CACTACEAE, PART 1. CACTUS FAMILY The Cereoid Cacti

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Trees, shrubs, climbers, mat-formers, some columnar or globular to caespitose or epiphytic. ROOTS usually diffuse and wide-spreading, some tuber-like. STEMS (long shoots) semi-succulent to succulent, mostly green to gray, usually glabrous, cylindric to strongly flattened, sometimes prominently ribbed and usually constricted at bases of branches or (in Opuntia) elongating by annually produced segments. AREOLES (short shoots) cushion-like, in axils of long shoot leaves, circular to elongate, sometimes partially to wholly divided into two parts, usually bearing trichomes, leaves (spines and rarely also fleshy, laminate to subterete leaves) and flowers. LEAVES (of long shoot) alternate, simple, petiolate to sessile, estipulate, fleshy, laminate to minute conic projections or obsolete, borne on obscure to prominent tubercles (enlargements of leaf bases and adjacent stem tissues), these sometimes coalescing into vertical ribs. SPINES lignified, persistent (or falling with areoles), commonly the central-most (central spines) surrounded by usually finer peripheral ones (radial spines), but in subfamily Opuntioideae short, fine, deciduous, usually retrorsely barbed spines (glochids) also present. INFLORESCENCE of 1(-few) flowers per areole, secondarily clustered variously at or near apices of stems, rarely on stalks as corymbs or panicles. FLOWERS perfect or rarely imperfect, actinomorphic to zygomorphic, epigynous, rarely perigynous (in spp. of Pereskia), with a nectariferous floral tube (hypanthium fused to surrounding stem tissue) of varying lengths and usually bearing areoles; tepals few to many, at least the innermost showy, rarely differentiated into sepals and petals; stamens several to many, borne on the floral tube; ovary of few to many carpels embedded in specialized stem tissues, 1-loculed; style 1; stigma lobes varying in number. FRUIT fleshy, juicy or dry, spiny, scaly or smooth, indehiscent or splitting irregularly, or circumscissile, or opening by slit(s) or a basal pore. SEEDS several to numerous, some bony-arillate (Opuntioideae), obovoid to lenticular reniform, to winged, shiny to dull, smooth to ornate. x = 11. --Approximately 110 genera and 1500 spp., widespread throughout the Western Hemisphere with centers of diversity in Mexico, Brazil, and the Andean regions. (Greek: kaktos = a kind of prickly plant). Benson, L. 1982. The Cacti of the United States and Canada. Stanford, CA, Stanford Univ. Press; Bravo-Hollis, H., and H. Sánchez-Mejorada. 1978, 1991. Las Cactáceas de México. Ed. 2, 3 vols. Univ. Nacional Autónoma de México, México; Britton N. L., and J. N. Rose. 1919-1923. The Cactaceae. 4 vols. Carnegie Inst. Wash. Publ. 248.

- 1' Stems not constricted or constricted only at bases of unsegmented branches, leafless or bearing minute leaves (scales or protuberances); areoles *not* bearing glochids; seeds small, brown, red or black, *not* encased in bony arils.
 - 2. Stems cylindric, columnar or arching to sprawling, 15-100+ times longer than wide, branched (at least in age), vertically ribbed.
 - 3. Shrubs inconspicuous, erect but soon arching or vine-like; stems (when young) papillose-canescent, 0.6-2 cm thick; roots tuber-like; spines to 0.5 cm long

 *Peniocereus**
 - 3' Shrubs or trees massive, erect; stems glabrous, 10-75+ cm thick; roots extensive, subsurface, diffuse; spines 1-11 cm long.
 - 4. Ribs 5-7; sterile branch portions bearing spine clusters of 7-10 short subulate spines; apical fertile stem portions bearing spine clusters of numerous long, gray

		4'	fruits Ribs spine	Lophocereus 12-24; all stem portions bearing spine clusters of 11-29+ stiff, slender to stout es; flowers solitary in areole, 6-12 cm long, 4-6 cm wide; areoles on fruits or spineless. Plants to 15 m tall; stem solitary, ultimately branching ca. 2.5 m above the narrower base; flowers (8-)10-12 cm long, the inner tepals white aging black; fruits spineless, ellipsoid to ovoid, 4-8 cm long. Carnegiea Plants to 6 m tall; stem branching at broad base; flowers 6-9 cm long; the inner tepals white aging lavender to rose; fruits spiny but spines deciduous	
	۵.			when fruits fully ripen, globose, 3-5(-6) cm long	
2'				or, if appearing cylindric, then not more than 10 times longer than wide, caespitose to mound-like, vertically ribbed or, if not ribbed, commonly strongly	
		elically tuberculate.			
	6.			nd fruits bearing well developed spiny areoles, these usually deciduous when	
	•			ripens Echinocereus	
	6'	Flow	vers a	nd fruits spineless (but scales of floral tube are spine-tipped in Echinocactus).	
		7.	Sterr	ns vertically ribbed.	
			8.	Fruit copiously woolly; bracts of floral tube and fruit aristate to spine-tipped,	
			0,	nearly concealed by the wool	
			8'	Fruit glabrous; bracts of floral tube and fruit obtuse to acute, naked. 9. Fruit opening by a basal pore, yellow and leathery at maturity	
				Ferocactus	
				9' Fruit opening by various horizontal or vertical slits or, if by a basal pore, then fruit not yellow and leathery at maturity.	
				10. Lowermost central spine in areole (in ours) usually hooked at apex; uppermost central spine(s) in areole more or less flattened, almost	
				papery in some species	
				not strongly differentiated from other spines Echinomastus	
		7'	Sten	as tuberculate, or the ribs almost completely interrupted between the areoles.	
			11.	Flowers (7-10 mm long), tiny, apical; fruits brilliant red, indehiscent;	
				tubercles extremely short (protruding 1.5-2.5 mm), hidden by short pale gray spines	
			11'	Flowers small to large (15+ mm long) either apical or well below stem apex;	
				fruits various in color and dehiscence pattern, but if red and indehiscent	
				(Mammillaria spp. and Coryphantha missouriensis), then always well below	
				stem apex; tubercles large (protruding 535+ mm), hidden or exposed, the spines larger (at least in mature plants).	
				12. Fruits juicy, indehiscent; seeds brown or black, pitted or, if smooth,	
				always reddish brown; bracts of floral tubes and fruits (when present)	
				narrow, linear to ovate; flowers and fruits strictly in axils of tubercles.	
				13. Tubercles of mature plants each with a longitudinal adaxial groove connecting the axillary part of areole to the spiny distal part;	
				flowers and fruits near stem apex (except C. recurvata and fruits of C. missouriensis)	
				13' Tubercles of mature plants never grooved between axillary and distal parts of the areole; flowers and fruits well below stem apex (excepting small plants of <i>M. viridiflora</i> or <i>M. wrightii</i>)	
				(excepting sinai plants of he. withytota of he. witgian)	

- 12' Fruits dry, usually dehiscent (except *Toumeya*); seeds black, nearly smooth, papillate or tuberculate; bracts of floral tubes and fruits broad (the basal ones wider than long), usually cordate; flowers and fruits often at edges of spine clusters, not strictly axillary.

 - 14' Lowermost central spine in areole (in ours) absent or all straight to curved, never hooked at apex; uppermost central spine(s) in areole terete or flattened, papery in *Toumeya*.
 - 15. Fruits fragile but not regularly dehiscent; all spines strongly flattened, the central spines papery and flexible *Toumeya*
 - 15' Fruits dehiscent by circumscissile or vertical sutures; central spines (when present) needle- to hair-like or blunt and corky in *Pediocactus peeblesianus*.
 - 16. Flowers and fruits of adult plants remote from spines (elongate areole); fruits dehiscing basally or by a longitudinal split, never by a circumscissile cap; floral remnants strongly persistent on fruit apex; central spines needle- or awl-like; southern and extreme western Arizona Echinomastus

Carnegiea Britton & Rose Saguaro, Giant Cactus

Massive columnar trees to 15+ m tall. STEM simple or the trunk bearing 1-6(-20+) upright-curving branches usually 2-2.5 m above ground, commonly in subwhorls, sometimes rebranched, to 75+ cm in diameter (widest at lowest branches), green, glabrous but woolly at apices; ribs 12-24, 3-4 cm high, continuous, increasing in number from the narrow base. LEAVES of long shoots minute or obsolete. AREOLES mostly circular, 6-8 mm in diameter, spaced about 2.5 cm apart on rib to nearly contiguous at stem apices, bearing short tan to gray wool. SPINES yellow to reddish brown, aging gray to gray-black, terete to angular, mostly bulbous-based, divergent; central-most spines stout, 3-5(-10) per areole, mostly 1-3 cm long, but the basal one longest, 3.5-5(-8) cm long; peripheral spines finer, 12-15(-19) per areole, 1-2 cm long. FLOWERS nocturnal but remaining open into morning, solitary in areoles, arranged in masses usually on south sides and below apices of the branches, perfect, actinomorphic, funnelform, (8-)10-12 cm long, 4-6 cm wide; ovary ovoid, bearing fleshy, elliptic scales, these ca. 2 mm long, apiculate, with axillary tufts of short white wool; floral tube scaly, ca. 6 cm long; outer tepals green; inner tepals waxy-white (drying black), reflexed, broadly obovate, ca. 2.5 cm long, apiculate; stamens numerous, exserted, the filaments and anthers cream-white; style and the ca. 12 stigma lobes cream-white. FRUITS maturing pale red, glabrous, scaly, spineless, ellipsoid to obovoid, 4-8 cm long, splitting longitudinally into 2-4 irregular radiating portions; pulp bright red, juicy, sweet. SEEDS numerous, deep red-brown appearing black, finely pitted, ca. 2 mm long, 1.8 mm wide. -- Monotypic genus, endemic to Sonoran Desert. (for Andrew Carnegie).

Carnegiea gigantea (Engelmann) Britton & Rose (gigantic). [Cereus giganteus Engelmann]. 2n = 22. --Upper Sonoran Desert zone, especially on hills and buttes: Cochise, Gila, Graham, La Paz, Maricopa, Mohave, Pima, Pinal, Santa Cruz, Yavapai, Yuma cos; below 1600 m (5200 ft); May-Jun, occasionally in

Sep; CA near Colorado River across from Yuma and Parker, AZ; Son., Mex. Arizona state flower and symbolic of the Sonoran Desert; spiritual tree of the Tohono O'odham Indians, its phenology used as basis of their calendar; multipurpose plant for food, flour, wine, oilseed; staves used for walking or probing, fences. Crosswhite, F. S. 1980. Desert Plants 2:2-61. Steenbergh, W. F., and C. H. Lowe. 1977. Ecology of the Saguaro II. Nat'l. Park Service Scientific Monographic Series No. 8.

Lophocereus Britton & Rose Senita

Columnar shrubs, erect, to 6.5 m tall. STEM much branched from base and sparingly above, 6-20 cm in diameter, glabrous; ribs 5-15, prominent. LEAVES of long shoots minute protrusions. AREOLES circular to elliptic, to ca. 2 cm apart on rib of lower stem to nearly contiguous on rib of upper stem. SPINES of areoles on sterile stem portions angular-subulate, 8-15 (or nearly absent in monstrose forms) per areole, to 22 mm long, those of areoles on apical flower-bearing stem portions weak, flattened, twisted, ca. 15-50, to 7.5(-11) cm long, obscuring the stem. FLOWERS nocturnal but sometimes remaining open next morning, 1-several per areole, mostly lateral, perfect, actinomorphic, malodorous, short-funnelform, 2.5-4 cm long, 2-3 cm wide; ovary ovoid, bearing a few small deltoid scales with naked or nearly naked axils; floral tube scaly; inner tepals whitish to deep pink or coral pink, sometimes reflexed, oblanceolate to oblong, obtuse to acuminate; stamens many, exserted, slender; style pinkish to white; stigma lobes 5-6, white. FRUITS greenish to red, glabrous, scaly, spineless, obovoid to globose, 2-4 cm long, splitting irregularly; pulp usually red, fleshy. SEEDS numerous, black, shiny, obovate, 2.2-3 mm long. --2 spp.; U.S.; Baja C., Sin., Son. in Mex. (Greek: lopho = tuft, referring to bristle-bearing reproductive shoots + cereus = an old generic name for columnar cacti). Felger, R. S., and C. H. Lowe. 1967. Ecology: 48:530-536. Lindsay, G. 1963. Cact. Succ. J. (Los Angeles) 35:176-192.

Lophocereus schottii (Engelmann) Britton & Rose (for A. Schott). Senita. --Shrubs to 6.5 m tall. STEM branches erect, green, aging grayish with faint, waxy chevrons, 10-20 cm in diameter; ribs (in ours) 5-6(-7), to 3.5 cm high, longitudinally continuous. AREOLES circular to broadly elliptic, to 13 mm long, yellow- to tan-woolly, to ca. 2 cm apart on rib to nearly contiguous on rib apices. SPINES of lower areoles reddish, turning brown or gray to blackish, angular-subulate, to 22 mm long, bulbous-based; spines of middle areoles transitional, or those of upper areoles usually to tan or reddish aging gray, ca. 25-50+ per areole, up to 7.5

(-11) cm long, weak, flattened, twisted. FLOWERS 2.5-4 cm long, 2-4 cm in diameter; floral tube scaly, to 2.5 cm long; outer tepals dark with pale margins; inner tepals whitish to deep pink, oblanceolate, obtuse, to 1.5 cm long; stamen filaments white, the anthers yellow; style and stigma lobes white. FRUITS few-scaled, spineless, splitting irregularly, pulp sour. SEEDS glossy, tessellate polygonal cells, 2-2.3 mm long, 1.8-2.2 mm wide. 2n = 22. --Widespread in Sonoran Desert, flats, washes and low hills on sand, lava and granitic substrates; sw Pima Co.; 350-500 m (1200-1700 ft); May-Jun; Mex., in Baja C., Baja C. Sur, Sin., Son. Arizona specimens belong to var. schottii if other varieties are recognized. Two monstrose forms (Baja C.) have ribs replaced by irregular knobs and nearly spineless lower stems; one often cultivated as Totem Pole Cactus.

Peniocereus (A. Berger) Britton & Rose

Low, erect, arching or sprawling shrubs, 1-3 m tall, arising from 1-many tuber-like roots. STEM simple to much branched, basally cylindric but distally with either obscure to prominent ribs or (in some Mexican species, dimorphic with young stems always conspicuously 3-8-winged, and with mature stems ribbed), papillose-pubescent when young, 0.5-3.5(-6.5) cm in diameter; ribs 3-9(-20), obscure to prominent. LEAVES linear-deltoid, ca. 1 mm long. AREOLES circular to elliptic, 1-8 mm in diameter, widely separated to nearly contiguous on rib. SPINES conic with swollen bases, subulate, sometimes bristle-like, 2-25 mm long. FLOWERS usually nocturnal, solitary, subterminal or lateral, perfect, actinomorphic (or floral tube curved), salverform but flaring abruptly near apex, mostly 8-25 cm long, 5-12 cm wide; ovary ovoid to ellipsoid, bearing low tubercles with woolly, spiny areoles; floral tube scaly usually bearing bristles in axils; inner tepals commonly white, sometimes lightly tinged cream, rose, red or green (bright red in one

Mexican species), lanceolate, attenuate. Stamens many, exserted; style and the 9-12 stigma lobes white to yellow-white. FRUITS scarlet to carmine or purple, papillose-canescent to glabrate, spiny, obpyriform, ovoid to ellipsoid, 3-10.5 cm long, indehiscent; pulp reddish, fleshy. SEEDS numerous, black, rugose or tessellate, sometimes pitted, 1-4 mm long (in ours). -Species ca. 20, deserts and dry tropical forests, sw U.S.; nc, w and s Mex. Delimitation of genus is debated: here to include *Peniocereus*, *Neoevansia* W. T. Marshall and *Wilcoxia* sensu Britton & Rose (excluding type species) but excludes *Acanthocereus* (Engelmann ex A. Berger) Britton & Rose and *Nyctocereus* (A. Berger) Britton & Rose. (Greek: *penios* = thread, referring to stem size + *Cereus* = an old generic name for columnar cacti). Sánchez-Mejorada, H. 1974. *Revision del Género* Peniocereus (*Las Cactaceas*). Gobierno del Estado de México, Dirección de Agricultura y Ganadería, Toluca, Méx. Sanchez-Mejorada, H. 1973. Cact. y Suc. Méx. 18: 13-27.

Peniocereus greggii (Engelmann) Britton & Rose (for Josiah Gregg). Desert Night-blooming Cereus. --Shrubs erect to sprawling, sparingly branched, inconspicuous, 0.4-1.2(-3) m tall; root solitary, large, light-brown, napiform, usually 15-30 cm long, 5--12 cm wide, but much larger ones are known. STEM gray-green to gray to purple, the distal parts 8-25 mm in diameter, bearing 4-6 prominent, angular, papillose-canescent ribs, the basal parts usually narrowed, brown and cylindric. AREOLES white-woolly, aging gray to blackish, (3.5-)4.5-12(-15) mm apart on each rib. SPINES black to yellowish-white, (9-)11-15(-17) per areole, usually in 3 vertical rows; apical ones black, subulate to 1 mm long; basal 3-5 spines yellowish white throughout to only at tips, thinner, to 3 mm long, appressed, puberulent when young. FLOWERS 15-25 cm long, 5-12 cm wide; floral tube papillose-canescent, the scales green tipped red or brown; tepals 4-7 cm long, lanceolate, attenuate to mucronate, the outer ones greenish white with brown to reddish midstripes, the inner ones white or lightly tinged cream or pink or rarely all pale rose pink; stamen filaments white, the anthers very pale cream-yellow. FRUITS bright red darkening in age, spiny, ellipsoid, snouted, 3-10.5 cm long, 2-5 cm in diameter; pulp red, fleshy, edible. SEEDS black, tessellate, wrinkled at hilum region, ca. 3-4 mm long, 2-2.5 mm wide. --2 vars., both in the flora.

Var. greggii --AREOLES elliptic, ca. 4-5 mm long, 2 mm wide, the apical spines tending to be directed forward, the basal ones, backward. FLOWERS 15-19(-21) cm long, 5-6(-9.5) cm wide. FRUITS 3-5(-8) cm long, 2-3 cm wide. 2n = 22. --Chihuahuan Desert, sandy or gravelly loams, along washes and on creosote-bush flats or gentle slopes: Cochise Co.; 1200-1500 m (3900-5000 ft); May-Jun; NM, TX; Chih., Coah., Dgo., Son., Zac., Mex.

Var. transmontanus (Engelmann) Backeberg (across the mountains). --AREOLES nearly circular, ca. 2 mm in wide; spines in a radial pattern. FLOWERS 16-22(-25) cm long, 7-8(-12) cm wide. FRUITS (6-) 7.5-10.5 cm long, 3-5 cm wide. 2n = 22. --Sonoran Desert, sandy or gravelly loams, creosote-bush bursage flats, edges of washes and on slopes of small hills: Cochise, Gila, Graham, La Paz, Maricopa, Pima, Pinal, Santa Cruz, Yavapai, Yuma cos.; 300-1100 m (1000-3500 ft); May-Jul; Son., Mex.

Peniocereus striatus (Brandegee) F. Buxbaum (grooved). Sweet Potato Cactus, Jacamatraca, Cardoncillo. --Suberect to sprawling shrubs, very inconspicuous, 25-75 cm tall, arising from a cluster of ca. 12 or more light-brown, radiating tuberous roots, these 10-15 cm long, 4-7 cm wide. STEM commonly much branched, green to brown or purple, mostly ca. 6 mm in diameter, papillose-canescent, bearing 6-9 broad, flat-topped ribs, these to 2 mm broad, narrowing beneath, 0.5 mm tall, separated by narrow grooves. AREOLES yellow-tan-woolly, aging white, 5-20 mm apart on the rib. SPINES yellowish white, some black-tipped to all black, nearly acicular, weak and easily broken off, 5-16 per areole, 1.5-4 mm long, scurfy when young, the radial spines encircling the 2-3 erect central spines, the basal 3-5 spines usually the longest, appressed, scurfy when young. FLOWERS (5-)7-8 cm long, 5-6 cm wide; floral tube canescent, the scales green-purple to reddish; tepals lanceolate to oblanceolate, attenuate to apiculate, 18-25 mm long, the outer

ones reddish to green-purple, the inner ones white or lightly tinted rose; stamens ca. 1 cm long, the filaments white, the anthers pale cream yellow. FRUITS scarlet, obpyriform to ovoid, bristly spiny, 2.5-5 cm long, 1.5-2.5 cm wide; pulp red, fleshy, bitter. SEEDS 1-2 mm long, 0.8-1.3 mm wide, black, tessellate, wrinkled near hilum region. --Sonoran Desert, sandy to rocky flats and small hills: s Pima Co.; 150-450 m (500-1500 ft); Aug; s Baja C., Baja C. Sur, Sin., Son., Mex.

Stenocereus (A. Berger) Riccobono

Columnar trees or shrubs, to 15+ m tall. STEM erect, arching or procumbent to prostrate, usually branched, the trunk, when present, to 40 cm in diameter, glabrous; ribs 4-20, rounded and vertically continuous to strongly tuberculate. LEAVES of long shoots minute or obsolete. AREOLES circular to elliptic, 0.5-4 cm apart on rib. SPINES terete to angular, divergent, to 28 per areole; central-most spines stout or absent, but sometimes flattened and deflexed, to 7.5 cm long; peripheral spines weaker, to 3.5 cm FLOWERS nocturnal or diurnal, solitary, subterminal or lateral, perfect, actinomorphic to zygomorphic, campanulate, funnelform to salverform, (4-)6-12 cm long, (3-)5-10 cm wide; ovary cylindric, ovoid to globose, bearing fleshy bracts, usually green with reddish apices, triangular, subtending axillary trichomes and up to 18 spines per areole; floral tube scaly; inner tepals white to rose, rarely yellow or red, oblong to obovate, obtuse; stamens many, included to strongly exserted, the filaments slender; style white; stigma lobes up to 15, white. FRUITS green to red, glabrous, scaly, often spiny (spine clusters deciduous from ripe fruits), glabrous, globose to ovoid, 3-8 cm long, indehiscent or splitting irregularly; pulp white, red to purplish, fleshy, mostly edible. SEEDS numerous, brownish, dull, verrucose, or less commonly, black glossy, finely pitted, 0.7-3 mm long. --18-20 spp.; sc AZ, Mex., coastal C. Amer., n S. Amer. and W. Ind. (Greek: Steno = narrow, with reference to stems + Cereus = an old generic name for columnar cacti).

Stenocereus thurberi (Engelmann) F. Buxbaum (for George Thurber). Organ Pipe Cactus, Pitaya Dulce. --Shrubs to 6 m tall. STEM much branched from the base, sometimes rebranched above, erect, green, the branches to 12-20 cm in diameter; ribs (12-)15-17(-20), 9-15 mm high. AREOLES subcircular, 4-6 mm in diameter, ca. 1-2 cm apart on rib, mostly red-brown woolly, aging gray. SPINES red-brown, coated whitish, aging gray with dark tips, terete, mostly bulbous-based, divergent; central-most spines 3-5 per areole, slender, the longest 17-32 mm long; peripheral spines 6-11, finer, 1-2 cm long. FLOWERS mostly subterminal, funnelform, 6-9 cm long, 3.5-6 cm wide; floral tube 2-4.5 cm long; outer tepals green, tinged red or rose-red to purplish, obovate; inner tepals white aging lavender or rose-pink with white margins, reflexed, oblong, to 2 cm long, 7 mm broad; stamen filaments cream-white, the anthers yellowish; style white; stigma lobes ca. 9, white. FRUITS reddish with green scales, glabrous, with deciduous spiny areoles, globose, 3-5(-6.5) cm long and wide; pulp juicy, red, sweet. SEEDS black, glossy, finely pitted, obovate, ca. 2 mm long and 1.2 mm wide. --2(-4) vars; AZ; nw Mex.

Var. thurberi. --FLOWERS white, fading lavender, 6-9 cm long, the perianth 4-6(-7) cm in diameter; floral tube 4-4.5 cm long. 2n = 22. [Cereus thurberi Engelmann, Lemaireocereus thurberi (Engelmann) Britton & Rose]. --Widespread in Sonoran Desert, adjacent thorn forests mostly on hills and bajadas: w Pima Co., but scattered individuals in Maricopa, Pinal and e Pima cos.; below 1100 m (3700 ft); Apr-Jul; Baja C., Baja C. Sur, Sin., Son., Mex. Gibson, A. C. 1990. Cact. Succ. J. (Los Angeles) 62:13-24.

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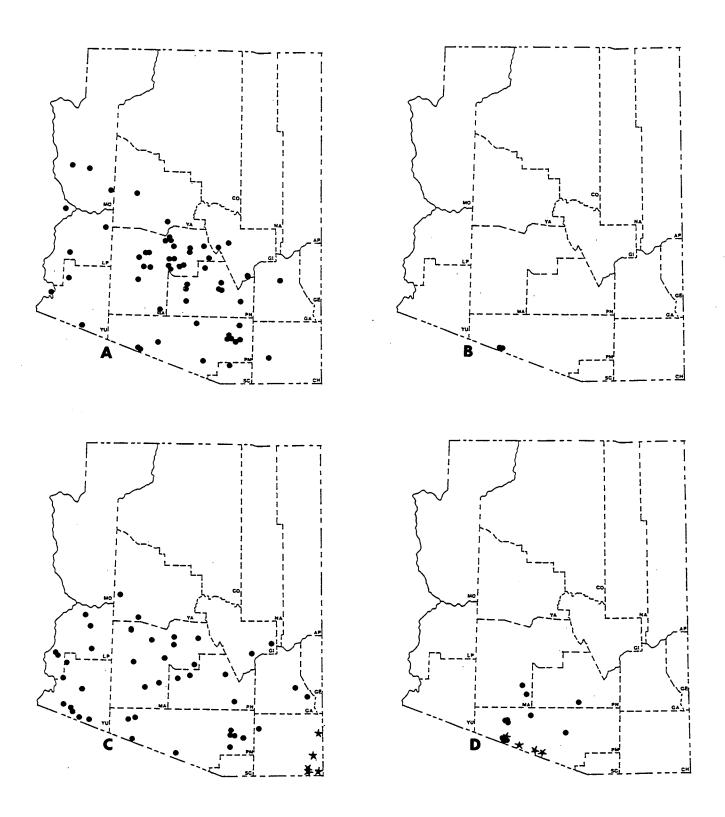


Figure 1. Distribution of: A. Carnegiea gigantea; B. Lophocereus schottii; C. Peniocereus greggii var. greggii (stars) and var. transmontanus (dots); D. Peniocereus striatus (stars) and Stenocereus thurberi (dots).