OPUNTIA CACTI OF NORTH AMERICA—AN OVERVIEW

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Abstract

The Cactaceae are a diversified group of New World plants with a wide array of evolutionary and ecological strategies that has given them the ability to adapt to many different habitats. The family is both interesting and challenging because of its varied morphology, adaptations to the environment, and reproductive systems. Of the groups within the cactus family, the opuntias are one of the most successful and widespread, but they exhibit many taxonomic difficulties and are, therefore, not well understood.

Key Words: Cactaceae, taxonomy, diversity, adaptation, reproductive strategies

Resumen

Las cactáceas son un grupo de plantas muy diversificado con una impresionante colección de estrategias evolutivas y ecológicas que les ha dado la habilidad de adaptarse a muchos hábitats diferentes en el nuevo mundo. Esta familia es interesante y desafiante debido a su variación morfológica, diversas adaptaciones al medio ambiente, y a sus sistemas de reproducción. Dentro de los grupos de la familia de las cactáceas, las opuntias son de los más exitosos y ampliamente distribuidas, pero presentan muchas dificultades taxonómicas y por lo tanto no son del todo entendidas.

The Cactaceae are an exciting and challenging group of plants because of their varied morphology and succulence, their showy flowers, their adaptations to the environment, and their reproductive strategies. The family has ca. 1600 species in ca. 115 genera (Barthlott & Hunt 1993). Cacti occur naturally from just south of the Arctic Circle in Canada to the tip of Patagonia in South America. Native cacti are restricted to the New World, except for one species, *Rhipsalis baccifera* (Miller) W. T. Stearn or mistletoe cactus of tropical Americas, which prehistorically migrated to Africa, Madagascar and Ceylon (Barthlott 1983). The sticky small fruits of *R. baccifera* were presumably carried across the Atlantic Ocean by birds.

Cacti grow at altitudes from below sea level (e.g., at Death Valley, CA) to over 4,500 m in the Andes; and in climates having no measurable rainfall to more than 500 cm of annual precipitation. Cacti vary in size from that of a large marble to as tall as 20+ m and weighing several tons.

There are three centers of cactus diversity: (1) central Mexico, from where the North American cacti have evolved, 2) the Andean region, and 3) Brazil. The dispersal of species radiating from these three centers has overlapped very little, except for human introductions. There is a subcenter extending from northern South America, northward through the Antilles and West Indies to Florida. The origin of all cacti is probably in South America, perhaps 90-100 million years ago (Gibson & Nobel 1986). However, there are no fossil records known beyond the desert packrat (*Neotoma* sp.) middens of the Pleistocene (McCarten 1981).

Taxonomy

The discovery of betalains in cacti helped taxonomists understand the phylogenetic position of the Cactaceae. Betalains are reddish pigments found in a small, related group of families in the order Caryophyllales (Carnations order). Other flowering plants have similarly colored pigments called anthocyanins, which are synthesized via a different chemical pathway. Betalains get their name from red beets (the genus *Beta* in the Chenopodiaceae), which are red in color due to the presence of the betalain, betanin. Certain betalains are responsible for the red to purple pricklypear pads, particularly when under stress as in *Opuntia macrocentra* Engelmann. The Cactaceae were once classified near the carrot family (Apiaceae), but now the family is placed in a very different order, the Caryophyllales, along with the only other betalain-producing angiosperm families, Achatocarpaceae, Aizoaceae, Amaranthaceae, Basellaceae, Chenopodiaceae, Didieriaceae, Nyctaginaceae, Phytolaccaceae, and Portulacaceae (Cronquist 1988).

Barthlott (1988) presented a phylogeny of the Cactaceae. There are three subfamilies of cacti—the phylogenetically basal Pereskioideae, the

Opuntioideae (the subfamily we are specifically interested in for this symposium), and the most derived and speciose Cactoideae, comprising some 80% of all cacti. The greatest diversity of cacti is in South America.

The Opuntioideae differ from all other cacti in having glochids (small, barbed, and deciduous spines) and seeds that are completely enwrapped by a funicular stalk, which becomes hard and bony. The largest genus in this subfamily is *Opuntia*, and in its very broad sense numbers perhaps 200 species (Barthlott & Hunt 1993).

The opuntias (representatives of the subfamily Opuntioideae) of the United States total 5 genera, 61 species, 18-20 additional varieties and many interspecific hybrids (Pinkava, ined.). The true chollas (*Cylindropuntia*, Fig. 1) have cylindric stem segments and completely deciduous spine sheaths. *Cylindropuntia* has 20 species, six additional varieties and at least nine named interspecific hybrids in the United States. The club-chollas (*Grusonia*, Fig. 2) are low mat- or clump-formers with cylindric to spheric stem segments having spines with only the tips being sheathed. In the United States, there are eight species and one interspecific hybrid of club-chollas. The prickly-pears (*Opuntia sensu stricto*, Fig. 3) have mostly flattened stem segments and are completely without spine sheaths. There are 31 species, 12-14 additional varieties and at least seven named interspecific hybrids in the United States alone.

Two other genera of the Opuntioideae, *Nopalea* and *Consolea*, are found only in Florida in the United States. *Nopalea* (Fig. 4) has a flower modified for hummingbird pollination. The flower is somewhat tubular in shape with red to orange tepals that are almost completely closed, but with protruding stamens and stigmas. The *Nopalea* flower also has a nectar chamber covered by an extension of the style near its base. Just one species (*N. cochinellifera* (L.) Salm-Dyck) is found in the United States and has naturalized from cultivation in central Florida. The genus *Consolea* (Fig. 5), has short, orange to red, slightly bilaterally symmetric flowers, with wide-opening petals and a nectar chamber similar to that of *Nopalea*. There is one species in the United States, the nearly extinct native *C. corallicola* Small from the Florida Keys, a species of special concern in this symposium.

Ecology

Opuntias, and cacti in general, are widespread and have adapted to many diverse habitats. One hypothesis is that they occupy areas where there is little competition from other plants, particularly when growing under extreme conditions. In

Fig. 1. Example of *Cylindropuntia*, *C. spinosior* (Engelmann) Knuth, the cane cholla.

Fig. 2. Example of *Grusonia*, *G. kunzei* (Rose) Pinkava, the Kunze club-cholla.

the United States, opuntias occur commonly in all four North American deserts: Chihuahuan, Sonoran and Mojave hot deserts and the Great Basin cold desert. In respect to the opuntias, prickly-pears, for example, thrive in arid, shallow and well-drained soils, but also on over-grazed sites and other disturbed areas, many attributable to human activities. In general, the greater the habitat disturbance the less the plant competition, but if too severe, of course, cacti also disappear. Cacti also do well in dry, tropical deciduous forests where there is little shade much of the year because of leaf-drop, even though the competing plants are close together. Epiphytic cacti, which are found mostly in the wet tropics, grow in open areas on branches of trees. Their roots are kept relatively dry in the open air or in a scanty substrate. All cacti require good drainage; long term accumulation of water is detrimental to them. But, cacti can do well and grow faster under hydroponics, if well aerated.

Cacti utilize high PAR (Photosynthetically Active Radiation) (for details see Gibson & Nobel 1986). They do poorly and etiolate rapidly in shade. However, shade is beneficial and often necessary during the critical stages of germination and juvenile development, such as when growing in association with nurse plants. Some cacti, e.g., the saguaro (*Carnegiea gigantea* (Engelmann) Britton & Rose) often outgrow, even outlive, these nurse plants.

Morphology

The morphology of cacti is often, at first, bizarre-looking, but close study reveals only an exaggeration of well-known features. All cacti have alternate leaves along the axis of a long-shoot/short-shoot growth pattern. As is true for virtually all plants, there is an axillary bud at the upper leaf base; however, in cacti this bud barely elongates and is called the short-shoot or areole.

In prickly-pears, the long-shoots are the pads (stem segments also called cladodes) and the fruit coverings (pericarpels). Each pad, in its first year only, produces areoles with subtending conic leaves (Fig. 6). The short-shoot areole produces leaves modified into spines of two kinds—permanent spines with their bases embedded in cork (those which can puncture your finger but remain on the plant) and small, barbed, easily dislodged glochids (those which break off easily and stay with your finger). Hormone concentrations during the very early development of the spine determine if it will be a regular spine, a glochid, or something intermediate between these structures which is rare in nature (Mauseth & Halperin 1975). Spines are produced from the short-shoot areole spirally

Fig. 3. Example of *Opuntia*, *O. basilaris* Engelmann & Bigelow, the beavertail prickly-pear.

from its margin to its apex. Spines elongate from the base and are larger in diameter at the base, but cells within the spine die from the apex to the base. The microscopic barbs of the glochid tip are created when an epidermal cell overrides the epidermal cell below it (Robinson 1974). The base of the glochid has an abscission layer (thin-walled cells) that is easily broken by contact. Short-shoots (areoles) also, on occasion, produce long-shoots including branches and flowers.

Tubercles (or podaria) are swellings below the conic leaves of the pad (long-shoot). The upper part of the conic leaf is the blade, which abscises in a week or two at a notch. The leaf base, or petiole, and adjacent stem tissues are fused together forming the tubercle. The tubercle may elongate and swell such as in species of pincushion cacti (*Mammillaria* spp.). If the raised tubercles align vertically around the stem they can coalesce with those directly above and below forming ribs, like those of the saguaro.

The flowers of cacti are quite variable, but there are some general features that are shared by the whole family. The ovary of the flower (the ovule-bearing part of the pistil) is completely embedded within the stem—a modified pad or long-shoot. Non-cactus flowers are positioned on top of the stem and vascular strands (veins) enter from the stem below. However, cactus flowers have veins from the surrounding stem that enter at the top and sides of the ovary, split and extend upward into the style and downward toward the ovules of the ovary. This unique vasculature provides evidence as to the derivation of the inferior ovary of a cactus flower from a stem that protrudes outward and engulfs the ovary. What is generally called a "fruit" is actually a fused combination of long-shoot coverings (technically called pericarpels) and the true botanical fruit, the mature ovary. So, when we eat the fleshy fruits of prickly-pears, called tunas, we are eating primarily stem tissue (after removing the glochids and spines, of course). Because the pericarpel is composed of stem tissue, it, like a first-year regular pad, produces conic leaves and areoles on its sides that, in turn, produce glochids and sometimes spines, or even flower buds.

Adaptations

Cacti have no escapability and therefore are subject completely to their environs. Two major problems exist for cacti, particularly those in arid climates: temperature extremes and lack of available water. However, several adaptations allow them to cope with these difficulties.

Freezing temperatures in the United States limit distributions by destroying the growing api-

Fig. 4. Example of *Nopalea*, *N. auberi* (Pfeiffer) Salm-Dyck, the lengua de vaca.

cal meristems (stem tips) of many cacti at the northern edges of their ranges and on northern north-facing slopes. This freezing effect may be moderated somewhat by stem tips having protection via pubescence and/or spines or by having depressed summits.

High temperature effects may be reduced by evasion from direct insolation by tilting toward the sun such that only the smaller top surface gets direct sun and not the sides, e.g., barrel cacti (*Ferocactus* species); or by an orientation of pads of prickly-pears such that minimal surface area (at edges of, not faces of pads) is exposed to direct sunlight during the hottest periods of the day. Water is conserved by a reduction of leaf surfaces from broad blades to spines and the reduction of stem surface area by having an efficient shape in relation to surface area/volume ratios, such as in barrel and globular cacti. Also, there is shading of surfaces by pubescence and/or spines and by the formation of ribs and elongate tubercles. A specialization of prickly-pears in Arizona is a metabolic shutdown (aestivation, similar to hibernation), which occurs during non-growing seasons so that only minimum metabolic maintenance takes place (Nisbet & Patten 1974).

Water absorption from rainfall is maximized in most cacti by the presence of a shallow, widespread root system, which often extends out several feet from the main plant body. Cacti also quickly produce tiny "rain roots," which efficiently absorb water after rains, but which quickly die when water is no longer available. The retention of water within the cactus is enhanced by lowering transpiration rates via: 1) having leaves reduced to spines which lowers surface area; 2) having a heavy wax coating (cuticle) on surfaces, impeding direct water loss to the atmosphere; 3) having daytime closure of stomata; and 4) being succulent wherein water adheres to complex carbohydrates called mucilage. Mucilage holds water very tightly, requiring energy to free the water. In some cacti, ribs allow the stems to expand and contract like the pleated part of an accordion both daily and seasonally, allowing for gains and losses of water. Cacti also conserve water by quickly sealing any breaks in the stem's surface caused by animals, humans, or weather. Szarek (in Gibson and Nobel 1986) experimented with a teddy-bear cholla (*Cylindropuntia bigelovii* (Engelmann) Knuth) by severing it from its base, then tying it to a ring stand in the desert. It survived three years without any contact with the soil. The scar tissue that formed where the plant was cut quickly cut off the loss of water.

Crassulacean Acid Metabolism (CAM) provides a method for photosynthesis to occur while stomata are closed during the daytime. This tim-

Fig. 5. Example of *Consolea*, *C. falcata* (Ekman & Werdermann) Knuth.

ing of stomatal opening is common in cacti and other succulents but is the reverse of most other plants. In CAM, the stomata open at night, allowing for the exchange of gases when temperatures and transpiration rates are lower. Incoming CO_2 is converted to stored malic acid in the cells during nighttime. The next day, the malic acid is converted back to CO_2, which can then be used to carry out photosynthesis and the making of carbohydrates using light energy.

As a result of these adaptations, cacti thrive in arid environments. They have adapted well to the extremes of their physical surroundings and have the morphology and physiology to survive these environmental adversities.

Reproductive Strategies of Opuntioid Cacti

The opuntioid genera have evolved rapidly and successfully by taking advantage of a combination of several reproductive strategies: 1) sexual reproduction which promotes active gene exchange and helps to maintain genetic variability, including the development of dioecy and gynodioecy that increases outcrossing and the genetic diversity of populations; 2) cloning via vegetative propagules such as detached stem segments and fruits, and via sprouting from roots or non-sexual seeds; 3) polyploidization allowing for additional DNA that can, in turn, mutate providing genetic novelties and yet maintain the status quo in unchanged genome copies; 4) interspecific hybridization allowing for the exchange of genes between once genetically separated or partially separated populations via hybrid fertility.

Flowers in the Cactaceae are usually perfect, containing both functional pistils and stamens. Such flowers can either outcross with other individuals or be self-fertile and pollinate themselves (del Carmen Mandujano et al. 1996; McFarland et al. 1989; Osborn et al. 1988; Ross 1981). However, a very limited number of cacti have been reported to be dioecious, androdioecious, gynodioecious, or trioecious (Fleming et al. 1994; Hoffman 1992; Parfitt 1985; Valiente-Banuet et al. 1997). The opuntias have evolved some exceptions to synoecy (= hermaphroditism, having perfect flowers) as well. Within the genus *Opuntia*, Parfitt (1985) documents *O. stenopetala* Engelmann as dioecious (with separate pistillate and staminate individuals). More recently, *Consolea corallicola* was discovered to be cryptically dioecious (with functionally separate pistillate and staminate plants, but appearing morphologically bisexual) (Negron-Ortiz 1998) and five taxa in the genus *Cylindropuntia* (including *C. calmalliana* (Coulter) Knuth, *C. molesta* (Brandegee) Knuth, and *C. wolfii* (Benson) Baker) from southern Califor-

Fig. 6. Long-shoot pad of *Opuntia aurea* Baxter showing the spiral arrangement of short-shoots (areoles) at the bases of conic, long-shoot leaves. Photo by Martin Ganz.

nia and Baja California appear to be gynodioecious (with perfect- and pistillate-flowered individuals) (Rebman 1998).

Asexual reproduction is a common occurrence for many opuntias. The most prevalent type of cloning in this group is vegetative propagation by stem or cladode detachment (Fig. 7). The terminal stem segments of many species (e.g., *Cylindropuntia leptocaulis* (DeCondolle) Knuth, *Opuntia fragilis* (Nuttal) Haworth, and *O. pubescens* Wendland) detach with ease from the parent plant and readily take root creating clonal individuals (Fig. 7). By this mechanism, some opuntias can develop natural populations that appear to be dense monocultures of clonal individuals. Some of these species frequently referred to as "jumping cacti" (e.g., *Cylindropuntia bigelovii, C. fulgida* (Engelmann) Knuth, and *C. molesta*) bear retrorsely-barbed spines on their easily dislodged stem segments and are dispersed by attachment to some mobile vector such as animals. In these taxa, the success of this type of dispersal mechanism may be responsible for much of the species' distributional patterns.

The fleshy fruits of some opuntias, e.g., *Cylindropuntia cholla* (Weber) Knuth and *C. fulgida* can also become vegetative propagules. Since the pericarpel surrounding the ovary is actually stem tissue and has the ability to generate new organs such as adventitious roots and stems, the fruits can drop from the parent plant and develop into clonal individuals.

Another type of asexual reproduction that has been documented in *Opuntia* is adventive embryony (Davis 1966). In this form of vegetative propagation, a diploid mother cell is translocated into the embryo sac and without fertilization develops into a clonal embryo that is produced inside of the seed. Thus, the individual that germinates from the seed is actually a clone of the parent plant.

The high frequency of vegetative propagation in opuntias can help to maintain particular genetic combinations, perpetuate hybrids, develop dense populations, and readily colonize new localities.

Cytogenetic analyses in the Cactaceae have been a very useful taxonomic tool for distinguishing species and documenting natural hybrid populations (e.g., Baker & Pinkava 1987; Pinkava & McLeod 1971; Pinkava & Parfitt 1982; Pinkava et al. 1973, 1985, 1998; Powell et al. 1991). The Cactaceae have a base number of $x = 11$ and polyploidy is the most common type of chromosomal variation, although aneuploidy, secondary association, cytomixis, extranuclear bodies (Ross 1981), inversions (Pinkava et al. 1973), and translocations (Pinkava et al. 1985) have been discovered.

Fig. 7. Young clonal individuals of the teddy-bear cholla (*Cylindropuntia bigelovii* (Engelmann) Knuth) take root near the base of an older plant as a result of vegetative propagation by stem detachment.

Although polyploidy occurs in only about 28% of all cacti investigated thus far, it plays a more important role in the evolution of the subfamily Opuntioideae (64.3%), than in the Cactoideae (12.9%) and the Pereskioideae (0.0%) (Pinkava et al. 1998). The highest levels of ploidy in the opuntioid group occur in the South American taxa—*Austrocylindropuntia* (11*x*), *Miqueliopuntia* (ca. 20*x*), and *Tephrocactus* (30*x*).

According to Pinkava et al. (1998), the origin of most polyploid cactus species is probably from fertilization involving unreduced gametes. This mechanism was determined as the main factor in polyploidization because: 1) macropollen has been found positively staining with cotton blue in diploid species; 2) many opuntioid taxa are both 2*x* and 3*x*, but not 4*x*, suggesting that triploid individuals are produced from the union of a reduced gamete (1*x*) and an unreduced gamete (2*x*) and then reproduce vegetatively, rather than from 2*x* × 4*x* hybridizations; 3) the morphology of interspecific and intergeneric hybrids derived from parents with different ploidy levels show genome dosage effects on character expression, making them more similar to the parent of higher genome dosage than to the parent of lower dosage.

Polyploidy adds supplementary DNA to a species' genome. This process can facilitate the introduction of novel features by mutation without displacing proven adaptations. In other words, polyploidy, as part of an evolutionary mechanism, may help to bring about something new without much detrimental impact. It appears that polyploidy may be one of the main driving factors in the diversification of opuntias due to its common occurrence. This process may also be responsible for some reproductive strategies in the Cactaceae, i.e., gynodioecy and trioecy, since all cactus species determined thus far that stray from synoecy are polyploid.

Hybridization coupled with polyploidy, the perennial habit, and asexual reproduction all play a role in increasing the complexity of the evolutionary processes of the Cactaceae. In our studies of opuntias, intraspecific, interspecific, and intergeneric hybrids have been determined by intermediacy in morphological characters such as flower color and size, fruit shape, texture, and spination; reduced pollen stainability; proximity to putative parents; and overlapping flower phenology. The commonality of hybrid events in many opuntioid taxa blurs species' boundaries and has led to much difficulty in accurately delineating taxa.

Hybrids can be rare and sterile, quite common and self-fertile, or backcross to the parent taxa. The effects of gene introgression between sympatric parental species have allowed certain hybrid genotypes to survive and thrive (Anderson and Stebbins 1954). In cacti, hybridization in association with polyploidy and vegetative propagation may even yield new species able to invade habitats different from both parent taxa, such as for *Cylindropuntia prolifera* (Engelmann) Knuth (Mayer et al. 2000).

Various techniques traditionally employed to help elucidate hybrid events and taxa include morphological studies, chromosome counts, and lactophenol pollen stains. Unfortunately, most of these studies have their limitations when examining very complex hybrid processes. It is hoped that future chemical and molecular analyses will help to unravel and provide much more insight into the reticulate evolution that seems prevalent in the phylogenies of many opuntias.

Taxonomic Challenges

The opuntias have long been a taxonomic problem for a variety of reasons. 1.) Dried specimens of cacti used for morphological studies usually are poorly prepared and many characteristics are lost or altered during herbarium specimen preparation. As a result, type specimens are often inadequate and non-descriptive causing subsequent nomenclatural difficulties (i.e., *Cylindropuntia* typology, in Rebman 1995). 2.) Like all cacti, it is difficult to make good herbarium specimens of opuntias due to all of the cutting, scraping, flattening, and drying that is required. For this reason, many botanists do not collect opuntias and herbarium collections are usually very depauperate in cactus specimens. This oversight creates a lack of distributional knowledge and an incomplete record of morphological variability present in most species, and should be considered one of the biggest limitations to the taxonomic research in the opuntias. 3.) Many vegetative characters can be quite drastically influenced by environmental factors. Morphological features such as growth habit, stem pubescence, spine length and number per areole can be phenotypically plastic and may change significantly depending upon local growing conditions. 4.) Many opuntias hybridize with other sympatric taxa producing novel, combined, or intermediate character states between species which can blur the boundaries between species. 5.) The opuntias can reproduce by vegetative propagation, adventive embryony, and self-fertility. These reproductive mechanisms help to sustain particular genetic combinations, perpetuate hybrids and as a result, create taxonomic enigmas for the systematist. 6.) There is a lack of interest by amateur collectors and hobbyists thus providing little knowledge of species from cultivated plants. 7.) There is a deficiency of detailed botanical investigations (e.g., systematic monographs and population studies) focusing on the various genera within the opuntioid group.

Of the groups within the Cactaceae, the opuntias are an extremely diversified and dominant component in many plant communities found throughout the New World, especially in arid regions. However, they are still one of the least understood groups in the cactus family. Although a lot of recent knowledge has been gained about the opuntioids and their evolutionary and ecological strategies, they are still an enigmatic group. There is no doubt that many discoveries about their natural history and phylogeny which have yet to be encountered will help us to better understand this fascinating and challenging group of cacti.

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References Cited

Anderson, E., and G. L. Stebbins, Jr. 1954. Hybridization as an evolutionary stimulus. Evolution 8: 378-388.

Baker, M. A., and D. J. Pinkava. 1987. A cytological and morphometric analysis of a triploid apomict, *Opuntia* (*kelvinensis* (subgenus *Cylindropuntia*, Cactaceae). Brittonia 39: 387-401.

Barthlott, W. 1983. Biogeography and evolution in neo- and paleotropical Rhipsalinae, pp. 41-248. *In* K. Kubitzki [ed.]. Dispersal and Distribution. Sonderbd. naturnaturwiss. Ver. Hamburg 7, Hamburg.

Barthlott, W. 1988. Über die systematischen Gliederungen der Cactaceae. Beitr. Biol. Pflanzen 63: 17-40.

Barthlott, W., and D. R. Hunt. 1993. Cactaceae, pp. 161-196. *In* K. Kubitzki [ed.], The Families and Genera of Vascular Plants. Vol. II. Flowering Plants. Springer Verlag Berlin.

Del Carmen Mandujano, M., C. Montaña, and L. E. Eguiarte. 1996. Reproductive ecology and inbreeding depression *in Opuntia rastrera* (Cactaceae) in the Chihuahuan Desert: Why are sexually derived recruitments so rare? Amer. Jour. Bot. 83: 63-70.

Cronquist, A. 1988. The Evolution and Classification of Flowering Plants. Ed. 2. New York Botanical Garden, Bronx.

Davis, G. L. 1966. Systematic Embryology of the Angiosperms. Wiley & Sons, Inc., New York.

Fleming, T. H., S. Maurice, S. L. Buchmann, and M. D. Tuttle. 1994. Reproductive biology and relative male and female fitness in a trioecious cactus, *Pachycereus pringlei* (Cactaceae). Amer. Journ. Bot. 81: 858-867.

Gibson, A. C., and P. S. Nobel. 1986. The Cactus Primer. Harvard Univ. Press, Cambridge, MA.

Hoffman, M. T. 1992. Functional dioecy in *Echinocereus coccineus* (Cactaceae): Breeding system, sex ratios, and geographic range of floral dimorphism. Amer. Journ. Bot. 79: 1382-1388.

Mauseth, J. D., and W. Halperin. 1975. Hormonal control of organogenesis in *Opuntia polyacantha* (Cactaceae). Amer. Journ. Bot. 62: 869-877.

MAYER, M., J. REBMAN, AND L. WILLIAMS. 2000. Molecular evidence for the hybrid origin of *Opuntia prolifera* (Cactaceae). Madroño 47: 109-115.

MCCARTEN, N. 1981. Fossil cacti and other succulents from the late Pleistocene. Cact. Succ. Journ. (U.S.) 53: 122-123.

MCFARLAND, J. D., P. G. KEVAN, AND M. A. LANE. 1989. Pollination biology of *Opuntia imbricata* (Cactaceae) in southern Colorado. Can. Journ. Bot. 67: 24-28.

NEGRÓN-ORTIZ, V. 1998. Reproductive biology of a rare cactus, *Opuntia spinosossima* (Cactaceae), in the Florida Keys: why is seed set very low? Sex. Plant Reprod. 11: 208-212.

NISBET, R. A., AND D. T. PATTEN. 1974. Seasonal temperature acclimation of a prickly-pear cactus in south-central Arizona. Oecologia 15: 345-352.

OSBORN, M. M., P. G. KEVAN, AND M. A. LANE. 1988. Pollination biology of *Opuntia polyacantha* and *Opuntia phaeacantha* (Cactaceae) in southern Colorado. Pl. Syst. Evol. 159: 85-94.

PARFITT, B. D. 1985. Dioecy in North American Cactaceae: A review. Sida 11: 200-206.

PINKAVA, D. J., M. A. BAKER, B. D. PARFITT, M. W. MOHLENBROCK, AND R. D. WORTHINGTON. 1985. Chromosome numbers in some cacti of western North America—V. Syst. Bot. 10: 471-483.

PINKAVA, D. J., AND M. G. MCLEOD. 1971. Chromosome numbers in some cacti of western North America. Brittonia 23: 171-176.

PINKAVA, D. J., M. G. MCLEOD, L. A. MCGILL, AND R. C. BROWN. 1973. Chromosome numbers in some cacti of western North America—II. Brittonia 25: 2-9.

PINKAVA, D. J., AND B. D. PARFITT. 1982. Chromosome numbers in some cacti of western North America—IV. Bull. Torrey Bot. Club 109: 121-128.

PINKAVA, D. J., J. REBMAN, AND M. BAKER. 1998. Chromosome numbers in some cacti of western North America—VII. Haseltonia 6: 32-41.

PINKAVA, D. J. 2001 (ined.). The Opuntioideae (Cactaceae). *In* Editorial Committee. Flora of North America. Oxford Univ. Press, New York.

POWELL, A. M., A. D. ZIMMERMAN, AND R. A. HILSENBECK. 1991. Experimental documentation of natural hybridization in Cactaceae: Origin of Lloyd's Hedgehog Cactus, *Echinocereus* (*lloydii*. Plant Syst. Evol. 178: 107-122.

REBMAN, J. 1995. Biosystematics of *Opuntia* subgenus *Cylindropuntia* (Cactaceae), the chollas of Lower California, Mexico. Ph.D. dissertation. Arizona State University, Tempe, AZ.

REBMAN, J. 1998. A new cholla (Cactaceae) from Baja California, Mexico. Haseltonia 6: 17-21.

ROBINSON, H. 1974. Scanning electron microscope studies of the spines and glochids of the Opuntioideae (Cactaceae). Amer. Journ. Bot. 61: 278-283.

ROSS, R. 1981. Chromosome counts, cytology, and reproduction in the Cactaceae. Amer. Journ. Bot. 68: 463-470.

VALIENTE-BANUET, A., A. ROJAS-MARTÍNEZ, M. DEL CORO ARIZMENDI, AND P. DÁVILA. 1997. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalaensis* and *Neobuxbaumia macrocephala*) in the Tehuacan Valley, central Mexico. Amer. Jour. Bot. 84: 452-455.