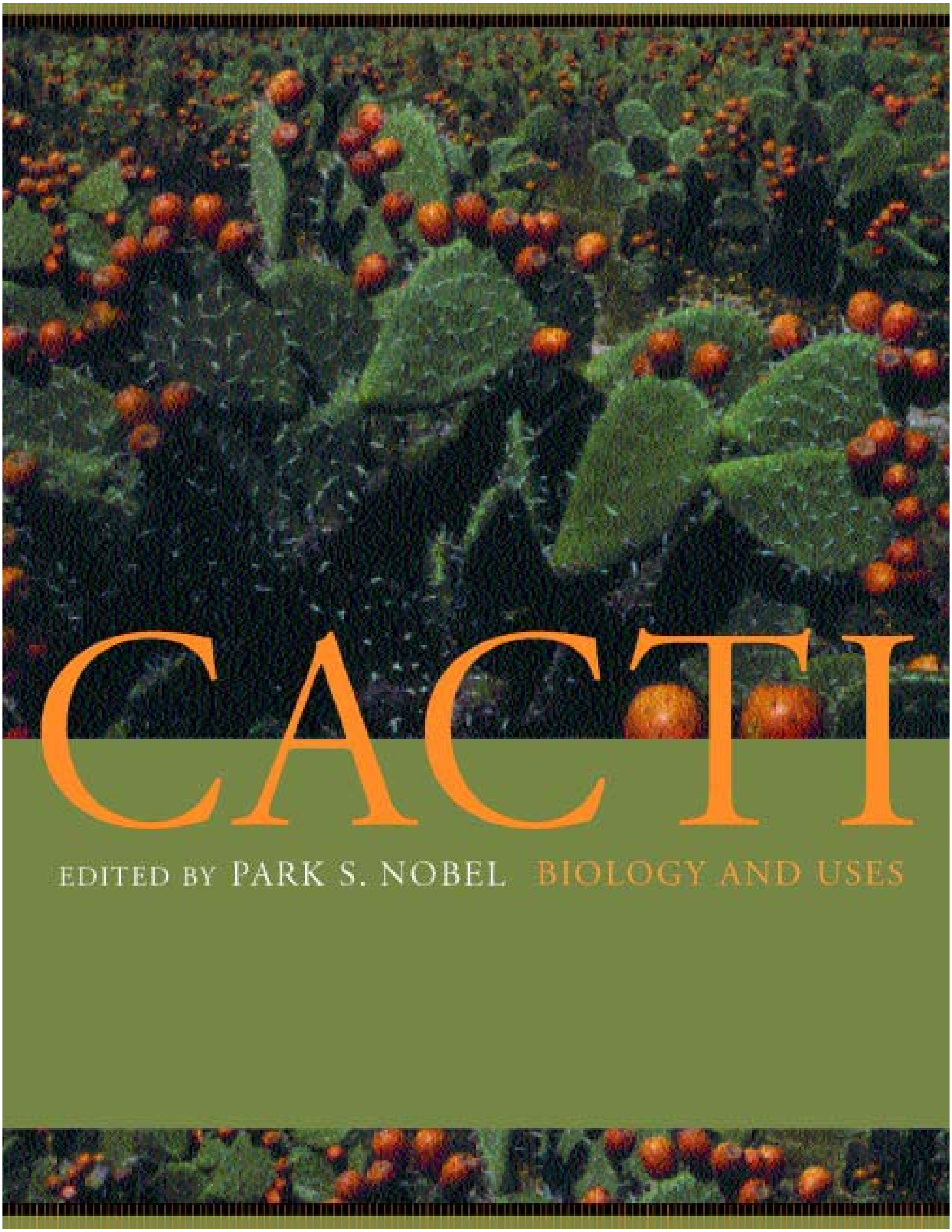

CACTI

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BIOLOGY AND USES

CHAPTER

› 9 ‹

MESOAMERICAN DOMESTICATION AND DIFFUSION

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Introduction

Mesoamerica, the culturally defined region from central Mexico to northwestern Costa Rica (Fig. 9.1), is one of the most important centers of domestication of plants in the world (Harlan 1975). Archaeological studies suggest that domestication of plants in this region was initiated approximately 9,600 years ago (Flannery 1986). Dressler (1953) estimated that about 100 cultivated species (e.g., maize, beans, squashes, tomatoes, avocados, and prickly pears) were domesticated by pre-Columbian cultures of Mesoamerica. Actually, ethnobotanical studies indicate that several hundred species were domesticated, some only in a beginning stage and others to advanced stages, but many have been poorly studied because they are only regionally or locally important. Apart from *Opuntia* spp. and *Hylocereus undatus,* cacti are commonly omitted from checklists of domesticated plants. Nevertheless, archaeologists have revealed that several species of *Opuntia* as well as columnar and barrel cacti were among the most important plant resources utilized by humans in prehistoric Mesoamerica (Callen 1967; Smith 1967, 1986), and ethnobotanists have documented that dozens of species of cacti are currently utilized by indigenous peoples of this

Figure 9.1. Mesoamerica and states for the Mexican part of the region (Matos 1994; Vargas 1994).

area, indicating that several species of *Opuntia* and columnar cacti are in advanced stages of domestication (Colunga 1984; Casas et al. 1997a, 1999a, b).

Domestication is an evolutionary process resulting from the manipulation of living organisms by humans. In this process, humans select and breed phenotypes with characteristics they consider advantageous; i.e., individual plants with better qualities as food, medicine, and other uses. Other evolutionary forces, such as genetic drift, also intervene in the selection process and may be significant in small populations caused by humans due to the isolation of individual plants or resulting from perturbation and fragmentation of natural habitats or transplantation of wild individuals into human habitats. Throughout history, human migrations, displacement of human settlements, commerce, cultural exchange, as well as conquest and colonization of new areas have been accompanied by the movement of plant and animal populations (individuals and/or their propagules) from one region to another. In some cases, migration has isolated individuals from their parental populations, and the influence of artificial selection under different cultural and environmental contexts can determine particular routes of domestication. In other cases, migration has reestablished contact between variants previously separated by natural or human processes, giving rise to new combinations of genes that are available for artificial selection. Through domestication, plant populations become morphologically, physiologically, and/or behaviorally divergent from their wild ancestors (Darwin 1868; Harlan 1992). But, as in general evolutionary processes, the inherited, genetically controlled divergence can be considered a domestication process.

Domestication of plants has generally been associated with cultivation (Harlan 1992), because artificial selection more probably occurs under successive generations of harvest and propagation of the desired phenotypes. However, domestication can also act under different forms of manipulation of wild plant populations *in situ,* including species of cacti (Casas et al. 1997b). Indeed, Mesoamerican indigenous peoples commonly practice a broad spectrum of interactions with plants (Alcorn 1984; Colunga 1984; Bye 1993; Casas et al. 1996, 1997a). Casas et al. (1996) group these forms of plant management into those occurring *in situ* (in the wild) and those occurring *ex situ.* Through interactions *in situ,* humans may take products from nature without significant perturbations, but they may also alter the structure of plant populations by increasing the quantity of target species or particular phenotypes. The main interactions *in situ* are: (1) gathering, which is the taking of useful plant products directly from natural populations; (2) tolerance, including practices directed to maintain, within human-made environments, useful plants already occurring there; (3) enhancement, directed to increase the population density of useful plant species, including the sowing of seeds or the intentional propagation of vegetative structures in places occupied by wild plant populations; and (4) protection, which includes conscious activities, such as the elimination of competitors or predators, fertilization, and pruning to safeguard critical wild plants. Plant management *ex situ* includes interactions taking place outside natural populations, in habitats created and controlled by humans, including: (1) transplantation of entire individuals and (2) sowing and planting of sexual or vegetative propagules (Casas et al. 1996, 1997a,b).

Variation among the species composing a plant community or the individuals forming a population, their differences in quality as useful resources, and the selective attitude of humans in taking advantage of some species and particular individuals and not others are the most important principles in artificial selection of plants. Ethnobotanical studies in Mesoamerica have revealed that this attitude is common among indigenous peoples and that it occurs under different interactions between humans and plants, not only under cultivation. In gathering, people usually make choices among individual plants based on their quality as a food, such as flavor, size, color, and presence of toxic substances (Casas et al. 1996, 1997a, 1999b). This selection may give rise to other types of interaction involving domestication. When they are found during the clearing of forest areas, the edible wild plant species and the preferred variants may be spared, enhanced, and/or protected *in situ,* whereas those species and variants whose edible parts are not preferred by people are eliminated. Over the long term such selective attitudes may modify vegetation patches in which the phenotypes desirable to humans have a better opportunity to be components of the community, and the selected components may increase their frequency in populations, another facet of plant domestication.

This chapter examines cultural and biological aspects related to the use and management of cacti among peoples of Mexican Mesoamerica and analyzes how domestication is occurring in some species. Comparisons of morphology between wild and manipulated populations of *Opuntia* and *Stenocereus* species are used to illustrate patterns of artificial selection and evolutionary trends resulting from domestication under different forms of management. This information is discussed to determine how domestication might be occurring in other cacti. The diffusion of cacti, especially platyopuntias, into other regions of the world is reviewed to examine trends in domestication of these species outside of Mesoamerica.

Human-Cactus Interactions in Mesoamerica

Archaeological and Historical Evidence

Mexico is apparently the richest area for cactus species in the world (Bravo-Hollis 1978). Cacti are among the main components of the tropical deciduous and thorn-scrub forests of subhumid tropics as well as arid and semiarid zones, which cover nearly two-thirds of the country (Toledo and Ordóñez 1993). Archaeological studies in the Tehuacán Valley, Puebla (MacNeish 1967), and at Guilá Naquitz, Oaxaca (Flannery 1986), suggest that the region was inhabited by humans probably from 14,000 years before present (BP) and have found there the oldest evidence of plant domestication in the New World. Since ancient times, people of this area have used a broad spectrum of plant and animal species as resources, and cacti have been among the most important because of their abundance, diversity, and edible parts.

Prehistoric human colonization of the Mexican territory most likely occurred in a north-south direction. According to this theory, people arrived from northern Aridoamerica, the vast territory occupied by the Sonoran and Chihuahuan deserts, where prehistoric bands of hunter-gatherers interacted for a long time with cacti as main resources. Inhabitants of the prehistoric Mesoamerica exhibited a strong cultural utilization of cacti, developed by their ancestors from Aridoamerica and their own experience with local arid and semiarid environments. Later on, continual migrations of peoples (including the Aztecs) from northern Mexico into Mesoamerica progressively reinforced the development of cactus utilization among the great civilizations; this utilization persists until today.

TABLE 9.1
Archaeological remains of cacti in caves of the Tehuacán Valley (Puebla, P) and Guilá Naquitz (Oaxaca, O) in central Mexico

Species	Phase, with radiocarbon date (years before present, BP) in parentheses								
	Ajuereado *(14,000 – 8,800)*	*El Riego* *(8,800 – 7,000)*	*Coxcatlán* *(7,000 – 5,400)*	*Abejas* *(5,400 – 4,300)*	*Purrón* *(4,300 – 3,500)*	*Ajalpan* *(3,500 – 2,800)*	*Sta. María* *(2,800 – 2,150)*	*Palo Blanco* *(2,150 – 1,300)*	*Venta Salada* *(1,300 – 500)*
Cephalocereus columna trajani		P	P			P	P		
Echinocactus platyacanthus		P						P	
Escontria chiotilla			P					P	
Ferocactus flavovirens								P	P
Myrtillocactus geometrizans		P	P						P
Opuntia spp.	P, O	P, O	P, O	P, O	P, O	P, O	P, O	P, O	P, O
Pachycereus hollianus		P	P	P					
P. weberi		P	P	P			P	P	
Stenocereus stellatus				P				P	

Adapted from MacNeish (1967) and Smith (1967, 1986).

Smith (1967) reported remains of nine cactus species (Table 9.1) from archaeological excavations of prehistoric Mesoamerican sites in caves of the Tehuacán Valley. For caves at Guilá Naquitz, Smith (1986) reports stems, fruits, and seeds of *Opuntia* species in almost all of the stratigraphic zones studied, from nearly 12,000 years BP, as well as a gumball that could have come from a columnar cactus. Callen (1967) identified the following types of cactus remains in human coprolites of Tehuacán: (1) "*Opuntia,*" which might represent some of the 18 species of this genus existing in the region (Arias et al. 1997); (2) "*Lemaireocereus,*" which might represent some of the 13 species of columnar cacti of the genera *Escontria, Myrtillocactus, Pachycereus, Polaskia,* and *Stenocereus* (Casas et al. 1999a); and (3) "cactus tissue," from unidentified cacti. Callen (1967) further found that in the earliest coprolites from the El Riego phase (8,500–7,000 years BP), these types of cactus remains were a part of a wild food diet, along with *Setaria* spp. seeds, pochote (*Ceiba parvifolia*) roots, maguey (*Agave* spp.) leaves, and meat. In the Coxcatlán phase (7,000–5,500 years BP), stem tissue and fruits of "*Opuntia*" and "*Lemaireocereus*" were equally dominant materials. In the Abejas (5,500–3,300 years BP), Ajalpan (3,500–2,900 years BP), Santa María (2,900–2,200 years BP), Palo Blanco (2,200–1,300 years BP), and Venta Salada (1,300–460 years BP) phases, findings suggest that consumption of "*Lemaireocereus*" stem tissue, fruits, and seeds were more important than products of "*Opuntia*"; and during the Ajalpan and Santa María phases, "*Lemaireocereus*" was the principal plant constituent of human diets.

The importance of cacti in Mesoamerican cultures can be recognized in pre-Columbian codices, which contain many toponymic glyphs referring to the names of cacti or their parts. Among the most famous are *Tenochtitlán* ("place of stony prickly pears" in Náhuatl), the original name of Mexico City, and *Nochistlán* ("place of prickly pears" in Náhuatl), in the state of Oaxaca. Historical information on utilization of cacti can be found in *La Historia General y Natural de las Indias,* published by Oviedo y Valdés in 1535. The Barberini Codex from 1552 (De la Cruz and Badiano 1964) includes information on medicinal utilization of *Tlatocnochtli,* a species of *Opuntia,* and a description of *Teonochtli,* identified as *Stenocereus* sp. by Bravo-Hollis (1978). The *Florentino Codex* (Sahagún 1970) contains a section dedicated to the description of the "diversity of tunas," which includes a list of variants of *Opuntia* species and their uses as edible fruits and stems. Estrada (1989) identified *Cacanochnopalli* (a Náhuatl term) as *O. megarhiza, Tecolnochnopalli* as *O. streptacantha, Uitzocuitlapalli* as *Aporocactus flagelliformis, Nopalxochitl* as

Epiphyllum ackermanii, Teonochtli as *Hylocereus undatus, Peyotl* as *Lophophora williamsii* (now commonly known as "peyote"), as well as several types of *Tecomitl* as *Mammillaria, Echinocactus,* and *Ferocactus* species. The *Florentino Codex* also includes information on two columnar cacti, one of them called *Netzolli,* which is probably *Escontria chiotilla,* and *Teunochtli,* which could be a species of *Stenocereus* (Casas et al. 1999a). The books of Francisco Hernández in the 16th century describe several species of cacti utilized as medicine, among them several species of *Opuntia,* two columnar cacti identified as *Myrtillocactus geometrizans,* and a possible *Stenocereus* species called *Teonochtli* (Hernández 1959). The *Geographic Relations of the XVI Century* described the cultivation of *Opuntia* species for the production of cochineal and contains a reference to the columnar cactus *Teonochtli,* the "Relation of Acatlán" (Acuña 1985). Based on these sources, cacti were clearly utilized as food (fruits, young stems, and in some cases the flowers and seeds) and medicine (fruits, stems, and roots).

In the 16th century, Oviedo y Valdés (1535) and Sahagún (1985) described how the harvest of fruits of *Opuntia* spp. and columnar cacti was crucial for subsistence of some pre-Columbian and post-Conquest peoples from northern and central Mexico. For example, indigenous people migrated during the summer from the coast of the Gulf of Mexico to the highlands of the northern plateau, looking for the fruits of platyopuntias. In this region, people stayed for two months, migrating from place to place consuming fruits.

Smith (1967) considered that species of *Opuntia* could have been among the first plants subject to human manipulation in the Tehuacán Valley, but no archaeological evidence exists. Apparently, *Opuntia* was cultivated in the 16th century for the production of cochineal (*Opuntia ficus-indica, O. tomentosa* var. *hernandezii,* and *Nopalea cochenillifera*). However, cultivation of *Opuntia* and columnar cacti for the production of fruits, as currently occurs, was not clearly recorded. The only document that indicates such cultivation is the book of Sahagún (1985), in which the wild variants are distinguished from others (presumably cultivated). This omission could be because the Spaniards did not consider fruits of cacti as important resources and therefore did not describe them, as was the case for many other plants cultivated by natives (Casas et al. 1999a). Such omission could also be explained if cultivation of these plants started more recently. Further studies can provide information on the changes of cacti under domestication, which would be helpful to estimate the antiquity of cactus domestication.

Ethnobotanical Information

According to the compendium of the Cactaceae of Mexico by Bravo-Hollis (1978; Bravo-Hollis and Sánchez-Mejorada 1991), about 850 cactus species occur within the Mexican territory and 420 in the Mesoamerican region. Ethnobotanical studies in the region have documented a total of 118 cacti species utilized by indigenous peoples (Table 9.2). Useful cacti include *Opuntia* species, epiphytes, as well as columnar, spherical, barrel, and shrubby cacti. Among the columnar cacti, nearly half of the species are uncultivated giant columnar cacti, some about 15 m tall, with slow vegetative growth, which flower only after decades (Casas et al. 1999a). However, 23 species of columnar cacti (Table 9.2) are 2 to 8 m high. They grow faster than the giant columnar cacti, and flower 6 to 8 years after seed germination (2–4 years after vegetative propagation); most of them reproduce vegetatively and are cultivated.

Cacti are used mainly for their fruits, which may be consumed both fresh and dried and are used to prepare jams (Table 9.2). With the exception of subfamily Pereskioideae, fruits of nearly all species of cacti are consumed by people (Bravo-Hollis 1978). Fruits of 83 species (Table 9.2) are the most commonly consumed, and it is possible to distinguish: (1) species producing sweet juicy fruits, which are "good quality fruits" and are commonly harvested; (2) species whose fruits are of "regular quality" and are collected only occasionally, because of the scarcity of individual plants or populations, tall branches, long or abundant spines, or lack of tastiness; and (3) species whose fruits do not contain juicy pulp and are consumed only during food scarcity. The main groups of cacti producing edible fruits are columnar cacti and *Hylocereus* species with fruits called *pitayas* and *pitahayas,* respectively (Chapter 11); some *Mammillaria* species with fruits called *chilitos;* and, most important, *Opuntia* species (Chapter 10), whose sweet fruits are called *tunas* and consumed fresh, and whose sour fruits are called *xoconoztles* (from the Náhuatl *xocotl,* meaning sour, and *nochtli,* prickly pear) and are utilized as greens, condiments (boiled or fried), or as an ingredient for several other dishes. Colunga (1984) identified as *xoconoztles* variants of the species *Opuntia joconstle, O. lasiacantha, O. leucotricha,* and *O. streptacantha* as well as the red variant *jitomatilli* of *O. megacantha,* which is utilized as a substitute for tomato, and the variant *brevas* of *Opuntia robusta* var. *robusta,* whose peel is consumed fried, resembling French fried potatoes.

From the useful species of cacti reported, the stems of 62 species are cut and fed (after removal of the spines) as fodder to domestic donkeys, cows, and goats (Table 9.2).

TABLE 9.2
Species of cacti from Mexican Mesoamerica

Species	Uses[a]	Type[b]	Status[c]	Mexican states[d]	Reference
Acanthocereus pentagonus	1**, 5, 7, 8	Shr	w	7, 16, 19, 21	Caballero (1992)
A. subinermis	5, 7	Shr	w, c	7, 16	Casas et al. (2001)
Aporocactus flagelliformis	8, 9	Shr	c	General	Bravo-Hollis (1978)
Backebergia militaris	1, 2	G col	w	9, 15	Casas et al. (1999a)
Cephalocereus apicicephalium	1, 2	G col	w	16	"
C. chrysacanthus	1*, 2	G col	w	14, 16	"
C. collinsii	1*, 2	S col	w	16	"
C. columna-trajani	1*, 2, 6	G col	w	14	"
C. guerreronis	1, 2	S col	w	15	"
C. nizandensis	1, 2	G col	w	16	"
C. palmeri var. *sartorianus*	1*, 2	G col	w	16	"
C. purpusii	1, 2	S col	w	9	"
C. quadricentralis	1, 2	S col	w	16	"
C. senilis	9	G col	w, c	6, 7	Bravo-Hollis (1978)
C. totolapensis	1, 2	G col	w	16	Casas et al. (1999a)
Coryphantha radians	2, 5	Sph	w	4, 5, 6, 16	Pennington (1963); Bravo-Hollis (1978)
C. pallida	2, 9	Sph	w	14, 16	Casas et al. (2001)
Echinocactus platyacanthus	5	Bar	w, m	4, 5, 6, 14, 16	Del Castillo and Trujillo (1991); Casas et al. (2001)
E. cinerascens	1, 8	Shr	w	4, 5, 6, 10, 11	Sánchez Mejorada (1982)
E. pulchellus	5	Shr	w	6, 14	Casas et al. (2001)
Escontria chiotilla	1**, 2, 3, 4, 5, 7, 11	S col	w, m	9, 14, 15, 16	Casas, et al. (1999a)
Ferocactus flavovirens	2	Sph	w	14, 16	Casas et al. (2001)
F. haematacanthus	1, 2	Sph	w	7, 14	Bravo-Hollis (1978); Casas et al. (2001)
F. histrix	1, 5	Bar	w	4, 5, 6, 14	Del Castillo and Trujillo (1991)
F. latispinus	1, 2, 5, 9	Sph	w	5, 6, 10, 11, 14, 16	Sánchez-Mejorada (1982); Casas et al. (2001)
F. macrodiscus	1, 5	Sph	w	4, 5, 14, 16	Pennington (1963); Casas et al. (2001)
F. recurvus	5	Bar	w	14, 16	Bravo-Hollis (1978); Casas et al. (2001)
F. robustus	2	Sph	w	14, 16	Casas et al. (2001)
Heliocereus cinnabarinus	1	Ep	w, m	21	Berlin et al. (1973)
H. elegantissimus	1, 8, 9	Ep	w, m, c	10, 13, 16	Guerra (1986); Cedillo (1990)
H. speciosus	8, 9	Ep	w, c	10	Bravo-Hollis (1978)
H. schrankii	9	Ep	w, c	6, 14, 16	Casas et al. (2001)
Hylocereus ocamponis	1*	Ep	w	8, 9	A. Casas (unpublished observation)
H. purpusii	1	Ep	w, c	1, 2, 8, 9, 14, 16	Bravo-Hollis (1978); Casas et al. (2001)
H. stenopterus	1*	Ep	w	16	Bravo-Hollis (1978)
H. undatus	1**, 9	Ep	c	General	Martínez (1993)

[a] Uses: 1 = edible fruits (*regular quality, **good quality); 2 = fodder; 3 = alcoholic beverage; 4 = edible seeds; 5 = edible stems and flowers; 6 = house construction; 7 = living fences; 8 = medicine; 9 = ornamental; 10 = adhesive; 11 = fuel wood.

[b] Type: Op = *Opuntia*; Ep = epiphyte; Sph = spherical; G col = giant columnar; S col = small columnar; Bar = barrel; Shr = shrubby.

[c] Cultural status: w = wild; m = managed *in situ*; c = cultivated.

[d] Numbers for Mexican states (see Figure 9.1) are as follows: 1 = Nayarit; 2 = Jalisco; 3 = San Luis Potosí; 4 = Guanajuato; 5 = Queretaro; 6 = Hidalgo; 7 = Verzcruz; 8 = Colima; 9 = Michoacán; 10 = México; 11 = Mexico City; 12 = Tlaxcala; 13 = Morelos; 14 = Puebla; 15 = Guerrero; 16 = Oaxaca; 17 = Yucatán; 18 = Chiapas; 19 = Zacatecas.

TABLE 9.2 *(continued)*

Species	Uses	Type	Status	Mexican states	Reference
Lophophora williamsii	8	Sph	w	3, 19	Pennington (1963); Martínez (1993)
Mammillaria carnea	1, 2	Sph	w	6, 14, 15, 16	Bravo-Hollis (1978); Casas et al. (2001)
M. collina	9	Sph	w, c	7, 14, 16	Bravo-Hollis (1978); Casas et al. (2001)
M. discolor	5	Sph	w	7, 14	Bravo-Hollis (1978)
M. haageana	5, 9	Sph	w, c	7, 14, 16	Pennington (1963); Casas et al. (2001)
M. magnimamma	1**	Sph	w	7, 9 10, 11, 12, 14	Bravo-Hollis (1978)
Melocactus maxonii	5	Sph	w	16	"
M. ruestii	5	Sph	w	16,18	"
Mitrocereus fulviceps	1*, 2, 6	G col	w	14, 16	Casas et al. (1999a)
Myrtillocactus geometrizans	1**, 2, 3, 5, 7	S col	w, m	9, 15, 16	"
M. schenkii	1**, 2, 3, 5, 7	S col	w, m, c	14, 16	"
Neobuxbaumia macrocephala	1, 2, 6	G col	w	14	"
N. mezcalaensis	1**, 2, 4, 5, 6	G col	w	9, 13, 14, 15, 16	"
N. multiareolata	1, 2	G col	w	15	"
N. scoparia	1, 2	G col	w	16	"
N. tetetzo	1**, 2, 4, 5, 6	G col	w	14, 16	"
Nopalea auberi	5, 8, 9	Op	w, c	13, General	Bravo-Hollis (1978); Casas et al. (2001)
N. cochenillifera	2, 5, 8	Op	w, m, c	16, General	Pennington (1969); Bravo-Hollis (1978)
N. dejecta	2, 5	Op	c	7, 18	Bravo-Hollis (1978)
N. escuintlensis	1**	Op	w	18	"
N. lutea	1**	Op	w	18	"
N. karwinskiana	8	Op	w	9, 15, 16	Bravo-Hollis (1978); Martínez (1993)
Nopalxochia ackermanii	9	Ep	w, c	7, 16	Bravo-Hollis (1978)
N. conzatitianum	9	Ep	w, c	16	"
N. macdougallii	9	Ep	w, c	18	"
N. phyllantoides	9	Ep	w, c	7, 14	"
Opuntia amyclaea	1*, 9	Op	c	General	"
O. atropes	1, 11	Op	w, m	4, 9, 10, 13, 15	Bravo-Hollis (1978); Colunga (1984)
O. bensonii	1**	Op	w	9	Bravo-Hollis (1978)
O. crassa	1**, 11	Op	c	4, 11	Bravo-Hollis (1978); Colunga (1984)
O. decumbens	2, 5, 11	Op	w	14, 15, 16	Casas et al. (2001)
O. ficus-indica	1**, 2, 5, 8, 10, 11	Op	c	General	Bravo-Hollis (1978); Colunga (1984)
O. fuliginosa	1**, 11	Op	w, m	4, 8, 9	Colunga (1984)
O. huajuapensis	1, 2, 3, 5, 8, 9	Op	w	14, 16	Casas et al. (2001)
O. hyptiacantha	1**, 2, 11	Op	w, m	4, 10, 11	Bravo-Hollis (1978); Colunga (1984)
O. imbricata	1*, 2, 5, 8	Op	w	4, 5, 10, 11	Sánchez Mejorada (1982)
O. jaliscana	1**, 11	Op	w, m	4, 9	Bravo-Hollis (1978); Colunga (1984)
O. joconostle	1**, 11	Op	w, m, c	4, 5, 9, 10, 11	Martínez (1993)
O. kleiniae	7	Op	c	14	Arias et al. (1997)

(*continued on next page*)

TABLE 9.2 *(continued)*

Species	Uses	Type	Status	Mexican states	Reference
O. lasiacantha	1*, 2, 9, 11	Op	w, m, c	4, 10, 11, 14, 16	Bravo-Hollis (1978)
O. leptocaulis	1, 2, 5, 8	Op	w	5, 6, 14, 16	Sánchez Mejorada (1982); Felger and Moser (1983)
O. leucotricha	1**, 2, 11	Op	w, m	4, 5, 6	Bravo-Hollis (1978); Colunga (1984)
O. megacantha	1**, 11	Op	w, m, c	4	Colunga (1984)
O. nerpicolor	1*, 5	Op	w		Sánchez Mejorada (1982)
O. pilifera	1*, 2, 11	Op	w, m	14, 16	Bravo-Hollis (1978); Casas et al. (2001)
O. robusta	1**, 2, 5, 11	Op	w, m, c	4, 5, 6, 9	Bravo-Hollis (1978); Colunga (1984)
O. spinulifera	1**	Op	c	10	Bravo-Hollis (1978)
O. stenopetala	2, 8	Op	w	4, 5, 6	Sánchez Mejorada (1982)
O. streptacantha	1**, 2, 5, 3, 11	Op	w, m, c	4, 5, 6, 14, 16	Bravo-Hollis (1978); Colunga (1984)
O. tehuantepecana	1*, 5, 8	Op	w	16, 18	Barrera et al. (1976)
O. tomentosa	1**, 2, 5, 11	Op	w, m, c	10, 11	Bravo-Hollis (1978)
O. undulata	1**, 11	Op	c	General	Bravo-Hollis (1978); Colunga (1984)
O. velutina	1**, 8, 11	Op	w, m	13, 14, 15, 16	Colunga (1984)
Pachycereus grandis	1**, 2, 4	G col	w	10, 13, 14	Casas et al. (1999a)
P. hollianus	1**, 2, 3, 4, 7	S col	w, m, c	14	"
P. marginatus	1**, 2, 7, 8	S col	w, m, c	10, 14, 16	"
P. pecten-aboriginum	1**, 2, 4, 6, 8, 11	G col	w, m	9, 15, 16	"
P. weberi	1**, 2, 3, 4, 6, 11	G col	w, m	9, 14, 15, 16	"
Peniocereus serpentinus	9	Shr	w, c	14	Arias et al. (1997)
Pereskia grandiflora	8	Shr	c	3	Alcorn (1984)
P. lychnidiflora	7	Shr	w, c	16, 18	Bravo-Hollis (1978); Martínez (1993)
Pereskiopsis aquosa	1**, 5, 8	Shr	w, c	4, 13	Bravo-Hollis (1978)
P. rotundifolia	7, 8	Shr	w, c	13, 14, 15, 16, 18	Arias et al. (1997)
P. velutina	7	Shr	w, c	5	Bravo-Hollis (1978)
Polaskia chende	1**, 2, 4, 7, 11	S col	w, m	14, 16	Casas et al. (1999a)
P. chichipe	1**, 2, 4, 7, 11	S col	w, m, c	14, 16	"
Rhipsalis baccifera	1**, 2, 3, 4, 6	G col	w, m	9, 13, 15, 16	"
Selenicereus donkelaarii	8	Ep	w	17	Martínez (1993)
S. grandiflorus	1**, 2, 3, 4, 5, 7	S col	c	14, 15, 16	Casas et al. (1999a)
S. spinulosus	1**, 2, 3, 4, 6	S col	w, m, c	14, 15, 16	"
Stenocereus beneckei	1*, 2, 7	S col	w	10, 13, 15	"
S. chacalapensis	1**, 2	G col	w	16	"
S. chrysocarpus	1**, 2	G col	w, m	9	"
S. eichlamii	1**	S col	w	18	Bravo-Hollis (1978)
S. fricii	1**, 2, 4, 7	S col	w, m, c	2, 9, 8	Casas et al. (1999a)
S. montanus	1*	S col	w	2, 8	Bravo-Hollis (1978)
S. pruinosus	1*, 2, 7, 11	S col	w, m, c	7, 14, 16	Casas et al. (1999a)
S. queretaroensis	1**, 2, 7	S col	w, m, c	9	"
S. quevedonis	1**, 2, 4, 7	S col	w, m, c	9, 15	"
S. stellatus	1**, 2, 3, 4, 5, 7, 11	S col	w, m, c	13, 14, 15, 16,	"
S. standleyi	1**, 2, 4, 7	S col	w, m, c	9, 15	"
S. treleasei	1**, 2, 4, 7, 11	S col	w, m, c	16	"

Unfortunately, this list includes long-lived cacti that are commonly endangered by this utilization. An alcoholic drink called *colonche* or *nochoctli* may be prepared from fruits of 11 species (Table 9.2). Seeds of 17 species are consumed by people (Table 9.2). In general, seeds obtained from fresh or dried fruits are washed, dried, and roasted to prepare traditional sauces or ground into an edible paste that is consumed with maize tortillas.

Stems and sometimes flowers of 34 species are consumed by humans (Table 9.2). Stems of *Opuntia* spp. and columnar cacti have long been a common food (Callen 1967). At present, consuming young stems of *Opuntia* and *Acanthocereus* as vegetables and utilizing the stems of barrel cacti to prepare candies are locally common, but the young stems of columnar cacti are eaten only during food scarcity. Undoubtedly, cladodes of platyopuntias are by far the most appreciated plants for stem consumption, although many species may be consumed; among the preferred and even commercialized are variants of *O. atropes, O. fuliginosa, O. hyptiacantha, O. jaliscana, O. joconostle, O. megacantha, O. streptacantha, O. tomentosa, O. velutina,* and, of course, *O. ficus-indica* (Colunga 1984). Flower buds are commonly consumed after boiling, e.g., *Pereskiopsis* species, whose leaves are also consumed as greens.

Wood of 9 species of columnar cacti is used in construction of house roofs and fences, and 22 species of *Opuntia, Pereskia, Pereskiopsis,* and columnar cacti, among others, are grown as living fences and/or as barriers for soil protection in terraces of cultivated slopes (Table 9.2). A total of 22 species are utilized as medicine. Among the main diseases traditionally treated with cacti are stomach ache, gastric ulcers, rheumatism, dysentery, diabetes, obesity, and heart diseases (Chapter 13), and some species are used as analgesic, anti-inflammatory, or diuretic agents (Table 9.2).

Also appreciated for their beauty, cacti have been collected, cultivated, and some domesticated as ornamental plants in Mexico and other parts of the world (Chapter 8). For the scope of this chapter, only the 19 species considered as ornamental in rural Mexico are so counted (Table 9.2). The mucilage of *O. ficus-indica* and *Pachycereus hollianus* is utilized as an adhesive (Chapter 13). The dry stems of 25 species are utilized as a fuel for heating and to prepare food, and the stems of *Polaskia chichipe, P. chende,* and *Stenocereus stellatus* are sources of fuel wood for manufacturing pottery.

Peoples of Mexican Mesoamerica gather fruits and other useful products of cacti from wild populations (Table 9.2). In general, they gather fruits selectively, preferring larger fruits of species or variants with juicy pulp, sweeter or, for *xoconoztles,* sourer pulp, or thinner edible pericarp (thicker for *xoconoztles*), shorter and fewer spines, and deciduous areoles (Casas et al. 1997a). Similarly, for collecting edible stems, people take into account the thickness of stems and prefer fewer spines, less mucilage, lack of a bitter flavor, and no fibrous texture (Colunga et al. 1986). When they clear the vegetation for cultivating maize, peasants frequently tolerate or let stand individuals of 19 species of columnar cacti, variants of 13 species of *Opuntia,* and 5 species of other cacti (Table 9.2). They commonly plant vegetative propagules of the spared cacti, enhancing their local abundance. Because these compete with cultivated plants, people carefully select the individuals to spare. Their decisions take into account the usefulness and desirable characteristics of the species and individuals in terms of the products that they produce. About 46 species are cultivated by planting vegetative parts in home gardens or in agricultural plots where they serve as living fences or as barriers to prevent soil erosion (Table 9.2). Vigorous branches or cladodes from wild or cultivated individuals are irrigated, and ash is commonly used as a fertilizer. Individuals cultivated in home gardens may also be derived from seedlings established from seeds dispersed via bird, bat, or human feces. Because people often do not recognize variants of cactus species based on vegetative characteristics, decisions on eliminating or sparing individuals are made when the individuals first produce fruits.

Domestication of Cacti

Columnar Cacti

Although 12 species of columnar cacti are cultivated (Table 9.2), the only cases studied under controlled domestication process are *Stenocereus pruinosus* (Luna 1999), *S. queretaroensis* (Pimienta-Barrios and Nobel 1994), and *S. stellatus* (Casas et al. 1997a, 1999b,c). *Stenocereus pruinosus* occurs in southeast-central Mexico, *S. queretaroensis* in west-central Mexico, and *S. stellatus* is endemic to south-central Mexico (Fig. 9.2). These species occur in the wild in tropical deciduous and thorn-scrub forests, but some wild populations are managed *in situ* and all three species are cultivated (Casas et al. 1999a). They exhibit considerable morphological variation, especially in fruit characteristics, which is presumably partly under genetic control, partly influenced by environmental conditions, and partly the result of human manipulation.

According to archaeological information from caves in Tehuacán, *S. stellatus* has been used for nearly 5,000 years (MacNeish 1967; Smith 1967). Current indigenous groups use and manage this species and *S. pruinosus* mainly for

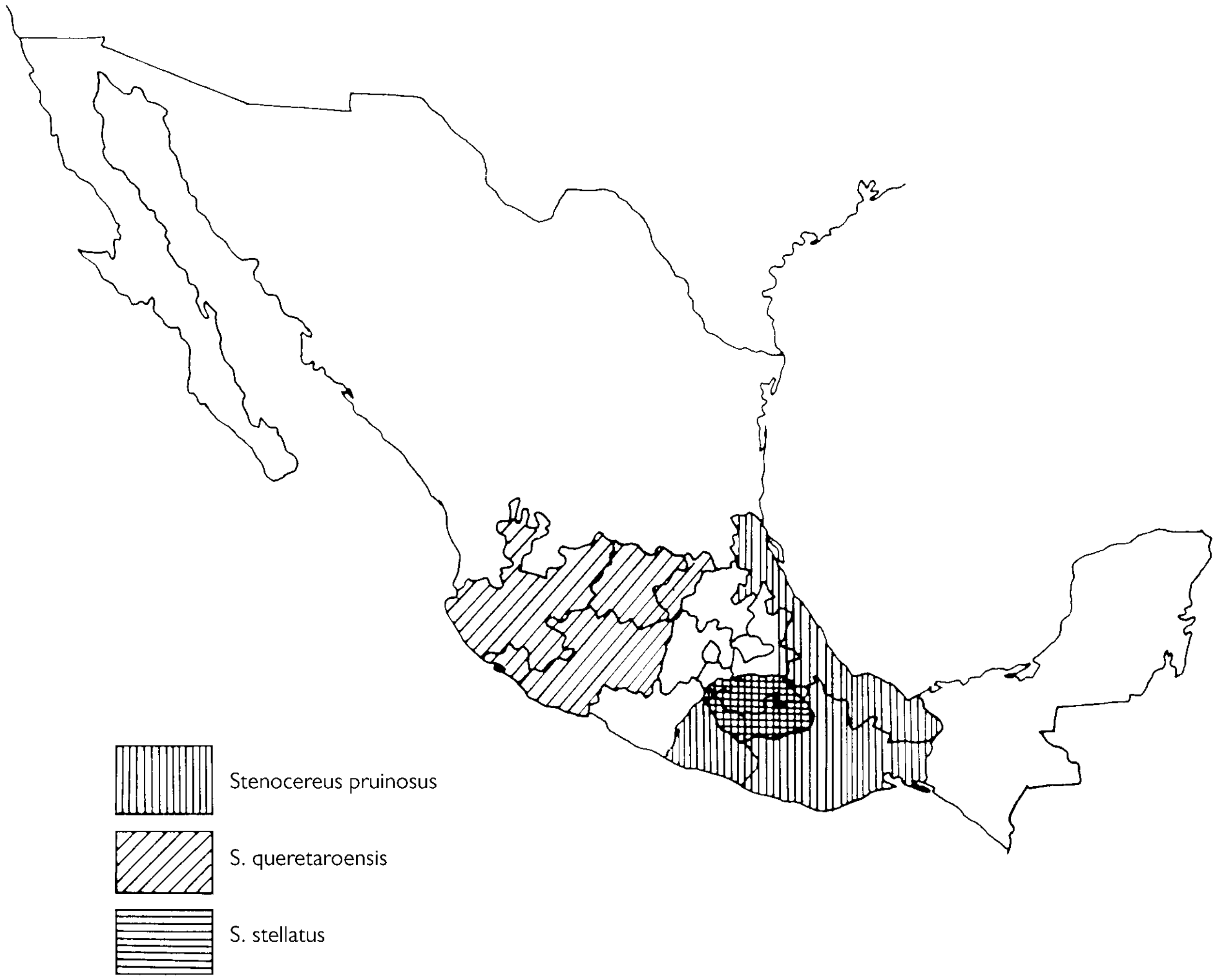

Figure 9.2. Range of *Stenocereus pruinosus, S. queretaroensis,* and *S. stellatus* (Pimienta-Barrios and Nobel 1994; Casas et al. 1997a; Luna 1999).

their edible fruits. Management *in situ* of wild populations of *S. pruinosus* and *S. stellatus* is carried out by keeping desirable phenotypes while removing others, and by cutting and planting branches of desirable phenotypes (Casas et al. 1997a, 1999a). Cultivation is practiced mainly in home gardens, where desirable phenotypes are vegetatively propagated and new variation is incorporated by volunteer seedlings. Similarly, relictual populations of *S. queretaroensis,* associated with pre-Columbian settlements, have been continuously used for long periods in southern Jalisco and Colima (Benz et al. 1997). This species is now widely cultivated in Jalisco and Guanajuato, most of this domestication apparently stemming from the 19th century (Pimienta-Barrios and Nobel 1994).

Pulp color, flavor, amount of edible matter, skin thickness, and spinyness of the mature fruits are the most significant characteristics used in folk classification of variants, assessing quality of products, and selecting individuals of these columnar cacti for propagation (Pimienta-Barrios and Nobel 1994; Casas et al. 1997a, 1999a,b; Luna 1999). Manipulation of these species involves artificial selection. This is particularly intense in home gardens, where manipulation is accomplished by continually planting and replacing individuals, but also is significant in managed populations *in situ,* where selection mainly increases frequencies of favorable phenotypes in wild populations (Casas et al. 1997a).

Where artificial selection has been significant, both management *in situ* and cultivation of *S. stellatus* may change morphology from that in wild populations, especially for those characters that are targets of human selection (Casas et al. 1997a, 1999a). Morphology was therefore compared among individuals from populations under different management regimes. Populations were sampled

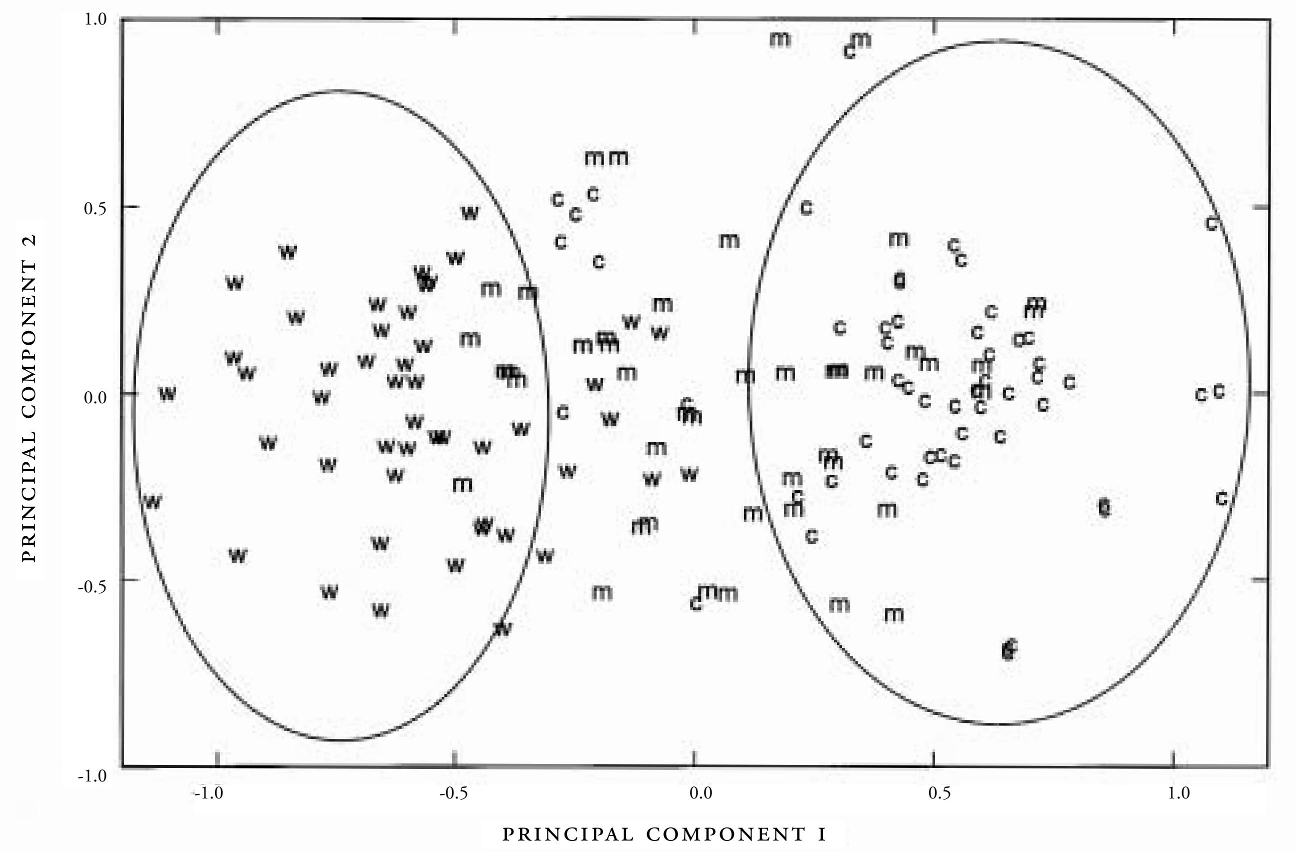

Figure 9.3. Principal component analysis of morphological variation for *Stenocereus stellatus* in the Tehuacán Valley, Puebla (w = wild; m = managed *in situ;* c = cultivated individuals; modified from Casas et al. 1999a). Characters analyzed include numbers and dimensions of fruits (and their parts), seeds, spines, and branches.

from the Tehuacán Valley (Fig. 9.3) and La Mixteca Baja to examine to what extent morphological variation in populations can be related to environmental factors.

Principal component analysis indicates morphological similarities among populations according to their management regime. Most wild individuals in the Tehuacán Valley occupy the left side of the figure, most cultivated ones are on the right side, and those from managed *in situ* populations predominate in the middle (Fig. 9.3). The most significant characters are fruit size, amount of pulp, and seed weight (positive values) and density of spines and skin thickness on fruits (negative values). Cultivated individuals have the largest and least spiny fruits, the thinnest peel, and the heaviest seeds. The number and dimensions of vegetative parts, fruits, and seeds are higher in La Mixteca, whereas the density of spines on the fruits is higher in the Tehuacán Valley. More intensive management leads to larger fruits with a higher proportion of pulp, more and heavier seeds, fewer spines per unit stem area, thinner fruit skin, and a higher proportion of individuals that produce fruits with a green skin and sweet pulp with a color other than red.

Thus, human management has influenced morphological divergence of both managed *in situ* and cultivated populations from wild populations of various species, so domestication may be caused not only by cultivation but also by management of wild populations (Casas et al. 1997a). Although the phenotypes of managed *in situ* and cultivated populations originate from wild populations, some cultivated phenotypes are rare or have not been observed in the wild. This is especially the case for individuals with large fruits and pulp colors other than red. Only 2.3% of the individuals sampled in wild populations have pink or yellow pulp, and other pulp colors (purple, orange, and white) are not observed in the wild (Casas et al. 1999b). On the other hand, 42% of individuals sampled in cultivated populations at La Mixteca have these phenotypes. Success of such phenotypes is low in the wild, and only under human protection (i.e., domestication of *S. stellatus*) are individuals with favorable characteristics that are scarce or absent in the wild protected and enhanced.

Variation in *S. stellatus* is influenced by environmental conditions, genetic differentiation, and other factors. The clearest environmental difference between the two regions is annual precipitation, higher in La Mixteca (average of 740 mm) than in the Tehuacán Valley (510 mm). In all populations, anthesis of *S. stellatus* is predominantly nocturnal, and bats are the most probable pollinators (Casas et al. 1999c). With bats as pollinators, movement of pollen between populations is expected, as bats can commute 30 km from their roosts (Sahley et al. 1993). Isolation by distance within regions is therefore unlikely between wild, managed *in situ,* and cultivated populations, because distances separating these populations are generally less than 10 km. In addition, flowering in wild and cultivated populations overlap by at least 75 days, indicating that temporal barriers for pollination between populations are also unlikely.

Stenocereus stellatus is out-crossing, and major differences exist between wild and cultivated populations. However, experimental crosses indicate pollen incompatibility between certain cultivated phenotypes, especially those with the greatest domestication. This can partly explain the morphological and genetic divergence among wild, managed, and cultivated populations. Nevertheless, the absence in wild populations of the phenotypes typical of home gardens may also be explained by failures in seed germination or in the establishment of these variants under wild conditions. Similar to results with *S. stellatus,* Luna (1999) analyzed the morphology of wild, managed *in situ,* and cultivated trees of *S. pruinosus,* finding significant differences in fruit mean weight: wild, 38 g; managed *in situ,* 70 g; and cultivated, 188 g. Seeds are larger and more numerous in cultivated variants. For *S. queretaroensis,* weights of fruit from wild trees (60–90 g) are higher than those from cultivated trees (over 130 g; Pimienta-Barrios and Nobel 1994). For *S. fricii* in Michoacán, fruit weight in wild populations is extremely variable but averages 130 g, whereas fruits of the cultivated variants average 230 g (Rebollar et al. 1997).

Opuntia *Species*

Opuntia ficus-indica, O. megacantha, O. streptacantha, O. robusta var. *larreyi,* and *O. joconostle* are the most commonly cultivated opuntias (Bravo-Hollis 1978). Yet in the El Bajío region of Guanajuato, Mexico, 16 *Opuntia* species are used for their edible products: young cladodes (nopalitos) and fruits (Colunga et al. 1986). The edible products of *Opuntia* are very important in the local peasant economy, because they are particularly abundant before the harvest season of maize and sometimes the latter is scarce; their commercialization determines about 20% of the annual income of local people (Colunga 1984). Interactions include gathering, tolerance, and enhancement *in situ* in areas cleared for agriculture, and cultivation in agricultural plots and home gardens.

The different utilization and management of *Opuntia* species and particular populations is due to the recognition of specific attributes and morphological differences among species and variants (Colunga 1984). Local people recognize nearly 70 variants belonging to the 16 species, which are broadly classified as 'manso' (docile) and 'de monte' (from the mountains). The 'manso' variants include plants whose edible products are of better quality but are dependent on humans for survival. These presumably domesticated variants include 17 of *Opuntia crassa, O. ficus-indica, O. megacantha, O. robusta* var. *larreyi,* and *O. undulata.* The 'de monte' variants do not depend on humans for survival and are presumably wild or weedy variants. Within the 'de monte' variants are plants producing fruits with thick sour edible peel named *xoconoztles* (including variants of *Opuntia joconostle* and two variants of *O. lasciacantha*), others producing fruits with thin peel and sour pulp called *jocotunas* that are consumed entire as greens (including variants of *Opuntia* aff. *leucotricha* and one variant of *O. streptacantha*), and others producing fruits with thin peel and sweet pulp called *tunas.* Among the characteristics for classifying and selecting phenotypes for differential management of *Opuntia* variants are fruit flavor, color, peel thickness and hardness, form, size, and spinyness as well as cladode size.

Colunga (1984) performed multivariate statistical analyses with 9 individuals of each of 70 variants of 16 species and considered 69 morphological characters to explore patterns of morphological similarity among the variants. These analyses consistently separated the 'manso' and the 'de monte' variants. Nearly 34 'de monte' variants of the species *O. atropes, O. fuliginosa, O. hyptiacantha, O. jaliscana, O. joconostle, O. lasiacantha, O. megacantha, O. streptacantha, O. tomentosa,* and *O. velutina* are managed *in situ* and are morphologically intermediate between the 'manso' and the 'de monte' variants. Thus, artificial selection apparently causes a morphological divergence not only between the wild and domesticated variants, but also between the wild and the managed *in situ* variants. The characters with higher significance in defining these groups relate to the dimensions of fruits and cladodes, the frequency of areoles on fruits and cladodes, fruit and seed form, and seed number and weight (Colunga et al. 1986). Of the species studied by Colunga (1984), *O. megacantha*

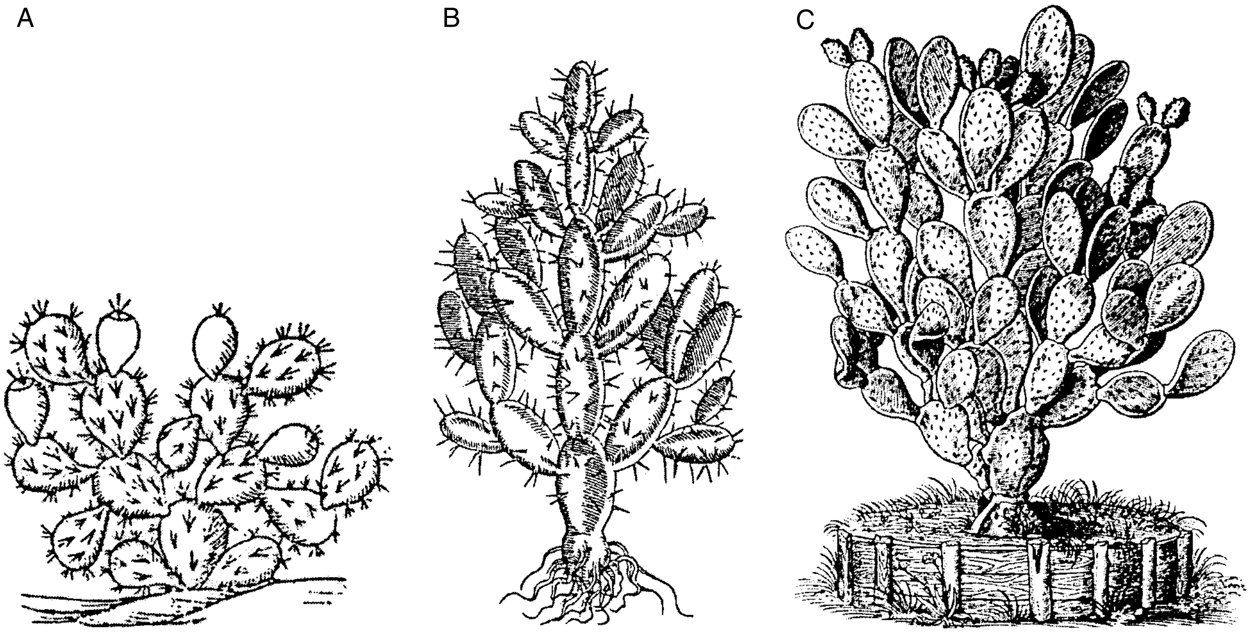

Figure 9.4. Various early depictions of opuntias: (A) the first opuntia depicted by a European illustrator (Oviedo y Valdés 1535); (B) drawing of an opuntia in Mattioli's 1558 edition of *De Materia Medica*; and (C) drawing of an opuntia in Mattioli's 1568 edition of *De Materia Medica.*

is the only taxon having wild, managed *in situ,* and domesticated/cultivated variants; based upon morphological data, the three types clearly form discrete groups according to their management (Colunga et al. 1986), as for *S. stellatus* (Fig. 9.3). Fruit, cladode, and seed dimensions are the most significant characters for this classification, and the management regime thus apparently plays a role in domestication of cacti.

Diffusion of Cacti to Other Regions of the World

Hundreds of species of cacti are presently part of plant collections in botanical gardens and some have become popular as ornamental plants worldwide. The "dragon fruit" *Hylocereus undatus* is an important crop in southeastern Asia after its introduction to the Philippines by Spaniards in the 16th century; trials are being conducted in Israel and the United States for cultivating it along with some of the fruit-producing columnar cacti (Chapter 11). But, undoubtedly, platyopuntias are the cacti most widespread out of their original range (Chapter 10), their dissemination having been initiated by humans after the conquest of the New World by Europeans. The first European to report on American platyopuntias was the Spanish state officer Oviedo y Valdés (1526), who wrote about two prickly pear cacti common on the island Hispaniola (now Haiti). In a later work (Oviedo y Valdés 1535), these plants were described in greater detail, one of them being depicted for the first time in the drawing of a European illustrator (Fig. 9.4A).

The wonder of the plants of the New World ("so beautiful and so different from ours," as Columbus wrote on his first pages about America) turned into bewilderment over the strangeness. The flora of the Old World did not include plants that were morphologically similar to platyopuntias, therefore Oviedo y Valdéz could not tell whether "this is a tree or rather a monster amidst trees," and he wrote that great painters, such as Leonardo da Vinci and Andrea Mantegna, would be necessary to describe it properly. His incredulity was shared by other European travelers, who in the subsequent 50 years talked about the plant, struck by some of its amazing features: leaves growing one upon the other into such a tree that it was impossible to find something "wilder or uglier" in the plant kingdom (Oviedo y Valdés 1526) and fruits that turned the urine red, which aroused great fear and became a prank played on newcomers. The fruits, called *tunas* by Oviedo y Valdés (1535), were commonly sold in markets; they were so delicious that his fellows "knew and ate [them] . . . with pleasure" and they were "as lovely as figs." The name given to the best-known species, *Opuntia ficus-indica,* reflects this supposed morphological resemblance and the geographical origin (the West Indies). The fruits of other opuntias mentioned by Oviedo y Valdés were mashed, dried, and used as dyestuff, while their cladodes were used in compresses to treat bone fractures, probably because of the anti-inflammatory action of mucilage (the "bone-fixing tree").

Colonial Period

When the Spanish conquistadors landed in Mexico, Oviedo y Valdés's curiosity was renewed and enhanced by the symbolic role that opuntias played in the complex Aztec cultural world. However, the interest in the commercial exploitation of the plant and especially in its fruits (offered as a present to the invaders in 1519 during Hernando Cortés's march on the Aztec capital [Diaz del Castillo 1991])did not go beyond a vague and cautious consideration, similar to that shown for many of the foods eaten by the American natives. Although Europeans liked its fruits as much or more than the local populations (Toribio de Motolinía 1541 and López de Gomara 1552, cited in Donkin 1977), the prickly pear was not introduced to Europe for food but as an ornamental plant. This was also the case for most American species that only later became staple crops and foods throughout Europe. One of the tasks of European travelers was to collect new and curious-looking plants, and prickly pears undoubtedly fell into that category.

Despite the lack of records, prickly pears are thought to have been first introduced to Europe in western Andalucía, probably in Seville. Beginning in 1495, this city had become the center of trade with the Americas through its *Casa de Contratación;* its numerous garden plants were acclimatized and studied for their medicinal properties (Valdes et al. 1992). Because of its importance to the Mesoamerican civilization, the first plant to be brought to Spain was probably *Opuntia ficus-indica.* This species, which was likely the one described by López de Gomara in 1552 (taking for granted that it was already known in Spain), seems to be represented in the first illustration of a specimen grown in Europe, published in the 1558 edition of *De Materia Medica* by the Italian physician Mattioli (Fig. 9.4B). A product of the plant, indirectly obtained by the insect that feeds on the plant, was apparently known and appreciated by the Spaniards more than the plant itself—the red dye, called *grana cochinilla* (cochineal). The conquistadors were impressed by the wonderful colors of Aztec artifacts, and probably as early as 1520—although the first record dates back only to 1543—small quantities of the dyestuff were brought to Spain. The new product met with instant success in European markets, because its dyeing power was ten times greater than kermes, the coloring matter used in the Old World and previously considered the best of red dyes. In the last quarter of the 16th century, Spain annually imported 70,000 to 90,000 kg of *grana cochinilla,* and this substance became one of the the most sought-after commodities from the American continent, preceded only by precious metals (Donkin 1977).

Spread of Platyopuntias in Europe

In the second half of the 16th century, prickly pears began to spread rapidly, first in many botanical gardens all over Europe. In the meantime, more knowledge about the plant arrived from America: Francisco Hernández from 1571 to 1576 and Sahagún in 1570 described several varieties, Cervantes de Salazar in 1554 pointed out that cladodes could easily take root, and G. Gómez de Cervantes in 1599 provided the first hints on growing techniques (Donkin 1977; Alvarez López 1946). Among European countries, Italy was particularly attracted to the new American plant—it was the Renaissance, arts and sciences were flourishing, and a deep interest in plants coming from the New World developed. Nonetheless, the prickly pear was always looked upon with suspicion. Galeotto Cei (1991) considered it so "malignant" that "however appreciated it may be in Italy, I would not wish to see or find it anywhere." A physician from Siena, Pier Andrea Mattioli, had a different attitude: he regarded the plant as "one of the wonders of nature," and his interest grew constantly in the various editions of his famous book (Mattioli 1558, 1568). No mention of prickly pears is made in the first issue of 1544 (Donkin 1977), whereas in 1558 the plant is depicted by a drawing, and two more illustrations are present in the 1568 version (Fig. 9.4C). The curious appearance of the plant, which in 1580 Soderini associated with the turkey to show the peculiarity of American nature (Tangiorgi Tomasi et al. 1990), helped it spread from botanical gardens to aristocratic estates all over Europe. In Italy, prickly pears were grown in Florence (Mattioli 1568). Dodonaeus in 1583 reported their dissemination into Germany and Holland and Gerard in 1596 into England (Alvarez López 1946).

More evidence of this popularity is provided by botanical drawings and engravings representing the plant, and by its appearance in the figurative arts. Platyopuntias are depicted in a painting by Bruegel the Elder ("Land of Plenty," 1567) as well as in some of the most beautiful botanical illustrations of the Renaissance, such as the watercolor of *Iconographia Plantarum* by Ulisse Aldovrandi (end of the 16th century; Baldini 1990) and the tables of *Hortus Eystehensis* (1600). The plant was highly rated and is considered necessary in a royal garden (Agostino del Riccio [undated but end of the 16th century], cited in Tangiorgi Tomasi et al. 1990), or thought to have occurred in Eden, as one of Switzer's 17th century xylographies shows.

History of Name

In the 17th century, prickly pears were "grown in the roof gardens of noblemen's mansions" (Bahuin 1650–1651, cited in Alvarez López 1946). Being closely linked to the botanical tradition of ancient Greece, Mattioli (1568) deemed impossible the acceptance of a new species and traced the newly discovered plants back to the flora of the classical world. In *Commentarii in sex Libros Pedacii Dioscoridis,* the prickly pear is mentioned in a chapter about the Mediterranean fig (*Ficus carica*). Two Indian figs are described: a large tree with branches that root, identified with the same plant mentioned by classical writers such as Theophrastus, Strabo, and Pliny; and another Indian fig, introduced from the West Indies "in our time," the fruits of which are called *tune* (tuna) by Indians. Mattioli believed the latter to be *Opuntia plinii,* the plant already described by the great Latin agronomist and named after Opunte, a town in Locrid (Greece), where grew a plant the leaves of which could root.

The fact that an American plant could be known to Greeks and Romans did not seem absurd to Mattioli and to many other European botanists after him. Some did raise doubts, such as the Spaniard Laguna in 1563, who "dared not affirm" that the prickly pear was Pliny's plant. Others did not seem to see the contradiction: in fact, Fragoso in 1572 and Rouvillium in 1587 believed it to be an American plant, but claimed it was already known by the ancients (Alvarez López 1946). Although Parkinson in 1619 stated with certainty that this could not be the plant described by Pliny, others persisted in believing the fallacy for a long time, essentially based on the observation that cladodes take root (Alvarez López 1946). The occurrence of the prickly pear in natural and cultural landscapes of Mediterranean Europe is so common, popular texts still say that this plant is a native species, or that it was introduced from the East Indies by the Arabs, as Gerard claimed in 1633. Considering that the various botanical names contain a semantic error, either based on the appearance of the fruits or on the geographical origin (*Cactus ficus-indica* Linnaeus, 1753; *Opuntia ficus-indica* [L.] Miller, 1768; *Cactus opuntiae,* Gussone, 1827–8; *Opuntia ficus-barbarica* Berger, 1912), one can perfectly agree with de Candolle (1883) when he said that "everything about this name is false and ridiculous!"

Naturalization in Europe

In northern Europe, platyopuntias cannot survive winter outside the privileged space of botanical gardens. In milder Mediterranean areas, the plants have found optimal environmental conditions, spreading and naturalizing so as to become one of the typical features of Mediterranean landscapes (Barbera et al. 1992). Prickly pear cacti can grow in places where the average minimal temperature does not go below 1 to 2°C, and average relative humidity does not remain lower than 40% for more than 1 month. In regions where the plants are common and commercially exploited, annual rainfall ranges from 400 to 600 mm, but they can also grow in areas with only 200 mm or up to 800 mm annually (in the latter case, the lithologic substrate must favor soil drainage). Under these conditions, platyopuntias grow independently of the lithologic matrix, even if they are typically found on volcanic soils and calcareous rocks, where they occur in scrub patches together with *Euphorbia dendroides, Artemisia arborescens, Calycotome infesta,* and other species (La Mantia et al. 2001). According to Le Houerou (1996), the major occurrence of platyopuntias in the western Mediterranean is due to a shorter and less severe dry season, which favors the natural spread of the species, in comparison with drier eastern regions. In addition to *O. ficus-indica,* other naturalized species growing on Mediterrean coasts are *O. decumana, O. dillenii, O. stricta, O. vulgaris, O. amyclaea,* and *O. robusta,* the last two of which inhabit frost-free areas only.

Dissemination of species was clearly encouraged by their widespread use in Mediterranean farming. After southern Spain, the first regions that knew and valued prickly pear were North Africa and Sicily, because of geographic contiguity or social and political relationships with the Spanish peninsula. Soon platyopuntias spread all over the Mediterranean coast and, taken aboard ship to prevent scurvy, followed European colonization and reached the remaining parts of Africa, Asia, and Australasia. In the Mediterranean, prickly pears turned out to be an inexhaustible source of products, first as a subsistence crop and later as a cash crop. The local populations immediately appreciated the new species, but neither cochineal production nor human consumption of young cladodes (nopalitos; both common in Mesoamerica) gained ground. Some attempts at cochineal culture were made, but only in the 19th century in Malta (1828), Algeria (1834), and Sicily (1860). The Spaniards, who held the monopoly of the cochineal industry, banned the export of insects until 1777, when the botanist N. J. Thierry de Menonville managed to introduce them to French dominions. Attempts at raising cochineal insects feeding on *O. ficus-indica* or *Nopalea cochenillifera* failed in the Mediterranean area, because these coccids cannot bear the combination of excessively low temperatures and frequent winter rainfall. The cochineal industry proved successful only in the Canary Islands, where it became a profitable economic activity, especially on the island of Lanzarote, and remains so since its introduction in 1826 to 1835 (Donkin 1977; Baranyovits 1978). On the other hand, the use of nopalitos for food has remained almost unknown in Europe; the only food habit that bears some resemblance to its use in Mesoamerica is found in some areas of inner Sicily, where the fruit skin is breaded and fried.

Platyopuntias in Sicily

In Sicily, *O. ficus-indica* became very popular and acquired considerable economic significance for its fruits. They became an important staple crop, but were also considered as a forage crop in extensively farmed inner regions. Platyopuntias were grown to ensure forage in times of emergency and were planted near rural buildings and animal shelters to form enclosures or dense scrub. They originally occurred as fruit plants in "pleasant gardens," as Bonanno reported in the 17th century, but their cultivation soon spread (Coppoler 1827), both in inner areas and on the coast, where they were to be found in "dry" orchards together with vines and olive, almond, carob, and pistachio trees. The fruit soon entered local markets: a platyopuntia is depicted on what seems to be a market stall in a still life by an unknown Sicilian painter who lived around 1640 and was named "maestro del ficodindia" (master of the prickly pear) because of this work (Barbera and Inglese 1993).

Platyopuntias had a leading role in the food habits of Sicilians. They were described as "the bread of the poor," and De Gasparin, a French agronomist who visited the island around 1840, said they were "the manna, the blessing of Sicily, the equivalent of the banana tree to equinoctial countries or the breadfruit tree to the Pacific Islands" (Biuso Varvaro 1895). The fruits can be eaten fresh, or are sun-dried and stored for the winter, following a peasant tradition. The juice, concentrated through boiling and seasoned with flour and spices, is used in recipes for special cakes called 'mostaccioli,' or for chutneys. The fruits were also used for ethanol production; in 1865 a plant in Catania obtained 2,500 liters per day and around 1940, in search of energy sources to ensure economic self-sufficiency to the country, this opportunity was again considered, and platyopuntias were extolled. Among other Sicilian rural traditions linked to this cactus are the production of a red dye obtained from the fruits of *O. dillenii* and the use of a decoction of dried flowers for diuretic purposes, a natural remedy that is still widely used and justified by the presence of a glucosidic flavonoid (isoramnethin) and a high potassium content. In Spain, the flowers were used to treat seizures in children in the 18th century. Convex cladodes served as plates in picnics, or as containers for the manna extruding from the tapped trunk of *Fraxinus angustifolia.* Sicilian farmers also use prickly pears for soil conservation, as mulch, and as windbreak hedges (Barbera 1994).

Fresh fruit production became the most important commercial exploitation, particularly beginning in the 19th century. In coastal areas, especially near the main towns, production flourished for local and export markets (Genoa, Marseille, London, and, from the 1850s, New York). Commercial success was favored by a cultivation technique called *scozzolatura,* whereby in autumn fruits of better quality and preservability than summer produce were obtained and put on the market when competition was less. The origins of this technique reflect the culture of the archaic Sicilian rural world. The agronomic chronicle by Alfonso Spagna (1884) gives an account of a quarrel breaking out, in a town not far from Palermo, between a farmer, who did not want to sell his product, and a merchant, who took his revenge by knocking down the fruits in full bloom. In Ventimiglia Sicula (famous for its delicious fruits that were sold in Palermo), a dispute arose between a son, who in May 1819 performed thinning to have bigger fruits, and a father who, ignoring the beneficial effect of this technique, removed all the fruits from the plant. In both cases and against all expectations, the plants blossomed again, and the late-ripening fruits were of higher quality.

Expansion to Other Mediterranean Regions

In Sicily, spineless forms were widely used for forage in the 1920s, when they were replaced—albeit keeping a minor role—by other crops that were thought to be more suitable for the climatic conditions of the region. From 1920 to 1930, the plant enjoyed great success in drier North African areas, being widely grown both in specialized farms as a forage crop and in extensive areas for erosion control, land reclamation, and rehabilitation. Platyopuntias were so important that Monjauze and Le Houerou (1965) regarded their dissemination as the "pre-arboricultural stage of farming," and described them as the plants that made possible the shift from nomadism to agriculture. Today in North Africa, especially in southern Tunisia, the vigorous action taken by programs against desertification, soil erosion, and dune movement, combined with the production of fodder for livestock, envisages the use of platyopuntias together with *Acacia* and *Atriplex* species (Chapter 12). To encourage forage production, much research was carried out in Tunisia and Algeria on cold-hardy species and clones of *O. ficus-indica,* many of which were brought from Mexico to be grown in arid highlands (Le Houérou 1996).

Platyopuntias are now common in arid regions that are subject to water and wind erosion. They prove effective in preventing soil loss, accumulating wind borne deposits, and reducing land degradation. They are also used to slow and direct sand movement, enhance the restoration of vegetative cover, stabilize the soil, and prevent water from destroying land terraces built to reduce runoff. The popularity of platyopuntias in North Africa is demonstrated by extensive cultivation areas begun in the 1950s, ranging from 700,000 to 1,000,000 hectares in Tunisia, Algeria, and Morocco (Nefzaoui and Ben Salem 2000).

Platyopuntias currently play a minor role in other Mediterranean countries. In Spain, Greece, and Turkey, they frequently occur in home orchards or vegetable gardens for human and animal consumption (fruits are particularly appreciated by pigs), but it is not common for commercial exploitation. They are also popular in Israel, where in the Negev Desert specialized farms covering hundreds of hectares can obtain two crops per year. The fruit of platyopuntias is called *sabra* in Israel, the same term used for people native to the country (because their character is like the fruit, spiny outside but sweet inside). Further indicating the exotic origin of the species are other popular names: e.g., the Arabs call it "Christian fig" and the French "Barbary fig" (from the ancient name of North Africa).

Conclusions and Future Prospects

Although a broad spectrum of cacti could have been crucial for sustenance of Mesoamerican people for a long time, only a few species have been recorded in archaeological excavations, and uncertainty exists about forms of utilization and management. The conjunction of archaeological and botanical research may clarify these aspects. In particular, Mesoamerican people currently utilize and manage many species of cacti. People presently decide how to manipulate cacti according to the quality of their products and their roles in human subsistence. The species and varieties cultivated or managed *in situ* are generally those with the most useful fruit characteristics. As found for *Stenocereus stellatus* (Casas et al. 1997a), cultivation is particularly intensive where the commercialization of fruits or their consumption by households leads to more and/or better fruits. Availability of plant resources is another crucial factor influencing their management; e.g., *S. stellatus* is intensively cultivated in places where wild populations are scarce, but not where they are abundant. Although species such as *Mitrocereus fulviceps, Neobuxbaumia tetetzo, N. mezcalaensis,* and *Pachycereus weberi* produce good quality fruits, and species of barrel cacti produce economically important stems (Table 9.2), they are not cultivated *ex situ,* because their slow growth makes the effort of sowing seeds and taking care of seedlings unrewarding for decades. Slow growth may not be relevant for decisions on managing wild populations of such species *in situ.* However, artificial selection favoring particular phenotypes *in situ* may reflect difficulties in increasing the frequency of desirable phenotypes by intentional direct propagation. Furthermore, when the seeds of desirable phenotypes are sown, the additive genetic variance of desirable traits can make it uncertain that the phenotypes selected are those expressed in the progeny. In contrast, the fixation of desirable characters in species with vegetative propagation, such as *S. pruinosus, S. queretaroensis,* or *S. stellatus* and *Opuntia* species, is relatively easy.

Artificial selection is carried out by identifying and subsequently increasing by vegetative propagation individuals that have desired phenotypes from wild, managed *in situ,* or cultivated populations. Artificial selection is also applied when plants of desired forms are preferentially spared or protected when land is cleared, or when seedlings are spared in cultivated populations until their fruits can be evaluated. Artificial selection has achieved significant results for species such as *Stenocereus fricii, S. griseus, S. pruinosus, S. queretaroensis,* and *S. stellatus* (Pimienta-Barrios and Nobel 1994; Casas et al. 1997a, 1999a, b; Rebollar et al. 1997), as well as for *Opuntia crassa, O. ficus-indica, O. megacantha, O. robusta* var. *larreyi, O. undulata,* and probably *O. joconostle* (Colunga 1984; Bravo-Hollis 1978). Artificial selection can also be significant for *Escontria chiotilla, Myrtillocactus geometrizans, M. schenckii, Pachycereus hollianus, P. marginatus, Polaskia chichipe,* and *P. chende* (Casas et al. 1999a) and variants of *Opuntia atropes, O. fuliginosa, O. hyptiacantha, O. jaliscana, O. joconostle, O. lasiacantha, O. megacantha, O. tomentosa, O. streptacantha,* and *O. velutina* (Colunga, 1984), which are intensely cultivated and/or managed *in situ* and which exhibit morphological variation in characters that are targets of human preference. The developing case studies of *Opuntia* and *Stenocereus* species provide a model of *in situ* and *ex situ* artificial selection that can help analyze patterns of domestication and can lead to hypotheses for testing in future research.

Ornamental cacti, *Hylocereus undatus,* columnar cacti, and *Opuntia* species are the main groups of the family Cactaceae diffused by humans in a process lasting about 500 years. Apart from *Opuntia,* particular forms of utilization and selection of these cacti should be documented in their new environments and under new human cultural conditions. The consequences of artificial selection in the evolution of these species needs to be evaluated. Particularly interesting will be a comparison in morphological and genetic changes developed during these 500 years in the context of human cultures and environments of the New and Old Worlds.

In any case, platyopuntias have become an integral part of the Mediterranean landscape and agricultural economy. To further develop its cultivation requires higher-quality and glochid-free fruits. Today, consumption is mostly confined to immigrants of rural origin, who are already familiar with the fruit in their homelands. In countries such as Belgium, France, Germany, and Great Britain, demand comes mainly from migrant workers from Italy and Africa. The market would expand considerably by attracting a different category of consumers—people curious about unusual and exotic products. The extension of the marketing period and the integration with produce from the southern hemisphere would increase consumption in the Mediterranean countries and ensure constant presence on the market. As for its use as a forage crop, the cloning of cold-hardy and salt-resistant varieties, or varieties with a higher protein content, as well as the introduction of this species in balanced diets, can increase consumption in arid and semiarid regions. The role played by platyopuntias in the economy and the environment, considering also the scenario of global climatic change and increasing desertification, should become increasingly important (Barbera 1995).

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