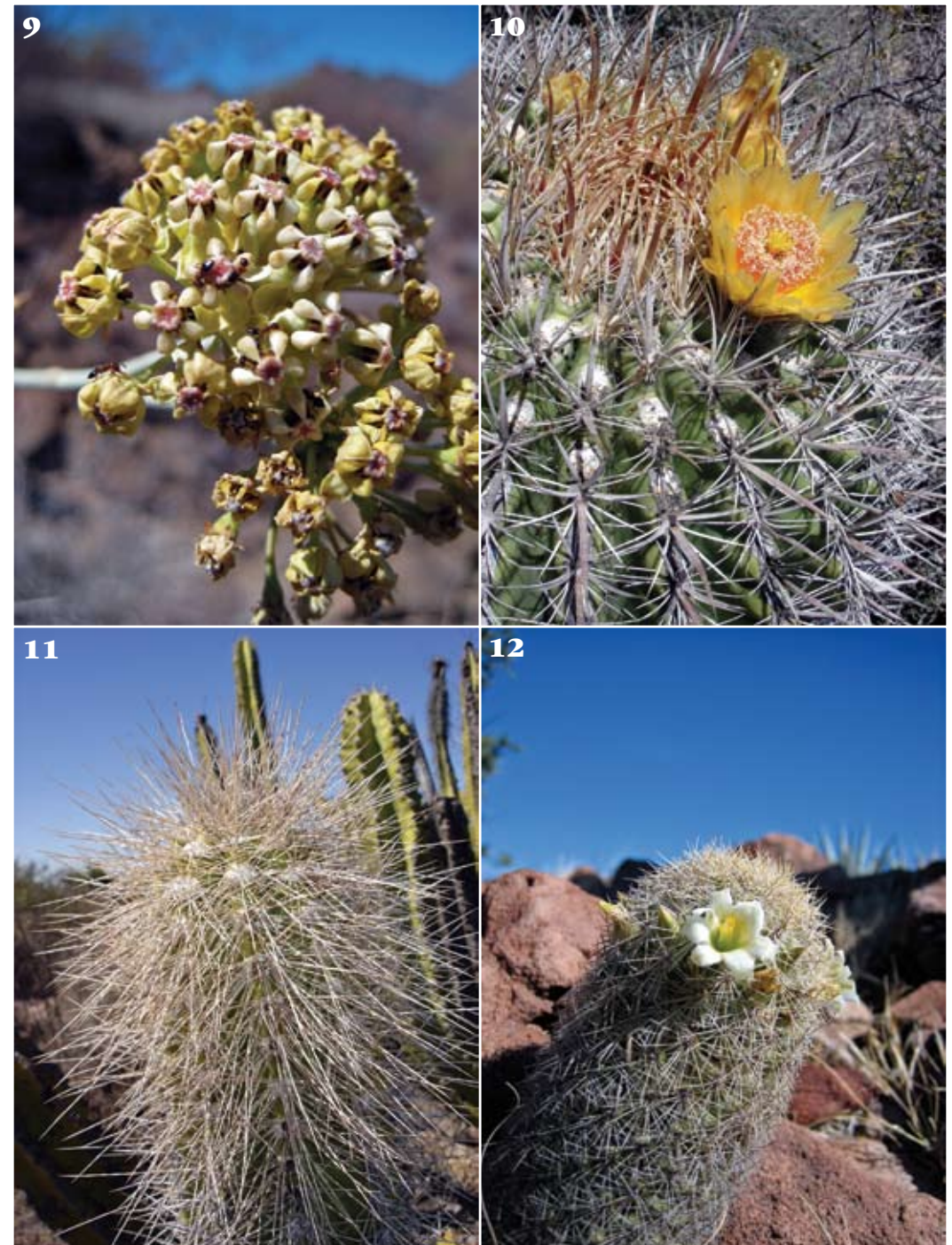
Coote, sea; choya, cholla güera; teddybear cholla

Trunk stout and straight, beset with persistent, dead, blackened joints. Cladodes extremely spiny; spines dull yellow. Inner tepals greenish yellow. Fruits yellow, somewhat fleshy. A clonal species; new plants grow from the fallen joints which break away even when scarcely brushed against. **Tiburón:** Widespread at lower elevations. **San Esteban:** Common along the Arroyo Limantour and scattered across the island. **Dátil:** Fairly common. **Alcatraz:** Rare at the E base of the mountain. **Geographic Range:** Sonora, Arizona, California, Nevada, Baja California, and Baja California Sur.

**Tiburón:** Tecomate, Whiting 9064. **San Esteban:** S end, Rempel 292 (RSA). Felger 7047. SW part, Wilder 07-83B (USON). **Alcatraz:** SE base of mountain, Felger 12827. NE base of mountain, Wilder 07-422 (USON). **Dátil:** NE side, 11 Apr 2007, Felger, observation.

***Cylindropuntia cholla* (F. A. C. WEBER) KNUTH***Opuntia cholla* F. A. C. WEBER

Chollas to about 1.5 m tall. Cladodes (joints) and fruits green, highly succulent and readily detaching, potentially forming new plants and clonal colonies. Flowers pink with relatively



**Figure 9.** *Asclepias albicans*, Sierra Kunkaak, Isla Tiburón, September 2007. **Figure 10.** *Ferocactus tiburonensis*, eastern bajada, Isla Tiburón, May 2007. **Figure 11.** *Lophocereus schottii*, eastern bajada, Isla Tiburón, May 2006. **Figure 12.** *Mammillaria estebanensis*, southwest corner, Isla San Esteban, March 2007.

few tepals. Fruits globose, persistent, and solitary or proliferating into short chains. **San Pedro Mártir:** Infrequent to locally common at higher elevations. Palmer reported it as “Choyer”; common on S. Pedro Martin [sic] Island” (Watson 1889: 52). **Geographic Range:** Widespread throughout the Baja California peninsula, including various Pacific and Gulf islands.

It is closely related to *C. fulgida* of the mainland and Sonoran islands, the distinctions being subtle (see Rebman 1995). The seeds of both species are likely not viable (Rebman 1995; Felger and Zimmerman 2000).

**Mártir:** 1887, *Palmer 419* (not seen, cited by Watson 1889: 52). Top of island, occasional, ca. 6 dm high, broad yellowish papery sheaths, very spiny, *Moran 8814* (CAS, SD). Lower (first) “plateau,” ca. 500 ft elev, not common, 4–5 ft high, *Felger 6357*. Summit, 300 m, localized population, plants 1.3 m tall, *Wilder 07–607* (USON).

***Cylindropuntia fulgida* (ENGELMANN) F. M. KUNTH var *fulgida***

*Opuntia fulgida* ENGELMANN var *fulgida*

Sea cotópl, sea icös cooxp; *choya*; jumping choya

Trunks seldom straight, often with several major branches from about mid height. Stems and fruits green all year, the fruits proliferating in pendulous chains. Propagation is vegetative from readily rooting fallen joints and fruits. *Cylindropuntia fulgida* is closely related to *C. cholla*, which is distinguished from *C. fulgida* in part by its single or short-chained and larger fruits, and broader and shallower floral scar on the fruits. **Tiburón:** Widespread across the lowlands. **San Pedro Nolasco:** Fairly common throughout the island except N-facing slopes; mostly on exposed ridges but also on other slopes. Most of the plants on this island are densely spined like var *fulgida*. **Alcatraz:** Common at the E base of the mountain. **Geographic Range:** S Arizona through much of Sonora, especially the W part of the state; also common on desert flats near Bahía Kino.

**Tiburón:** Arroyo Sauzal, generally rare, except interhill bench adjacent to waterhole, *Felger 10118*. S end of island, *Rempel 296* (RSA). **Nolasco:** 29 Mar 1937, *Rempel 296* (RSA). NE side of island, 28 Nov 2006, *Felger*, observation. **Alcatraz:** SE base of mountain, *Felger 12826*. E-base of mountain, *Wilder 07–428* (USON).

***Cylindropuntia fulgida* var *mamillata* (SCHOTT EX ENGELMANN) BACKEBERG**

This variety is distinguished from var *fulgida* by its fewer and shorter spines (the stem surface is not obscured by the spines) and tight-fitting sheaths (the spines sheaths are not papery). Rebman (1995: 163) cites a specimen of this variety from **San Esteban**, but we have not found it there. **San Pedro Nolasco:** Some plants, especially at lower elevations on the E side of the island, appear more like var *mamillata* than var *fulgida*. **Alcatraz:** Common on the coastal margins of the E flat. **Dátil:** Reported for the island by Felger (1966) and Felger and Lowe (1976). **Patos:** “Colonies of mature individuals laden with pendulant chains of fruits occur at the rocky ledges near the southeast shore and also on the flats near the base of the hill. Before clearing of the island in 1946 it occurred at least in the former site and was common” (Felger 1966: 359), and it was still common there in 2007. A few younger plants approach var *fulgida* in density of spines. **Cholludo:** Common in the understory of the cactus forest.

**San Esteban:** 13 Apr 1911, *Rose 16824* (US, not seen, cited by Rebman 1995: 163). **Nolasco:** E side of island, *Felger 12074*. **Alcatraz:** Common on coastal edge of flat, *Wilder 07–412* (USON). **Dátil:** Felger and Lowe 1976: 39. **Patos:** *Felger 7012*. Near SE shore, 1946, *Osario Tafal* (photo; Felger 1966: 353). S side of island, *Felger 07–58A, 07–58B* (USON). **Cholludo:** N face of island, abundant, *Felger 13422*. Seal Island, near Tiburón, 13 Apr 1911, *Rose 16813* (US, not seen, cited by Rebman 1995: 163).

***Cylindropuntia leptocaulis* (DE CANDOLLE) F. M. KNUTH**

*Opuntia leptocaulis* DE CANDOLLE

Iipxö; *siviri*; desert Christmas cholla

Slender-stemmed cholla to ca. 1 m. Young plants have a small tuberous root. Flowers pale yellowish to cream, 1.5–2 cm wide, opening late in the afternoon. Fruits fleshy, bright red or red-orange. **Tiburón:** At least in the lower coastal zone on the E bajada and the S shore. **Dátil:** Common along canyons at the NE side of the island and rare on the NW side; many plants had proliferating chains of two or three fruits. **Geographic Range:** Oklahoma and Texas to Arizona and S to Puebla, and lowlands of Sonora and Sinaloa.

**Tiburón:** S of Zozni Cmiipla and ca. 75 m inland, rare, *Wilder 06–162* (USON). [Presumably the S shore of the island], *Dawson 25 Jan 1940* (RSA). **Dátil:** NW part, *Felger 2777*. NE side, *Wilder 07–142* (USON).

***Cylindropuntia versicolor* (ENGELMANN EX J. M. COULTER) F. M. KNUTH**

*Opuntia versicolor* ENGELMANN EX J. M. COULTER

Heem icös cmaxlilca, hepem ihéem; *siviri*; staghorn cholla

Chollas often to about 1.5 m tall with an upright trunk and main stems, and spreading branches, the stems purple-brown during drier, cooler months. Inner tepals greenish yellow with red-brown tips; stamens yellow-green. Flowering March–early April. Fruits fleshy, yellow-green, usually persistent until the following year, often becoming enlarged and swollen, usually solitary or rarely in chains of two or three fruits. **Tiburón:** Widely scattered in the lowlands and rare in the Sierra Kunkaak. **Dátil:** Rare, only seen on steep rocky slopes near peak elevation on a brushy slope. **Geographic Range:** S-central Arizona to the Guaymas region in Sonora.

**Tiburón:** Punta Willard, *Harbison 19 Mar 1962* (SD, 51614 & 84157). Agua Dulce Bay, rather few, volcanic N slope, *Moran 12993* (SD). NW side of island, 29 Sep 2007, *Felger & Wilder*, observation. Tecomate, *Whiting 9016*. Coastal mountain E of Tecomate, 30 Sep 2007, *Wilder*, observation. **Dátil:** NE side of island, NE-facing slope near crest, rare, steep and rocky slope, *Felger 13471*.

***Echinocereus grandis* BRITTON & ROSE**

*Cactaceae* 3: 18, fig 18, pl 3.3; fig 3, 1922

Hant iipzx iteja caacöl; giant rainbow cactus

Plants reaching ca. 50 cm tall, the stems very thick, sometimes solitary but mostly with a few branches. Flowers whitish (on San Esteban), ca. 5–7 cm long and about as wide, the outer perianth segments pink-tinged. Endemic to **Islas Las Animas, San Lorenzo, and San Esteban**. **San Esteban:** Widespread and abundant from low to high elevations.

The flowers (Fig 2a) are relatively smaller and not very showy compared to other members of the genus in the Sonoran Desert, except for *E. websterianus* on San Pedro Nolasco, which likewise has smallish, dull-whitish flowers. One might think that these island endemics have less-showy flowers because of the relative lack of competition for pollinators with fewer other species of cacti (also see *Mammillaria estebanensis*). The flowers on *E. grandis* on Islas San Lorenzo and Las Animas (“San Lorenzo Norte”), however, are bright pink (Thomas Bowen, personal communication, 2006; Figure 2b). *Echinocereus grandis*, *E. scopulorum*, and *E. websterianus* are part of the *E. rigidissimus* group (Taylor 1985), which consists of six species in the Sonoran Desert region and SE Arizona and SW New Mexico.

**San Esteban:** 13 Apr 1911, *Rose 16823* (Holotype, NY, image). SE end of island, main canyon, flowers white, however one plant with pinkish flowers, *Felger 2610*. SE corner, seen from shore to summit, *Moran 8838* (SD). S end of island, *Rempel 294*. Arroyo Limantour, *Van Devender Apr 1992*.

***Echinocereus scopulorum* BRITTON & ROSE**

Hant iipzx iteja caacöl; Sonoran rainbow cactus

Stems usually solitary. Plants in the SW part of Tiburón are often exceptionally large (to ca. 40 cm tall). Flowers large and showy, 6–8 cm wide, the perianth deep rose-pink. Flowering April and July–August. **Tiburón:** Widely but thinly scattered in rocky places across the island but not seen on the lowland bajadas and valley plains. **Geographic Range:** W Sonora, from the Guaymas region N to the Sierra Seri and Sierra del Viejo near Caborca.

**Tiburón:** Willard Point, *Lindsay 3247* (SD). Arroyo Sauzal, rocky ledge adjacent to arroyo, ca. ½ mi S of waterhole, 44 cm tall, *Felger 10096*. Sierra Kunkaak, near Siimen Haax waterhole, *Wilder 06–471* (USON). Agua Dulce Bay, *Lindsay 3246* (SD). NW side of island, 29 Sep 2007, *Felger & Wilder*, observation.

***Echinocereus websterianus* G. E. LINDSAY**

*Cact Succ J* (US) 19: 153–154, figs 102, 103, 1947

Multiple-stemmed (cespitose), often 50–60 cm tall. Spines often pale golden-yellow. Flowers pale pink, about half as large as those of *E. scopulorum*. Flowering in spring, probably mostly March.

Endemic to **San Pedro Nolasco**, where it is abundant on steep, rocky slopes, growing with *Agave chryso glossa*, *Mammillaria multidigitata*, and *Opuntia* sp. This distinctive *Echinocereus* shares several features with *E. grandis*. Both have unusually large, thick, and multiple stems,

and flowers reduced in size and brightness of color as compared with *E. scopulorum*, their presumed closest relative. However, *E. websterianus* may be more closely related to *E. scopulorum* than to *E. grandis*.

**Nolasco:** 24 Feb 1947, *Lindsay & Bool 498* (Holotype, DS; Isotype, SD); *Dawson 1040*; *Felger 2228* (SD); *Rempel 301*.

***Ferocactus emoryi* (ENGELMANN) ORCUTT**

*F. covillei* BRITTON & ROSE

Siml caacöl, siml yapxöt cheel; *biznaga*; Coville barrel cactus

Robust barrel cactus with a single thick stem (reaching ca 1 m tall on the nearby mainland). All spines (including radials) thick and rigid; juvenile plants have markedly more-rigid spines than adult plants. Flowers reddish and fruits yellow and fleshy (nearby mainland population). **Alcatraz:** In 2007 we found three robust juvenile plants within a few meters of the maximum high tide. The plants were less than ca 20 cm tall and within 5 m of each other. These plants, rather recent arrivals on the island, represent the only record for this species on a Gulf of California island. The nearest population occurs on the sandy flats a few kilometers inland from the shore at Bahía Kino. It also occurs north of Bahía Kino in the Sierra Seri. **Geographic Range:** Southwestern Arizona to the Guaymas/Yaqui region in southern Sonora.

**Alcatraz:** NW side of island, cobble/shell rock berm along shore, three juvenile, healthy robust plants, *Felger 07–176* (photos).

***Ferocactus tiburonensis* (G. E. LINDSAY) BACKEBERG**

*F. wislizeni* var *tiburonensis* G. E. LINDSAY, *Cact Succ J* (US) 27: 166, fig 155, 1955

Siml; *biznaga*; Tiburón barrel cactus

Stem to 1+ m tall. “Spines usually heavily annulated [“ringed”], not clearly differentiated into radial and central series; the four most central spines terete, cruciform in arrangement, straight or somewhat twisted, the lower sometimes flattened and to 9 cm long; radial spines subulate, annulate, strongly resembling the centrals but not as heavy, though never setaceous” (Lindsay 1996: 175). On younger plants the central spine can be hooked and much stouter than the other spines. Flowers yellow, in spring (Fig 10). Fruits yellow and fleshy. The distinctive firm outer radial spines, a character first pointed out by Johnston (1924), sets *F. tiburonensis* apart from *F. wislizeni*. Taylor (1984) pointed out the distinctive seed coat morphology of *F. tiburonensis* (he treated it at the varietal rank). Backeberg treated it as a distinct species, an opinion substantiated by Felger and Zimmerman (2000).

**Tiburón:** Fairly widespread including the E bajada and ranging into the Sierra Kunkaak,

**Figure 13.** *Peniocereus striatus*, eastern bajada, Isla Tiburón, May 2007. **Figure 14.** *Stenocereus gummosus*, eastern bajada, Isla Tiburón, September 2006.



where it also occurs at higher elevations. Plants at higher elevations are being heavily impacted by the introduced bighorn sheep. **Geographic Range:** On Tiburón and the opposite coastal mainland from S of Bahía Kino to the vicinity of Tastiota. Much of the probable mainland habitat has been converted to agriculture and the few remaining populations are rapidly being lost to roads, shrimp farming, and other developments. *F. tiburonensis* and *F. wislizeni* are clearly allopatric, although the distance separating them remains unknown.

**Tiburón:** SE corner [Ensenada del Perro], 30 Apr 1952, *Lindsay 2229* (Holotype, DS). Ensenada Blanca, 29 Jan 1965, *Felger*, observation (Felger 1966: 181). Arroyo Sauzal, ¼ mi S of waterhole, infrequent and scattered on rocky slopes, pediments, and benches adjacent or near arroyo, *Felger 10098*. Tordillitos, *Felger 15473*. Coralitos, *Felger 15373*. 0.5 mi NW of Zozni Cmiipla, scattered plants, *Wilder 06–160* (USON). Ca. 2 km from shore, road to Pazj Hax waterhole, scattered plants, *Wilder 06–164* (USON). NW side of island, *Felger 07–86* (USON). Tecomate, W of village, *Whiting 9065*.

***Lophocereus schottii* (ENGELMANN) D. R. HUNT var *schottii***

*Pachycereus schottii* (ENGELMANN) BRITTON & ROSE var *schottii*

Hasahcápjö, hehe is quisil; *sinita*; senita, old man cactus

Multi-stemmed columnar cactus (Fig 11), the stems markedly dimorphic. Fruits rather small, juicy, red, and moderately sweet. Senita reaches maximum development on fine-textured soils of bajadas and valley plains and is uncommon on rockier soils and steep slopes. Reproductive populations with juvenile, seed-grown plants were observed only on Tiburón. The occasional occurrence of senitas on the smaller islands, often at higher elevations on rocky sites, indicates repeated introductions by birds.

**Tiburón:** Widely scattered at lower elevations, including bajadas on the east side of the island and especially the west-inclined bajada-plain on the east side of the Central (Agua Dulce) Valley. Occasional plants encountered on rocky hilltops. Reported by Rebman and others (2002) for **San Esteban** but we are unable to document it for the island. It is, however, on **San Lorenzo**, where there are a half dozen small stands of this cactus on the E side of the island near the N tip and east edge (Thomas Bowen, pers. comm. 2006). **Alcatraz:** A few straggly senitas occur near the top of the island. **Dátil:** Scattered colonies of several or more plants are localized in arroyos and slopes near the top of the island. **Patos:** Two specimens are evident in Osorio Tafal's 1946 photos near the SE shore. One of the senitas was still present in 1966 and was the only one then on the island (Felger 1966: 353, 359), but it was no longer present in 2007. Three other, half-grown senitas were present in 2007. **Cholludo:** Rare, observed at the top of the island. **Geographic Range:** (This species) NW Sinaloa to SW Arizona, Baja California peninsula, and many Gulf islands.

**Tiburón:** Arroyo de la Cruz, rather scarce, *Moran 13015* (SD). SW Central Valley, 2 Feb 1965, *Felger*, observation (Felger 1966: 236). Ca. ½ mi from shore, road to Pazj Hax waterhole, *Wilder 06–163* (photo). **Alcatraz:** “Limited numbers near the top of the island, with birds seeming to be the agents of dispersal” (Felger 1966: 137). Several on E coastal edge, and a population near the summit of the island, 16 Sep 2007, *Wilder 07–425* (photo). **Dátil:** NE side, widely scattered, *Felger 13469*. **Patos:** Near SE shore, 1946, *Osario Tafal* (photo; Felger 1966). Flats, SW of base of hill, 30 Sep 2007, *Wilder* (photo). **Cholludo:** Felger 1966: 418.

***Mammillaria estebanensis* LINDSAY**

*Cact Succ J* (US) 39: 31, 1967

*M. angelensis* R. T. CRAIG bis var *estebanensis* (G. E. LINDSAY) REPPENHAGGEN, *Die Gattung Mammillaria nach dem heutigen Stand meines Wissens* 1988: 34, 1981

*M. dioica* K. BRANDEGEE ssp *estebanensis* (G. E. LINDSAY) D. R. HUNT, *Mammillaria Postscripts* 7: 3, 1998

Often irregularly several-branched. Tubercle axils bear multiple bristles about as long as the tubercle. Flowers dull white: outer, larger tepals five, each with a broad greenish-red mid-stripe; inner tepals eight, nearly white with greenish tinge and slightly darker along the mid-stripe (Fig 12). Fruits bright red, fleshy, and delicious, often borne in a ring around the upper part of the stem. It is part of the *M. dioica* complex centered in the Baja California peninsula (Hunt and others 2006). **San Esteban:** Widespread, often growing with *Echinocereus grandis*.

**Geographic Range:** Endemic to Islas San Esteban and San Lorenzo. Not seen on Las Animas (Thomas Bowen, personal communication 2006).

**San Esteban:** 13 Jan 1961, *Lindsay 3002* (Holotype; SD). *Lindsay, 22356* (SD). *Moran 4078* (SD). Arroyo Limantour, common in rocks on gentle bajada and broad wash, *Van Deventer 90–525*.

***Mammillaria grahamii* ENGELMANN ssp *sheldonii* (BRITTON & ROSE) D. R. HUNT**

*M. sheldonii* (BRITTON & ROSE) BOEDEKER

*M. swinglei* (BRITTON & ROSE) BOEDEKER

Hant iipxzteja; viejito, cabeza de viejo; fishhook cactus

Small globose to cylindrical cactus, often with several branches from the base. Central spines usually hooked. Flowers whitish, the inner tepals with pale pink midstripes. Fruits fleshy and red or orange. **Tiburón:** Widely scattered across the island, often in rocky places. **Alcatraz:** Occasional along the rocky cobblestone margin of the E flat. **Geographic Range:** As broadly interpreted, *M. grahamii* ranges from SE California to W Texas, Chihuahua and Sonora nearly to the Sinaloa border. Subspecies *sheldonii* is endemic to the Gulf Coast of Sonora.

**Tiburón:** Ensenada Blanca, 160 m, *Felger 17625* (SD). E side of island, foothills of Sierra Kunkaak, *Wilder 05–16* (USON). Vicinity of Siimen Haax waterhole, *Wilder 06–452* (USON). Bahía Agua Dulce, *Lindsay 18 Mar 1962* (SD). NE side of island, *Felger 07–66A* (USON). **Alcatraz:** Rocky coastal bench at NE portion of flat, *Wilder 07–410* (USON).

***Mammillaria multidigitata* W. T. MARSHALL EX G. E. LINDSAY**

*Cact Succ J* (US) 19: 152, figs 99–100, 1947

Many-stemmed, low, spreading plant. Stems elongated, reaching 4–5 cm in diameter, somewhat flaccid, the tubercles and spines short, spines straight, or rarely a few areoles with the central spine curved or moderately hooked at the tip. Dioecious. Tepals white to cream; outer tepals ciliate-fringed and with a faint, pale-pink midstripe; inner tepals with entire or essentially entire margins, the tips broadly obtuse, except the three or so innermost tepals, which have acute tips. Stigma lobes five or six, chartreuse; pistillate flowers with relatively thick lobes, the staminate flowers with slender stigma lobes. Anthers of pistillate plants small and

Figure 15. *Ficus palmeri*, eastern base of Sierra Kunkaak, Isla Tiburón, May 2006.



indehiscent, those of the staminate plants larger, dehiscent and gold-yellow. Fruits clavate, red-orange to orange.

Endemic to **San Pedro Nolasco**, where it is abundant on steep, rocky slopes growing with *Agave chryso glossa*, *Echinocereus websterianus*, and *Opuntia* sp. The axillary bristles, dioecious plants, and flower color and structure point to a plausible relationship with *M. dioica* K. BRANDEGEE.

**Nolasco:** 27°50' N, 11°24' W, ca. 50 m, *Lindsay 24 Feb 1947* (Holotype, DS). *Johnston 3112* (CAS, image).

***Mammillaria tayloriorum* C. GLASS & R. FOSTER**

*Cact Succ J* (US) 47: 175, 1975

Plants single-stemmed or cespitose with several heads, branching from base, stems nearly globose to ca 15+ cm tall; with milky sap. Flowers small, inner tepals bright red-purple. Observed in early flower in mid-February when no other cactus on the island was seen in flower. Fruits elongated and red.

Endemic to **San Pedro Nolasco**; scattered along the E-facing side of the island near the ridgecrest (see Johnston 1924: 1115). Glass (1998) indicates that this species is allied to *M. standleyi* (BRITTON & ROSE) ORCUTT of E-central and SE Sonora and adjacent Chihuahua. We suggest that the Nolasco species might be more closely related to *M. bocensis* R. T. CRAIG of SW Sonora and NW Sinaloa.

**Nolasco:** *Glass & Foster 2686* (Holotype, POM). *Johnston 3121* (not seen, cited by Johnston 1924: 1115).

***Mammillaria* sp**

This cactus may be an undescribed species or a subspecies of *M. grahamii*. Stems often branched at base (clustered), spines not hooked, reddish purple; sap watery. Flowers cream-colored; bisexual. Fruits at first orange, becoming red at maturity. **Dátil:** Widespread and abundant. **Cholludo:** Abundant on the vegetated slope. **Geographic Range:** This mammillaria appears to be endemic to these two small islands.

**Dátil:** NE side, *Felger 13430* (ARIZ, SD). E side, half way up N-facing slope of peak, *Wilder 07–121* (USON). **Cholludo:** *Felger 1966: 418*.

***Opuntia engelmannii* SALM-DYCK EX ENGELMANN var *engelmannii***

Heel hayéen ipáii; nopah; desert prickly pear

Plant usually spreading or sprawling. Cladodes (pads) obovate to elliptic, mostly 20+ cm long. Flowers large, uniformly bright yellow, changing to yellow-orange (apricot color) as the flowers age; flowering in spring. Fruits purple-red including the pulp, ripening July and August, the pulp juicy and sweet. (Description mostly based on mainland populations.) **Alcatraz:** “East-facing slope of the mountain near peak elevation” (*Felger 1966: 138*) and the S-central side of flat. **Geographic Range:** N Mexico and SW United States. Parfitt and Pinkava (1988) recognize six varieties, with var *engelmannii* being the most widespread.

**Alcatraz:** S-central part of flat, two plants present, *Wilder 07–429*.

***Opuntia* sp**

Low, spreading to shrub-sized prickly pear, 1–1.5 (–2) m tall. Pads bright green, relatively flat and very succulent, glabrous and often shiny, and sometimes purplish at the areoles and margins of the pads. Many or most areoles on each pad spineless, or some areoles with one to few, usually deflexed spines. Flowers monochromatic, bright yellow and relatively large, mostly borne near the cladode tips. Fruits red-purple, with glochids only but some rather long, the epidermis glabrous. Flowering in spring.

**San Pedro Nolasco:** Common, especially on the E side of the island, where it is abundant and best developed on relatively deep-soil of E-facing slopes. This is the most favorable habitat on the island, where species richness is highest (*Felger and Lowe 1976*). The prickly pear population on this island seems to be dynamic. George Lindsay recorded the following information on the label of a herbarium specimen (#2225) “a platyopuntia which in 1947 covered large areas of the island in impenetrable thickets, but at the present time [1952] is rare... the large areas of dead opuntias are now covered with *Vaseyanthus insularis*, a few of the opuntias are left, one of which was in flower.” Richard Felger found it abundant and healthy during

the several times he visited the island, beginning in the 1960s.

**Geographic distribution:** Islands and island-like habitats at Guaymas and Bahía San Carlos including Isla Santa Catarina bordering the entrance to Bahía San Carlos, islands in Guaymas Harbor, and the N edge of the coastal plain near the vicinity of Las Guasimas. This prickly pear seems to be an undescribed species (Donald Pinkava, pers. comm.). On Nolasco it has been called *O. bravoana* E. M. BAXTER, a prickly pear from Baja California Sur, but apparently is not that species. *Opuntia bravoana*, as to the type, is a rather spiny plant, pubescent or glabrous, bearing fruits along the top and edges of the cladodes.

**Nolasco:** *Lindsay 2225* (DS). E side, common in granitic steep ravines, commonly observed *Ctenosaurus* lizard feeding on flowers, *Stinson & Robinson 29 Apr 1974* (SD).

***Pachycereus pringlei* (S. WATSON) BRITTON & ROSE**

**Xaasj, xcocni; cardón, sabueso**

Massive columnar cacti. The fruits and seeds were major food resources of the Comcáac. Common on all islands in the study area. **Tiburón:** Widespread throughout the island, especially at lower elevations. Dense stands occur on the bajada of the Valle de Águilar at the NE side of the island. **San Esteban:** Widespread on the island and especially well developed along Arroyo Limantour, the island's major drainage. **San Pedro Nolasco:** Abundant on all slope exposures except north-facing ones. Young plants occasionally become established on north-facing slopes, but topple over before reaching a meter or so in height. The loose soil on these slopes affords poor footing. A common demise of large cardons on favorable exposures (firmer rock) also appears to be loss of footing due to soil erosion and occasional severe storms. **San Pedro Mártir:** This cactus is the dominant landscape feature across the island. The largest ones are at higher elevations, where the majority of the island surface is a veritable cardón forest (Fig 4). In 2008 we found juvenile to adult plants abundant throughout the island. Seedlings and small plants were found in the open, growing among rocks that make up the island surface; nurse plants were not present. Upon reaching maturity, with many massive branches, the plants seem prone to toppling over, probably because of the loose rock and the effects of strong winds when the plants are well hydrated. Uprooted behemoths are seen across the island. Cardons on this and a few other Gulf islands near the Baja California peninsula are notable for having unusually short trunks or being trunkless, reaching a maximum height of about 5 m, and have been called "dwarfs" (Cody and others 1983; Johnston 1924; Moran 1968; Wilder and Felger, unpublished field notes). **Alcatraz:** Felger (1966: 139) reports that "Of the two species of arborescent columnar cacti on the island, *Carnegiea* is poorly established while *Pachycereus* is... the more common and widespread species." *Pachycereus* is common on the rocky ridges spreading NE from the mountain. **Dátil:** Densest on the NW part of island, but ranges throughout. **Cholludo:** It forms a nearly impenetrable forest on the NE-facing slope of the isle (Fig 6; Felger 1966: 306–308). **Patos:** "The 1946 photographs show a very thinly distributed stand across the flats where it is today absent except for one medium-sized plant. Two colonies are also visible in the older photographs, one at about half way up the south side of the hillslope and another at the rocky ledges near the southeast shore. The hillside colony consisted of larger individuals and seems to have been slightly bigger than the one near the shore" (Felger 1966: 360). In 1966 as well as in 2007, *Pachycereus* occurs in the same places, but the individual plants are markedly smaller than those shown in the 1946 photographs. The population is recovering, but the plants have not yet reached maximum size. In September 2007 we found several scattered stands of reproductive plants and a number of juveniles, primarily along the S shore and on the cone-shaped hill or mountain. The largest population was on the W side of the mountain, about 16–18 m below the



Figure 16. *Abronia maritima*, eastern flat, Isla Alcatraz, September 2007. All photos by Benjamin Wilder except where indicated.

summit. We counted 14 adult plants and 65 juveniles mostly less than 1 m tall, and few to 1.2 m. **Geographic Range:** Baja California peninsula, W Sonora, and most Gulf islands.

**Tiburón:** Arroyo Sauzal, *Felger 10119*. W of Tecomate, rocky hill, *Felger 6244*. **San Esteban:** SE corner of island, *Bostic 21 Jun 1965* (SD). **Nolasco:** Felger 1966: 98–103. **Mártir:** Summit, 1887, *Palmer 418* (GH, image). Forming a forest over upper part of island, branching from base, 18 Apr 1921, *Johnston 3160* (CAS, image). Very common, 25 Jan 1963, *Felger 6347*. 15 Apr 1966, *Moran 13038* (SD, UC). Small canyon at base of SE-facing slope that leads to island summit, *Felger 07–19* (USON). **Alcatraz:** N-facing slope, abundant, *Felger 13410*. **Dátil:** Occasional, *Moran 13036* (SD). NW part of island, *Felger 2553*. **Patos:** 1946, *Osario Tafal* (photos; Felger 1966: 352, 353). *Felger*, Aug 1964 (photo; Felger 1966: 356). N side of hill near summit, *Felger 07–57* (USON). **Cholludo:** Figure 5.

***Peniocereus striatus* (BRANDEGEE) BUXBAUM**

***Neoevansia striata* (BRANDEGEE) SÁNCHEZ-MEJORADA**

***N. diguetii* (F. A. C. WEBER) W. T. MARSHALL**

**Xtoox; sarramatraca, sacamatraca; night-blooming cereus**

Root system with about a dozen or more tuberous roots (Fig 13). The pencil-thin, grayish stems often scramble through spiny shrubs such as *Colubrina viridis* and *Lycium* spp. The slender stems seem out of place due to their comparatively high surface to volume ratio, but unusual adaptations help explain its presence in an arid environment. The stomata are in the furrows, or grooves, between the stem ribs, and as the stem shrinks during drought the ribs close off the furrows. In addition, SEM studies show that during drought the stomata are sealed by a covering of an amorphous-looking substance, perhaps a polysaccharide, which is water soluble (Felger and Henrickson 1997). **Tiburón:** Often common in scattered localities, including bajadas, valley plains, and rocky slopes. **Dátil:** Found growing in thorny shrubs just behind the beach at the NE side of the island. **Geographic Range:** SW Arizona to NW Sinaloa, both Baja California states, and Gulf islands.

**Tiburón:** El Sauz, *Harbison 20 Mar 1962* (SD). Mountains bordering SW part of Central Valley, 1200–1400 ft, *Felger 12434*. Hast Coopol, large volcanic hill S of Pazj Hax waterhole, *Wilder 07–382* (photo). Punta Perla, *Felger 74–14*. Valle de Águila, *Wilder 07–269* (USON). Tecomate, *Felger 8877*. **Dátil:** NE side, *Felger 9129*.

***Stenocereus gummosus* (ENGELMANN) GIBSON & HORAK**

**Ziix is ccapxl; pitaya agria**

Large sprawling, multi-stemmed cactus. Fruits succulent, delicious, and large (Fig 14). **Tiburón:** Common and widespread on bajadas, valley plains, and low hills. **San Esteban:** Abundant, especially along the arroyos and adjacent lower hillsides, extending to peak elevation. **Dátil:** A single plant was seen on a steep slope at the NE side of the island. Also on **Cholludo**. **Patos:** A single mature plant occurred on the island in 1946; it was no longer there in 1966. In 2007, we found one struggling juvenile at the S shore of the island. **Geographic Range:** Both states of Baja California, many Gulf islands, and the mainland coast of Sonora adjacent to Isla Tiburón. This distribution has led to the hypothesis that this species migrated via the Midriff islands from Baja California to the Sonoran mainland (Cody and others 1983), which is in part supported by molecular evidence (Clark-Tapia and Molina-Freaner 2003). Yet, the role of people in dispersing organisms, especially those with such delicious fruit as *pitaya agria*, should not be ignored (Felger and Moser 1985; Nabhan 2000; Yetman and Búrquez 1996).

**Tiburón:** Arroyo Sauzal, *Felger 2752*. Palo Fierro, *Felger 10343*. Near marine base [Punta Tormenta], *Knight 905* (UNM). Tecomate, *Whiting 9042*. **San Esteban:** *Felger 9187*. **Dátil:** Felger 1966: 418. **Patos:** Near S edge of island, 1946, *Osario Tafal* (photo; Felger 1966: 354, 359). S shore, 30 Sep 2007, *Wilder* (photo). **Cholludo:** Documented by Felger 1966: 418.

***Stenocereus thurberi* (ENGELMANN) BUXBAUM**

**Ool; pitaya dulce; organ pipe cactus**

Multi-stemmed columnar cactus. The fruit pulp is sweet, juicy, and delicious and has been a major food resource of the Comcáac; the small seeds are consumed along with the fruit pulp. This is the preferred fruit of the Comcáac (Cathy Moser Marlett and Stephen Mar-

lett, personal communication 2007), although the fruits of *pitaya agria* are also highly esteemed. On all Sonoran islands except Mártir and Patos. **Tiburón:** Widespread, from near the shore to the peaks. **San Esteban:** Scattered and not common except one canyon in the NW part of the island (Bowen 2003). **San Pedro Nolasco:** Widespread and one of the most conspicuous landscape elements on the island; generally not on N-facing slopes. **Alcatraz:** Rare at the E base of mountain. **Dátil:** More common on the relative arid W side of the island than on the E side. **Cholludo:** A major component of the cactus forest dominating the island (Felger and Lowe 1976). **Geographic Range:** SW Arizona to Sinaloa and SW Chihuahua, many Gulf islands, Baja California Sur, and S Baja California Norte.

**Tiburón:** S end, *Rempel 297*. Sauzal, *Felger 10097*. Tecomate, *Whiting 9038*. **San Esteban:** Center of island, *Felger 471*. S-central peak, *Felger 17549B*. SW part of island, rare, *Wilder 07-89b* (photo). **Nolasco:** Felger 1966: 99–103. **Alcatraz:** E-central base of mountain, rare, 16 Sep 2007, *Wilder 07-424* (photo). **Dátil:** Canyon at NW side, Felger 1966: 299. **Cholludo:** Figure 5.

### EUPHORBIACEAE (Spurge Family)

#### *Cnidoscolus palmeri* (S. WATSON) ROSE

Coáap; mala mujer, ortiguilla

Shrub to ca. 1.5 m tall with a moderately thick semisucculent caudex, the herbage beset with stout, stinging hairs or spines. Root systems with up to several dozen succulent, potato-like tuberous roots, each ca. 5–20 cm long, often compressed as they grow wedged between rocks. The tuberous roots, edible raw or cooked, were an important staple for the Comcáac (Felger and Moser 1985). *Cnidoscolus palmeri* seems to have its closest relative in *C. shrevei* I. M. JOHNSTON from Durango (Steinmann and Felger 1997). These are the smallest-leaved members of the genus. **Tiburón:** Known from the Sierra Kunkaak and mountains at the NE side of the island. **Dátil:** Fairly widespread but localized, and not in the most arid sites. **Geographic Range:** Coastal Sonora, in the Sierra Seri and the Sierra El Aguaje and mountains around Guaymas, and Baja California Sur.

**Tiburón:** Cerro San Miguel, cerca de la cima hasta [near the peak ca.] 400 m, *Quijada-Mascareñas 90T009*. Top of Sierra Caracol, *Knight 1058* (UNM). NE side of island, coastal mountains, higher elevations, *Felger 07-78*. **Dátil:** NE side, *Felger 13457*. E side, N-facing peak, *Wilder 07-110*. SE side, *Felger 17503*.

#### *Euphorbia lomelii* V. W. STEINMANN

*Pedilanthus macrocarpus* BENTHAM

Candelillo; slipper plant

Stems semisucculent, several to many, thick, mostly straight, unbranched to few-branched, with a white-waxy coating and copious white latex. Leaves to ca. 1 cm long and quickly deciduous. Cyathia 2–2.5 cm long, bilateral, the cyathia and flowers bright red-orange, visited by hummingbirds. The gland chamber of the involucre overflows with nectar, which often drips down the flowers. **San Pedro Nolasco:** Common on steep, rocky slopes on the E side of the island. This is only place we have found it on rocky substrate. **Geographic range:** Fine-textured soils of the coastal plains of Sonora from near Tastiota to NW Sinaloa, Baja California and Baja California Sur.

**Nolasco:** NE side of island, S-facing slope, *Felger 06-83*.

#### *Euphorbia misera* BENTHAM

Hamácj; jumetón; cliff spurge

Shrubs with copious milky sap, often 0.7–1.4 m tall, the stems semisucculent and flexible, appearing gnarled due to the knobby short shoots; multiple stemmed from the base, resembling *Jatropha cuneata* in architecture. **Tiburón:** Documented from rocky habitats along the W and N sides of the island. **San Esteban:** N-facing slopes at higher elevations. **Dátil:** Rocky slopes along the E side of the island. **Geographic Range:** S California to mid-Baja California, and the Sonora coast S to Cerro Tepopa.

**Tiburón:** Ensenada Blanca, *Felger 17272*. Pooj Iime, NW part of island, *Wilder 07-441*. NE side of island, *Felger 07-61*. **San Esteban:** N slope of high peak near SE corner of island,

400 m, *Moran 8852* (SD). N slope of NE peak, steep arroyo, 450 m, *Moran 13049* (SD). **Dátil:** NE side of island, steep rocky slopes, *Felger 9105, 13455*.

#### *Euphorbia xanti* ENGELMANN EX BOISSIER

Hehe ix cooxp; jumetón

Shrubs 0.5–2.5 m tall; stems semisucculent. **Tiburón:** Common on the bajada of the NE side of the island and rare in the Sierra Kunkaak (Wilder and others 2007). **Geographic Range:** Baja California Sur and adjacent Islas Tortuga and Monserrate, and coastal Sonora from near Desemboque San Ignacio to Bahía Kino and farther S near Guaymas.

**Tiburón:** Sierra Kunkaak, *Wilder 06-453*. Near Valle de Águila, *Wilder 07-232*.

#### *Jatropha cinerea* (ORTEGA) MÜLLER ARGOVENSIS

Hamísj, oot iquéjoc; sangregrado; ashy jatropha

Multiply-stemmed shrub to ca. 2.5 m tall, the stems semisucculent. Leaves quickly drought deciduous. **Tiburón:** Common and widespread in lowland habitats, especially on bajadas and valley plains. **Geographic distribution:** SW Arizona to Sinaloa, both states of Baja California, and many Gulf islands.

**Tiburón:** Palo Fierro, *Felger 10138*. Tecomate, *Felger 10195*.

#### *Jatropha cuneata* WIGGINS & ROLLINS

Haat; torote, matacora, sangregrado; limberbush

Xerophytic succulent; multiply-stemmed shrub, with succulent stems and thick and somewhat tuberous roots. Leaves quickly drought deciduous. **Tiburón, San Esteban, San Pedro Nolasco,** and **Dátil:** Widespread and common, especially on hot, dry sites including rocky slopes and S- and W-facing exposures, arid bajadas, desert flats, and washes. One of the most abundant shrubs in the region. **Geographic distribution:** NW Sinaloa to SW Arizona, most of the Baja California peninsula, and Gulf islands.

**Tiburón:** Ensenada Blanca, *Felger 10249*. Ensenada de la Cruz, *Felger 2590*. Palo Fierro, *Felger 8927*. **San Esteban:** SW corner, *Felger 16616*. Limantour, *Felger 16611*. **Nolasco:** NE side of island, S-facing slope, *Felger 06-83*. **Dátil:** NE end of island, *Felger 9123*.

### FOUQUIERIACEAE (Ocotillo Family)

#### *Fouquieria diguetii* (VAN TIEGHEM) I. M. JOHNSTON

Palo adán

Shrubs or small trees with semisucculent trunks and limbs. Leaves drought deciduous, appearing with each substantial rain. Flowers red. Somewhat resembling the common desert ocotillo (*F. splendens*) but more shrub- or tree-like and the flowers darker red. **San Pedro Nolasco:** Common throughout including the W side of the island. **San Esteban:** A photo shows two *Fouquieria* shrubs, the only ones known from the island. The stems are rather crooked like those of *F. diguetii* but the branching pattern looks more like *F. splendens*—it could be either species. **Geographic range:** Coastal Sonora from the vicinity of Tastiota southward to Puerto Yavaros and widespread on the Baja California peninsula.

We do not classify *F. splendens* ENGELMANN as a succulent due to its comparatively thinner and non-fleshy stems. It occurs on Tiburón and Dátil.

**Nolasco:** NE side of island, 150 m, S-facing slope, *Felger 06-90*. **San Esteban:** SE peak, highest point on the island, Apr 1980, *Thomas Bowen* (photo).

### LOASACEAE

#### *Eucnide rupestris* (BAILLON) H. J. THOMPSON & W. R. ERNST

Zaaj iti cocáai; Velcro plant

Non-seasonal annual, roots unusually small for the size of the plants; stems and petioles semisucculent. **Tiburón, San Esteban, San Pedro Nolasco, Dátil:** Usually growing from crevices in rocks, cliffs, and arroyo or canyon walls and mountains from the shore to higher elevations, rarely in sandy washes. **Geographic Range:** Gulf side of Baja California Sur to SE California, Gulf islands, and NW Sinaloa to SW Arizona.

**Tiburón:** Ensenada Blanca, *Felger 12241*. Arroyo Sauzal, *Felger 9993*. S-facing slope of

Sierra Kunkaak, 1115 ft, *Wilder 06–34*. Agua Dulce Bay, *Moran 12996* (SD). **San Esteban:** Arroyo Limantour, *Wilder 07–83*. N side of island, *Felger 15446*. SE corner, N slope of high peak, *Moran 8858* (SD). **Nolasco:** NE side of island, ca. 30 m below crest of island, *Felger 06–105*. **Dátil:** Ridgecrest on peak, *Wilder 07–112*. NE side, *Felger 9107*. NW side, *Felger 15354*. SE side, *Felger 17519*.

### MORACEAE (Mulberry Family)

#### *Ficus palmeri* S. WATSON

*F. petiolaris* KUNTH ssp. *palmeri* (S. WATSON) FELGER & LOWE  
Xpaasni; tescalama; cliff fig

Shrubs to small trees and occasionally large trees (Fig 15); young plants forming a thick semisucculent caudex. Root and stem bark whitish. Leaves gradually drought deciduous, 6–28 cm long, the blades often relatively firm, broadly ovate or less often oval, the base moderately cordate or not. This is the largest tree on the Gulf islands, and the leaves are notably large in comparison to most other Sonoran Desert trees and shrubs. This unique tree grows on sea cliffs, often high above the sea or sometimes in the reach of sea spray, sheer canyon walls, and mountain rock. The roots grasp the rock and cascade over the surface, and if they reach the canyon floor or moist soil the plant may develop into a tree, otherwise it remains dwarfed as a shrub. The fact that it can become established on exposed rock faces in the desert indicates adaptations that set it apart from typical woody trees. The figs are eaten by the Comcaac, fresh or usually cooked (Felger and Moser 1985: 348).

In extended drought the young as well as adult plants can become leafless, an adaptation that presumably allows them to thrive in their arid habitats. Young plants of the closely related sister species, *F. petiolaris*, likewise form a semisucculent caudex and grow on rock/cliff niches (for instance, Felger 1999; Felger and others 2001). The boundary between the two species can be fuzzy (Felger 1999), which led Felger and Lowe (1970) to regard them as subspecies.

**Tiburón:** This is the only island where *F. palmeri* occurs in arroyo bottoms, and in such habitats in the interior of the island it occasionally reaches 10 m, and one was estimated to be at least 18 m tall. It is most common in the canyons of Sierra Kunkaak and extends to peak elevation. It also grows on sea cliffs. **San Esteban:** Widely scattered and generally restricted to steep cliffs where it usually remains a facultatively dwarfed shrub and only rarely becomes a small tree. **San Pedro Nolasco:** Shrubs and small trees, mostly near the ridge crest of the island. **San Pedro Mártir:** Probably several hundred or more *Ficus* plants are thinly scattered along ridges and sea cliffs, mostly at higher elevations at the periphery of the island. **Alcatraz:** Rare on sea cliffs. **Dátil:** Scattered shrubs or small trees on cliff faces in the interior and coast. **Cholludo:** Several large shrubs on sea cliffs. **Geographic Range:** Endemic to the Sonoran Desert in W Sonora, Gulf islands, and the Baja California peninsula.

**Tiburón:** Ensenada de la Cruz, *Felger 9203*. Foothills of Sierra Kunkaak, SW side of mountain, *Felger 6951*. Hast Coopool, large volcanic hill S of Pazj Hax waterhole, *Wilder 07–375*. Sierra Kunkaak, *Wilder 05–23*. **San Esteban:** Cascajal, sea cliffs, *Felger 9192*. NE shore, *Felger 479*. SW part of island, *Wilder 07–89*. **Nolasco:** NE side of island, ca. 30 m below crest of island, *Felger 06–101*. **Mártir:** Island of San Martin [sic], 1887, *Palmer 413* (type collection, US 796147, image). 18 Apr 1921: In a rock hewn draw in midpart of island, *Johnston 3153* (CAS, image); Tree on high sea cliffs, *Johnston 3162* (CAS, UC, images). Shrub or small tree, 3–4 m high, *Felger 6354*. 125 m elev, 17 Mar 1971, *Hastings 71–63*. *Valiente-Banuet 604*. Small canyon at base of SE-facing slope that leads to island summit, *Felger 07–17*. **Alcatraz:** Single shrub, N side of highest peak at N side of island, 28 Jan 2008, *Felger & Wilder*, observation. **Dátil:** NE side, *Felger 13458*. SE side, sea cliff, *Felger 2560*. **Cholludo:** NW side, not common, cliff, *Felger 13413*.

### NYCTAGINACEAE (Four O'clock Family)

#### *Abronia maritima* NUTTALL EX S. WATSON var. *maritima*

Spitj cmajúic; alfombrilla playera; coastal sand verbena

Xerophytic succulent; mat-forming perennial with succulent stems and leaves (Fig 16). **Tiburón** and **Alcatraz:** Upper beaches and beach dunes. **Geographic Range:** This species oc-

curs on sandy seashores of S California to Nayarit, Islas Tres Marias, and the Gulf of California. Another subspecies occurs in the Cape Region of Baja California Sur.

**Tiburón:** N of Willard Point, *Moran 8748* (SD). Vicinity of Valle de Águila, beach, *Wilder 07–272*. Bahía Agua Dulce, high beach dunes, *Felger 1966: 253*. **Alcatraz:** E side, sandy beach, *Felger 14909*. Above beach dune, *Lowe 10 Nov 1969*. E part of flat, just inland, *Wilder 07–392*.

### PORTULACACEAE (Portulaca Family)

We classify these four species as semisucculents.

#### *Portulaca halimoides* L.

*P. parvula* A. GRAY  
Dwarf purslane

Diminutive summer annual (potentially fairly robust when well watered) with succulent leaves and slender stems. **Tiburón:** Known from the N and E margins of the island and likely to be more widespread. **Geographic Range:** Arid and tropical regions of the Americas; Sonoran Desert in Arizona and Sonora S to the vicinity of Hermosillo and the Baja California peninsula.

**Tiburón:** Zozni Cmiipla, *Wilder 06–350*. Bahía Agua Dulce, *Felger 10223*.

#### *Portulaca oleracea* L.

Verdolaga; Purslane

Summer annual, succulent throughout. **Tiburón:** Documented at widely separated localities, indicating widespread distribution on the island. **Geographic Range:** Worldwide in tropical to warm-temperate climates, including Baja California Norte y Sur and Sonora. It is often difficult to determine which populations might be native and which are non-native.

**Tiburón:** Ensenada de la Cruz, *Felger 12778*. Haap Hill, *Felger T74–24*.

#### *Portulaca umbraticola* KUNTH ssp. *lanceolata* (ENGELMANN) J. F. MATTHEWS & KETRON

Summer annual, distinguished from *P. oleracea* by a conspicuous collar like wing 1–2 mm wide surrounding the capsule rim, capsules opening above the middle to shed a flattish and shallow saucer-like lid; dull gray seeds with prominent peg like projections. **Tiburón:** Known from three widely separated localities, indicating widespread distribution on the island. **Geographic Range:** Widespread in the Americas with three subspecies.

**Tiburón:** Haap Hill, *Felger 76-T35*. Palo Fierro, *Felger 8940*. Bahía Agua Dulce, *Felger 10222*.

#### *Talinum paniculatum* (JACQUIN) GAERTNER

Rama de sapo; pink baby breath

Perennial herb from thick, fleshy, tuberous roots, flowering in the first season; appearing during the summer rainy season, virtually no trace of the plant is evident at other seasons. Stems and leaves succulent, the leaves 2.5–11+ cm long, falling quickly as the soil dries. Inflorescences of loose, open panicles 30–100 cm long. Flowers small, pink to dark red-purple, open for about three hours in the late afternoon. **Tiburón:** At the E shore near Estero San Miguel, at the bases of larger shrubs, and also documented from Sierra Kunkaak. **Geographic Range:** Arizona to Florida and through Mexico to South America and the west Indies.

**Tiburón:** Sierra Kunkaak, *Knight 910* (UNM). Zozni Cmiipla, 100–300 m inland, *Wilder 06–285*.

### RUSCACEAE

#### *Dasyliirion gentryi* BOGLER

Sotol

Large rosette-forming plant with short, semisucculent trunk. Leaves to ca. 1 m long, 12–17 mm wide not including the spines, green, relatively thin and flexible, rather flat but slightly channeled, the margins with many sharp, recurved and mostly forward-projecting spines 2.3–4.5 mm long. Flower stalks to ca. 2 m tall. The plants resemble *D. wheeleri* but differ in part by having leaves greener and not waxy. **Tiburón:** Higher elevations in the Sierra Kunkaak on steep rock slopes, canyon walls, and cliff faces. **Geographic Range:** Mountains in SW Chi-



huahua and SE Sonora and isolated mountains in W Sonora including the Sierra del Viejo (S of Caborca) and the Sierra el Aguaje (N of San Carlos).

**Tiburón:** Cerro San Miguel, común en ladera de lomerios y cerro San Miguel, junto con *Agave chrysoglossa*, en un cerro pequeño, ca. 200 m [common on hillsides and foothills, growing with *Agave chrysoglossa* on a small hill near 200 m], *Quijada-Mascareñas 91T018*. Cerro Kunkaak, 1200 m, *Scott 11 Apr 1978* (UNM 53273 & 53278). S-facing slope of Sierra Kunkaak, 354 m, 2 Jan 2006, *Wilder* (photo).

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