THE OPUNTIAS OF MISSISSIPPI

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Abstract: Literature on distributions, habitat characteristics, and identification of *Opuntia* species in the southeastern US is scant. Regional treatments of *Opuntia* are often ambiguous, limited studies based primarily on herbarium specimens. The present work provides a detailed description of the opuntias found in Mississippi along with their distributions and habitat descriptions. Observations, collections, and measurements were made from natural populations within Mississippi and other parts of the southeastern United States. Plants of all taxa were greenhouse grown for approximately two years to monitor morphological characteristics, which sometimes can be quite plastic. Our two-year study encompassed nearly 150 natural populations among several eastern states. Five species are recognized. Of these, *Opuntia cespitosa, O. humifusa,* and *O. pusilla* are the most common in Mississippi. *O. aff allairei* and *O. stricta* are found infrequently.

Introduction

The *Opuntia* species occurring in Mississippi and the eastern United States are a complex group. The taxonomy of the species has never been resolved fully, because they exhibit extreme morphological plasticity, they are poorly studied ecologically, they potentially intergrade to form hybrid taxa that express characters intermediate between well defined taxa, and they possess numerous critical morphological characters that are difficult to preserve in herbarium vouchers. This treatment deals with the ecology, morphological variation, and taxonomy of the group for Mississippi. As the flora for Mississippi remains incomplete, this also provides a preliminary treatment and account of the diversity and distribution of Cactaceae for the state.

Opuntia species (Cactaceae: Opuntioideae; Stevens 2001–2008) are biologically complex xerophytes. The genus is native to the Americas, and species can be found from Canada to the southernmost reaches of South America (Powell and Weedin 2004). The highest diversity is found in Mexico, where *Opuntia* species flourish in arid habitats because of their numerous xerophytic adaptations (DeFelice 2004), including thick, waxy cuticles that reduce the amount of water lost through transpiration; modified leaves and bud scales in the form of spines and glochids (Mauseth 2006), which decrease plant surface area and transpiration rates and affect thermoregulation (Lewis and Nobel 1977, Nobel 1978, 1983); rapid root growth and shallow root systems that maximize water uptake when long periods of drought are broken by rain; Crassulacean Acid Metabolism (CAM), which helps conserve water through the closing of stomata during hot daylight hours and utilizing CO_2 stored overnight for photosynthesis; and cells rich in polysaccharides, which readily bind water molecules, thus reducing desiccation if the plant is injured (Benson 1982; Rebman and Pinkava 2001).

The platyopuntias, or genera of opuntioid cacti with flat stems (cladodes, cladophylls, or pads), are commonly known as nopales or prickly pear cacti (Benson 1982; Wallace and Fairbrothers 1987; Hanselka and Paschal 1991; Mohamed-Yasseen 1996; Rebman and Pinkava 2001; DeFelice 2004). They can be prostrate to erect and even form small trees. Generally, they produce an abundance of many-seeded fruits, but also they are easily propagated from stem fragments. Many species easily disarticulate at the nodes, and thus form large clonal colonies by vegetative reproduction (Benson 1982; Rebman and Pinkava 2001).

Opuntia species are host to a variety of insect and mite species (Mann 1969) and are utilized by many animal species, including hu-

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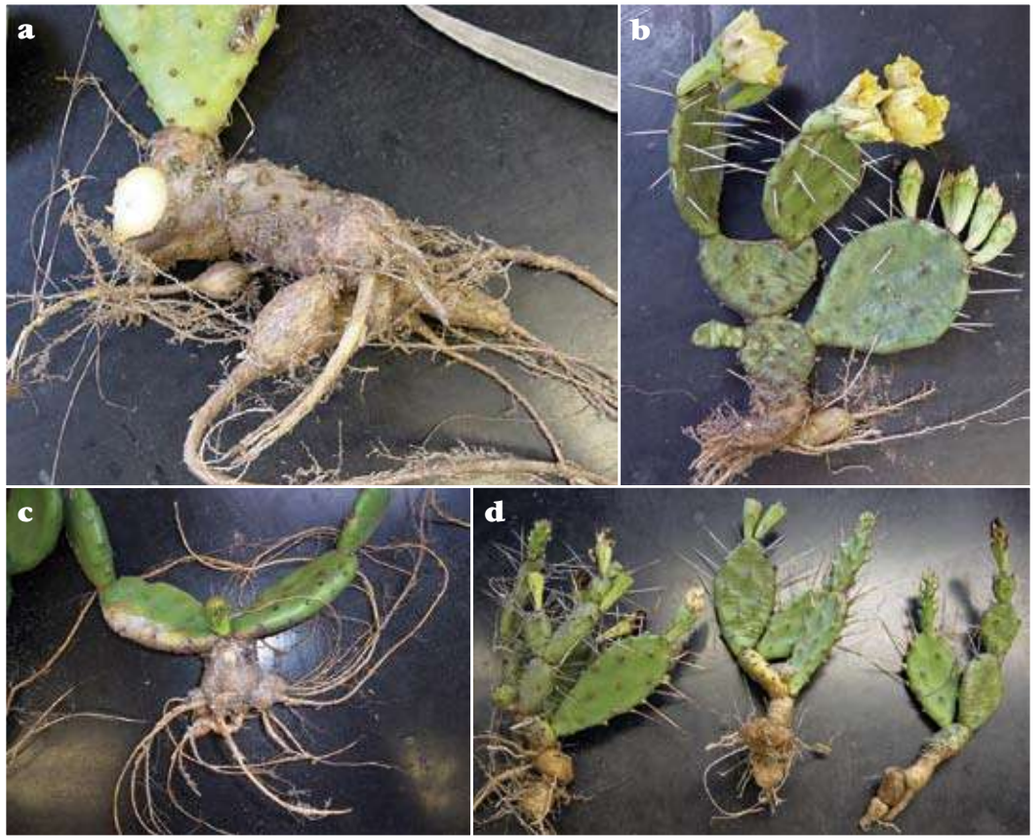


Figure 1. Tuberous roots of **(a)** *O.* aff *allairei,* **(b)** *O. cespitosa*, **(c)** *O. humifusa*, and **(d)** *O. pusilla*.

mans (Kalmbacher 1975; Benson 1982; Hanselka and Paschal 1991; Mohamed-Yasseen and others 1996; Melink and Riojas-Lopez 2001; Perez-Sandi 2001; DeFelice 2004). In most of their range, prickly pears are used as fodder for livestock (Hanselka and Paschal 1991; Mohamed-Yasseen 1996; Nefzaoui and Salem 2001; DeFelice 2004), and they are often grown for human consumption. Young pads are collected and made into a variety of consumable products. The fruit can be made into beverages, syrup, and a cheese-like product, or they can be consumed raw (Benson 1982; Mohamed-Yasseen 1996; Pimienta-Barrios 1997). The seeds were used by early California natives to produce a seed meal (Benson 1982; Mohamed-Yasseen 1996). Opuntias also are used ornamentally and medicinally, and they are commercially grown as host the cochineal insect (*Dactylopius coccus* Costa), an important source of natural red dye (Benson 1982; Pimienta-Barrios 1997; Vigueras and Portillo 1997; DeFelice 2004).

Opuntias are widely distributed in the southeastern US, where some species are planted for ornamental purposes. Many ornamental species are imported from the southwestern United States, such as *Opuntia engelmannii* Salm-Dyck ex Engelm., or other areas in the Americas (for instance, *O. ficus-indica* (L.) P. Mill.). The natural dispersal mechanisms of *Opuntia* is not well known, although Barlow (2001) suggested that extinction and population reductions of vertebrates have affected active dispersal. Bison, for example, are thought to have been major dispersers of *O. fragilis*, which has an extensive geographical range in the western United States (Mitich 1970). Jansen (1986) suggested that ancient megafauna consumed *Opuntia* fruit, and therefore would have been important dispersal agents. A great number of extant animals, such as deer, rabbits, coyotes, birds, and numerous reptiles, feed on *Opuntia* fruit and contribute to the dispersal of sexually produced propagules (Timmons 1941; Dean and Milton 2000; Melink and Riojas-López 2001). In addition, *Opuntia* species can probably be dispersed through hurricanes and other natural meteorological events (Majure and others 2007). Cladodes could be transported by water to shell middens, barrier islands, and shorelines, where they then would root and develop into new plants. Frego and Staniforth (1985) suggested that *O. fragilis* also could be transported along riparian systems by water.

Taxonomy of eastern US opuntias

The current status of the taxonomy of eastern *Opuntia* taxa is a work in progress. Roughly 190 years after *Cactus humifusus* was described by CS Rafinesque (1820), confusion remains about what species exist in the eastern United States. Questions of hybridization, specific status, varietal level status, and numerous morphological and physiological attributes remain unresolved. Pinkava (2003) recognizes five species of *Opuntia* in the eastern United States: *O. cubensis* Britton and Rose, *O. humifusa* (Raf.) Raf. (including varieties *humifusa* and *ammophila* Small), *O. pusilla* (Haw.) Haw., *O. stricta* (Haw.) Haw., and *O. triacantha* (Willdenow) Sweet. However, according to the PLANTS Database, based on taxonomic information from John Kartesz (Biota of North America Program; USDA, NRCS 2007), there are nine taxa: *O. ammophila* Small, *O. austrina* Small, *O.* ×*cubensis*, *O. dillenii* (Ker Gawler) Haw., *O. humifusa*, *O. macrorhiza* Engelm., *O. pusilla*, *O. stricta*, and *O. triacantha*. Kartesz included certain taxa at the specific level, for instance, *O. austrina* and *O. dillenii*, apparently based on a 1990 dissertation by JD Doyle (J Kartesz personal communication), which in no way conclusively segregates these taxa as separate species or even varieties (Doyle 1990).

Benson (1982) cited localities for populations of *O. austrina* (*O. humifusa* var *austrina* (Small) L. Benson) and *O. humifusa* var *hum-*

Key to the opuntias of Mississippi

1 Plants forming shrubs to sub-shrubs; stems ascending or erect, 0.5 to 1 m or more tall; inner tepals yellow; spines yellow or brownish, flattened, slightly curved; plants restricted to coastal areas or occasionally planted as ornamentals… ***O. stricta*** **(V)**

1 Plants forming clumps or mats; stems ascending, decumbent or trailing; 0.1 to 0.5 m tall; inner tepals yellow or yellow with red bases; spines white, brown, or gray, terete, straight, sometimes twisted longitudinally; plants inland or coastal. **2**

2 Cladodes small; 1–4 (–11) cm long, 0.7–2.2 (–5.1) cm wide, 3–9 (–16) mm thick; subcylindrical or laterally compressed (flat); easily disarticulating at the nodes; spines usually strongly retrorsely barbed to the touch, especially on terminal cladodes; 0–4 spines per areole…… ***O. pusilla*** **(III)**

2 Cladodes larger; 3.1–13.6 (32.5) cm long, 2.0–8.0 (–11.3) cm wide, 4–15 (–19) mm thick; laterally compressed (flat), not subcylindrical; not easily disarticulating at the nodes; spines not strongly retrosely barbed (except in younger spines of *O. humifusa*); 0–2 (–3) spines per areole…… **3**

3 Stems strongly ascending (during growing season); cladodes strongly tuberculate, usually elliptical in outline; spines normally absent, if present, one per areole, short, 15–18 mm long; not retrorsely barbed to the touch; inner tepals yellow with red bases …… ***O.*** **aff** ***allairei*** **(IV)**

3 Stems moderately ascending (during growing season), more often decumbent or trailing; cladodes ± tuberculate, elliptical or circular in outline; spines generally present on some plants, 0–2 (–3) per areole, long 20–71 mm long; spines sometimes retrorsely barbed to the touch; inner tepals wholly yellow, or yellow with red bases…… **4**

4 Cladodes dark green to bluish-green, slightly glaucous; mostly circular in outline, elliptical or obovate; generally slightly tuberculate; inner tepals yellow with dark red to red-orange bases; glochids crimson, reddish-brown, dark or light brown in age; spines 0–2(–3) per areole; when young with dark, castaneous bases; bony white or gray in age; not retrorsely barbed to the touch…… ***O. cespitosa*** **(II)**

4 Cladodes yellow-green, lime-green to dark green, not glaucous; mostly elliptical in outline, circular or obovate; ± tuberculate; inner tepals wholly yellow; glochids pale yellow to tan or light brown (sometimes nearly translucent); spines 0–2 per areole; when young with light brown or yellowish bases, white or gray in age; often retrorsely barbed to the touch…… ***O. humifusa*** **(I)**

ifusa from the Mississippi Gulf Coast. Based on observations of numerous populations of *Opuntia* within that region, and in line with Pinkava (2003), little distinction appears to exist between *O. humifusa* var *humifusa* and *O. austrina* in Mississippi, thus both are considered within *O. humifusa* in the present treatment. There is a great deal of morphological heterogeneity within populations, appearing to correlate with environmental heterogeneity (for instance, light vs. shade, soil composition). When working primarily from herbarium specimens, this type of environmentally induced morphological variation could easily be overlooked, resulting in taxonomic splitting of species. It is likely that *O. austrina* may exist as a distinct species in Florida, where it was described (Small 1903), but this remains to be verified.

The other two species previously recognized as native to Mississippi, *O. stricta* and *O. pusilla*, present fewer taxonomic difficulties outside of potential hybridization. Both are found in the eastern United States in coastal states from North Carolina to Texas (although the occurrence of *O. pusilla* in Louisiana has not been confirmed), particularly in coastal areas of those states. Most extant collections of these species are from barrier islands and sites directly adjacent to the Gulf and Atlantic coasts (Benson 1982; Pinkava 2003). As indicated here, two other taxa have been overlooked in botanical surveys of Mississippi and adjacent states: *O. cespitosa* Raf. and a species most accurately matching the description by Griffiths (1909) of *O. allairei* Griffiths.

Mississippi opuntias

The five native or naturalized species of *Opuntia* within Mississippi are *O. cespitosa* Raf., *O. humifusa* (Raf.) Raf., *O.* aff *allairei* Griffiths, *O. pusilla* (Haw.) Haw., and *O. stricta* (Haw.) Haw. A putative hybrid also occurs within Mississippi but will not be treated here, as more information will be needed to determine the taxonomic level at which this entity should be recognized. The five main taxa are treated below. Cladode characteristics used here are typical of live material. Herbarium specimens are much more difficult to determine, as cladode characteristics and flower color generally are poorly preserved and frequently not noted. We prefer to use live material for identifications, and when possible, specimens that are in flower. Flower color and general characteristics of the plants and the population should be noted, as single plants within a population might not have the typical characteristics of the species. Sterile specimens often can be misleading and result in misidentification, especially with herbarium specimens. Glochid color generally changes with the age of the plant or in those most heavily subjected to environmental stresses. True glochid color can sometimes be seen by extracting the inner glochids from the areoles. It is best to use younger cladodes when determining glochid colors.

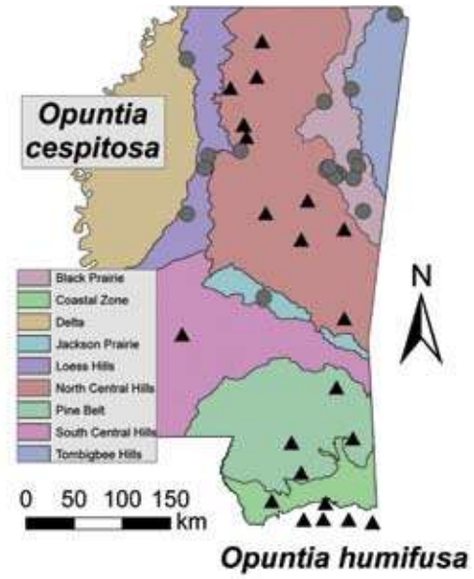


Figure 2. Distribution of *Opuntia humifusa* (black triangles) and *Opuntia cespitosa* (gray circles) in Mississippi.

Another morphological trait that has historically been used in species determinations is the presence or absence of tuberous root thickenings. Of the *Opuntia* species that occur in Mississippi, *O.* aff *allairei*, *O. cespitosa*, *O. humifusa*, and *O. pusilla* have been observed with thickened, tuberous roots (Fig 1). This characteristic has been used by many authors to distinguish *O. macrorhiza* (Engelmann 1850, 1856; Benson 1944, 1969, 1982; Gleason 1952; Lundell 1969) and *O. pollardii* Britton & Rose (syn. *O. humifusa* var *austrina* or *O. humifusa* var *humifusa*; Small 1903, 1913) from other species, such as *O. humifusa* and *O. pusilla*. However, tuberous roots are often found on plants growing in well-drained substrates, independent of the species (Weniger 1970; Doyle 1990; Powell and Weedin 2004; DJ Pinkava pers. comm.). Environmental factors are most likely the primary cause of this phenomenon, but this needs to be tested further.

All voucher specimens made during this study are housed in the Mississippi State University Herbarium (MISSA). Specimens were collected from nearly all locations given for the distribution of the taxa represented here, which includes over 100 specimens (including the putative hybrid taxon) from Mississippi. The distributions of *Opuntia* species given in this work are based partly on herbarium records, of which very few existed before this project. All herbarium records were revouchered when possible to verify the continued existence of an *Opuntia* species at a certain location. New localities were discovered through the use of soil maps, herbarium records of associate vegetation, and by word of mouth.

The following is a treatment of the known *Opuntia* taxa in Mississippi based on a thorough review and reconciliation of extant taxonomic works on the genus in North America. Measurements represented in the dichotomous

Figures 3a, b. *O. humifusa*: typical, trailing, and decumbent growth form, Grenada Co., MS and Horn Island, Jackson Co., MS. Photos: LC Majure and GN Ervin. **Figures 4.** *O. humifusa* with **(a)** and without **(b)** spines, Horn Island, Jackson Co., MS and DeSoto National Forest, Forrest Co., MS. **Figure 5.** Glochids of *O. humifusa,* Grenada Co., MS. **Figure 6.** Flower of *O. humifusa.*

key, as well as other characters, are based on live material from natural populations.

I. *Opuntia humifusa* (Raf.) Raf., *Med Fl US*. 2: 247. 1830.

Cactus humifusus Raf. 1820.
Opuntia pollardi Britton & Rose 1908.

Opuntia humifusa is the most widespread species in Mississippi, occurring naturally in four of nine physiographic regions; the north Central Hills, the south Central Hills, the Pine Belt, and the Coastal Zone (Fig 2), where it is sympatric with *O. pusilla* and *O. stricta*. This *Opuntia* species has many different morphological forms and, therefore, has been given many different names over many years (for instance, Britton & Rose 1919).

Two varieties have been recognized for Mississippi: *O. humifusa* var *humifusa* and *O. humifusa* var *austrina*. In this treatment, only *O. humifusa* is recognized. The variety *austrina* is supposed to be much larger, more erect, and have longer spines than the more common variety *humifusa*. Also, variety *austrina* is referred to as the variety occurring along coastal areas in deep sands of sand dunes and barrier islands (Benson 1982; Weakley 2003). This delineation is ambiguous, however, as other plants found farther inland share most of the same features as coastal populations. The degree of spine coverage, spine length and diameter, and pad turgidity are probably more a function of environmental variables acting on phenotype rather than genetic dissimilarity. Morphological variation also seems to coincide with latitude (Doyle 1990; Majure pers. obs.). However, because inland populations are typically highly disjunct, a degree of interpopulational genetic dissimilarity might be expected to result from a variety of biological mechanisms.

Opuntia humifusa is found on sandy substrates in pine forests, on barrier islands, low areas behind primary or secondary sand dunes, and scrub oak forests. Unlike inland populations of *O. pusilla*, inland localities for *O. humifusa* are generally removed somewhat from riparian systems. *O. humifusa* is associated with a variety of grasses, sedges, forbs, and woody vegetation common to sandhill communities. In southern Mississippi it commonly is found associated with *Gopherus polyphemus* Daudin (the endangered gopher tortoise), which is known to feed on the plants.

Morphological characteristics

Opuntia humifusa is generally a low, decumbent, trailing plant (Fig 3), but links of cladodes can reach heights of 30–40 cm and be more ascending in certain situations during the growing season, when the cladodes are turgid. It forms relatively small (< 4 m^2) to large populations (> 5 hectares) depending on the quality and quantity of suitable habitat.

Cladodes are generally yellow-green to dark green and become cross-wrinkled in the winter or under water stress. Cladode sizes are highly variable depending on microclimate, ranging from 3.1–8.5 (–17.7) cm long, to 2.0–5.2 (–9.0) cm wide, and 4–10 (–19) mm thick. They can be obovate, ovate, orbicular, or elliptical in shape. Cladodes, even from the same plant, can exhibit greatly divergent morphology.

Spines are yellowish or cream and mottled with reds and light browns generally in rings near the base of the spine when immature; they then turn a pale to bright white color with yellowish tips. Aging spines turn light or dark gray and have yellowish, brownish, or black tips. They range in length from 5–71 mm, and grow 0.7–1.3 mm in diameter at the base and are strongly retrorsely barbed when immature, with barbs wearing in age. *O. humifusa* has up to two spines per areole, but is often spineless (Fig 4). There is an outer chalky layer that covers the spines. In cases where this is rubbed off (for instance, after a hurricane), the spines appear light cream, light yellow, or even translucent. Spines can be erect, spreading, or slightly deflexed depending on the age of the cladode from which it is produced or the areole from which it is produced. For example, spines can become deflexed and appressed to a cladode if another cladode or flower is produced from the same areole, effectively limiting available space. Generally spines are erect or spreading and are produced from the uppermost portion of the cladode (upper ⅓ of the cladode, apex, margins) or the portion of the cladode that receives the most sunlight. Spineless plants can be produced easily by growing plants in shaded conditions where temperatures are decreased compared to a full-light scenario. Environmental conditions effect glochid lengths in the same manner.

Glochids are light yellow, tan, or more commonly translucent (Fig 5). Glochids darken in age from exposure to ambient effects (for instance, sunlight). Plants grown in a greenhouse were seen to have a terrestrial algae covering the glochids, turning them almost black. This also has been seen in natural populations. This could inevitably lead to misinterpretations of glochid color. Glochids form a compact fascicle within the areole, which typically are borne in a spiral arrangement, except in marginal areoles, where they often form a pin-cushion arrangement. Glochids range in length up to 6 mm, but variable glochid lengths can be seen in the same areole, where a shorter outer ring of glochids normally gives way to longer inner glochids. There can be up to three varying lengths of glochids within the areole.

Flowers and fruit The inner tepals in this species are completely yellow. Outer tepals are green with light colored margins. The style and stigma are white. Filaments of the stamens are yellowish or creamy colored. The anthers are yellow (Fig 6). The fruit of this species are pinkish, purplish (Fig 3), reddish, and can even be yellowish at maturity.

II. *Opuntia cespitosa* Raf., *Bulletin Botanique*. 2: 215-216. 1830.

Opuntia rafinesquii Engelm. 1856.

Opuntia cespitosa occurs in Mississippi mainly in the Black Prairie Physiographic Region, but plants have also been found in the Tombigbee Hills, north Central Hills, Jackson Prairie, and the Loess Hills (Fig 2).

In the Black Prairie it is found most commonly in acidic soils overlying chalk outcrops of the Pontotoc Ridge, where *Juniperus virginiana* L. forms a dominant canopy cover (Fig 7). Where it is found outside of the Black Prairie, it occurs in upland mixed pine and deciduous forests in dry clayey or silty-sandy soils or in sandy prairies. In Tennessee this species is commonly found in Juniper glades and barrens growing beside or over limestone outcrops. In Arkansas it occurs in shale barrens and granitic outcrops. Specimens of this species have also been seen from the black prairie and dolomite outcrops in Alabama, as well as portions of Kentucky and Virginia. In Missouri and Illinois this plant is found in sandy prairies. There is evidence that it also occurs in New York (Kalmbacher 1975). This taxon in Mississippi tends to grow in areas that are more mesic in nature (Fig 8) than those of *O. humifusa*, *O. pusilla*, and *O. stricta*.

This species has been included as synonymous with *O. humifusa* for quite some time (Britton and Rose 1920; Small 1933; Weniger 1970, 1984; Benson 1982; Anderson 2001; Hunt 2006), and has either been ignored as being different from typical *O. humifusa* (Benson 1982) or unseen by specialists (Pinkava 2003; Pinkava pers. comm.). Interestingly, although Benson (1982) excluded this taxon from his most recent treatment, he previously considered this eastern opuntia as a possible separate variety of *O. humifusa* (var *microsperma* Engelmann, Benson 1962).

Opuntia cespitosa deviates morphologically from the original description of *Cactus humifusus* Raf. (Rafinesque 1820) in having yellow tepals that are basally tinged red, among other characteristics. This species therefore is treated as separate from *O. humifusa* with one key difference being that *O. humifusa* has wholly yellow tepals (Rafinesque 1820; Radford and others 1968; Benson 1982; Wunderlin 1998; Pinkava 2003). Anderson (2001), states that *Opuntia humifusa* has yellow flowers, yet the photo of the plant that he includes under *O. humifusa* is a plant having yellow flowers with red centers. Hunt (2006), as well as many other authors (for instance, Britton and Rose 1920; Small 1933; Weniger 1970; Snow unpubl. data), state that *O. humifusa* can have yellow flowers or flowers with red centers, effectively lumping these two entities.

Engelmann (1856) and Small (1903, 1913) made the distinction between *O. cespitosa* and *O. humifusa*, but they were using at that time the invalid name *O. vulgaris* Mill. for *O. humifusa*. In the meantime these two taxa have been put into synonymy as *O. humifusa* var *humifusa*, the common prickly pear of the eastern United States, by many authors (Britton and Rose 1920; Weniger 1970; Benson 1982; Doyle 1990; Anderson 2001; Pinkava 2003; Hunt 2006). As no Rafinesque specimen of *O. humifusa* exists, Leuenberger (1993) typified *O. humifusa* using a specimen from Pennsylvania, considering that it was the only taxon inhabiting such a broad range in the eastern United States (Benson 1982). If *O. cespitosa* was typified as *O. humifusa*, then this typification will have to be reassessed. Habitat characteristics also are easily separable between the two species (Majure and Ervin unpubl. data).

The name *Opuntia cespitosa* comes from a species described by Rafinesque (1830) for a plant from the eastern United States. Although no flower color is mentioned, he described the plant as having very long spines and red glochids. The distribution he gives for the species is much more accurate than for other taxa that might be considered for this taxon (for instance, *O. grandiflora* Engelmann). Of course more work will be necessary to determine the correct taxonomic level of this taxon, as this species is similar to *O. humifusa* and could potentially just be a variety thereof. Some cytological work (Bowden 1945) suggests that this taxon is a tetraploid,

Figures 7a, b. Examples of mesic and *Juniper* dominated habitat of *O. cespitosa*, Oktibbeha Co., MS. **Figure 8.** *O. cespitosa* growth form, Oktibbeha Co., MS. **Figure 9.** Moderately glaucous cladodes of *O. cespitosa,* Lowndes Co., MS. **Figures 10a, b.** Typical flowers of *O. cespitosa.*

while *O. humifusa* is diploid. Contemporary cytological work needs to be completed on these taxa.

Morphological characteristics

At first glance this species can be mistaken for the more common *O. humifusa*. However, it is easily separated from *O. humifusa* in having red-centered flowers, reddish glochids, and slightly glaucous cladodes. These characteristics are maintained even when this species is planted in acidic, sterile, sandy soil. This species also is decumbent, low growing, and trailing (Fig 8), although heights of 30 cm or more can occasionally be reached, especially when the plant is surrounded by supporting vegetation.

Cladodes are normally dark green to moderately glaucous (Fig 9), obovate, orbicular, or elliptical. They are consistently more orbicular than *O. humifusa*. They range in size from 3.8–10.5 (–18.7) cm long, 3.2–8.0 (–11.3) cm wide and 4–10 (–19) mm thick. Cladodes become cross wrinkled during winter or in times of stress as well, and the plant becomes more purplish during times of stress, especially around the areoles.

Spines of *O. cespitosa* are usually bony white with castaneous colored or maroon bases during development and right after maturity, characteristics strikingly similar to those of *O. macrorhiza* as described by Powell and Weedin (2004). In age they become light to dark gray. Spine tips are light yellow or cream when young but usually darken in age, to almost black in some specimens. Spine tips are never retrorsely barbed to the touch, although they do possess microscopic barbs. These can easily be seen under moderate magnification. Spines range in size from 9.5–60 mm long and 0.7–1.05 mm in diameter at the base.

Glochids This species typically has crimson, reddish-brown, or dark brown glochids, although plants with light brown glochids are found. They range in length up to 7 mm long and generate the same patterns and varying lengths as those seen in *O. humifusa*.

Flowers and Fruit The flowers of this variety are quite striking in having dark yellow inner tepals that are dark red to orange-red basally extending to roughly ½ to ⅔ the length of the tepal (Fig 10). The outer tepals are green with light colored margins. The stigma lobes are white or a light cream color. Filaments generally are reddish, orangish, or dark yellow. Anthers are yellow. Pollen of this species is slightly larger than in *O. humifusa*, and its pollen contains more germinal pores than *O. humifusa* (Majure and Ervin unpubl. data). This is another characteristic that needs to be studied in more detail. The fruit of this species are pinkish, pale red, dark red, or purplish.

III. *Opuntia pusilla* (Haw.) Haw., *Syn Pl Succ* 195. 1812.

Cactus foliosus Willdenow 1813.
Cactus pusillus Haworth 1803.
Opuntia foliosa Salm-Dyck 1828.

Opuntia pusilla is most often considered to be a coastal species, as it is found on barrier islands, coastal shorelines, sand dunes, and shell middens in the coastal states from North Carolina to Texas (Radford and others 1968; Benson 1982; Wunderlin 1998), with the exception of Louisiana (Benson 1982; Pinkava 2003). However, we have found many populations of *O. pusilla* much farther inland, generally occurring on well-drained, acidic sand deposits along river systems. In Mississippi this species is found in the Tombigbee Hills, Black Prairie, south Central Hills, north Central Hills, Jackson Prairie, Pine Belt, and the Coastal Zone physiographic regions (Fig 11).

Opuntia pusilla can be dispersed easily by animals due to easy disarticulation of the cladodes and retrorsely barbed spines, which hook into the fur, skin, or clothing. The fragments drop and root to form new plants if the environment is suitable for continued growth. Dispersal by flooding events also could play an important role in the movement of populations of this species. A morphologically similar species, *O. fragilis* (Nutt.) Haw., is presumed to be spread along riparian areas by floods (Frego and Staniforth 1985).

Opuntia pusilla is highly morphologically plastic (Majure and Ervin unpubl. data) like many other *Opuntia* species. Small (1933) recognized two species (*O. drummondii* Graham and *O. tracyi* Britton) based on cladode and fruit morphology, with one species having subcylindric cladodes and the other possessing flat cladodes. These are characteristics of cladodes that can be seen on the same plant, within and among populations, and most likely has something to do with environmental variables. However, larger forms that appear to be intermediate between *O. pusilla* and *O. humifusa* have been found and moderately conform to the description of *O. drummondii*.

Use of the name *O. pusilla* is somewhat debatable (D Pinkava pers. comm.). As Britton and Rose (1919) note, the type locality for this species is unknown. It is usually said to be from South America, but Schumann believed it to be from the West Indies. It is

Figure 11. Distribution of *O. pusilla* in Mississippi.

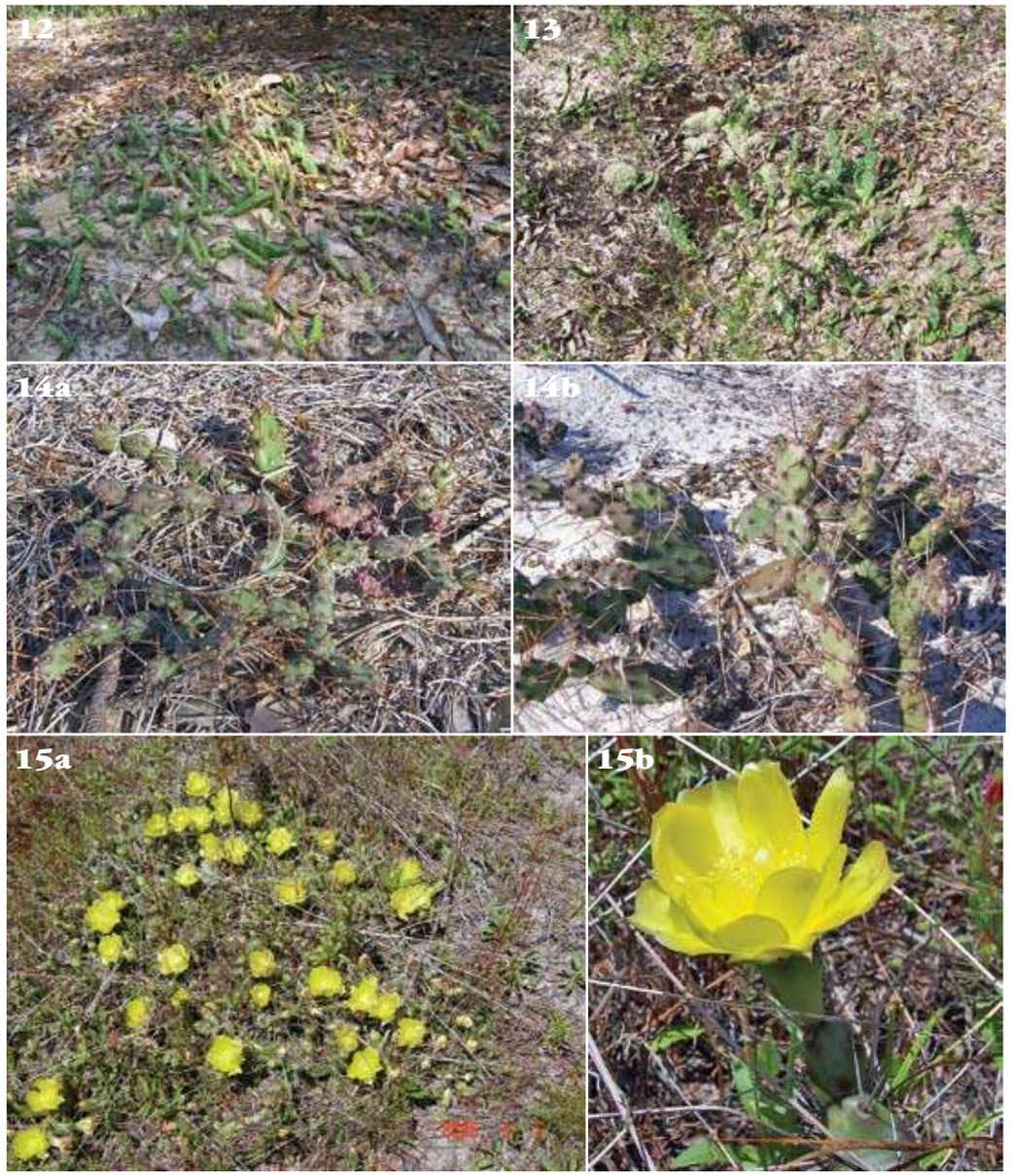


Figure 12. Etiolated pads of *O. pusilla* grown under heavy shade along the Chunky River, Lauderdale Co., MS. **Figure 13.** Pads of *O. pusilla* after the removal of dense canopy cover, along the Chunky River, Lauderdale Co., MS. **Figures 14a, b.** Growth forms of *O. pusilla* with pads **(a)** sub-cylindric or **(b)** flattened, Horn Island, Jackson Co., MS. **Figures 15a, b.** Flowers of *O. pusilla*, Deaton Preserve, Greene Co., MS.

quite possible that this name for our plants should be abandoned, and one of the species described from the southeastern US should be used in its place.

Morphological characteristics

Opuntia pusilla, as the name implies, is a small plant. It often forms small mounds or patches of cladodes from 5–15 cm tall that are easily hidden in grasses, forbs, and shrubs. Patch sizes increase as terminal cladodes disarticulate throughout the year and fall around the existing plant. These pads form new plants that maintain this cycle, steadily increasing the patch diameter. Of course, many cladodes fall back into the parent plant and increase the overall density of stems radiating from a central location, and many pads are dispersed away from the parent plant. Under prolonged periods of shading this species tends to form smaller and smaller cladodes that eventually resemble juvenile plants (Fig 12). Only when the canopy cover is removed (for instance, after a flooding event, beaver activity, etc) do the plants start to recuperate (Fig 13; Majure 2007). It is not known at what reduced light level this species starts to suffer effects from shading nor for how long etiolated plants can remain in this state. More work needs to be done to test this observation.

Cladodes range from 1.0–4.0 (–11.0) cm long, 7–22 (–51) mm wide, and 3–9 (–16) mm thick. Cladode shapes tend to be ellipsoid, obovate, or rotund in outline and are subcylindrical or commonly flat (Fig 14). The most turgid and subcylindrical cladodes are found along coastal areas, especially on the barrier islands. In winter the cladodes become transversely cross-wrinkled and turn a purplish color, especially at the areoles.

Spines on this species are strongly retrorsely barbed when immature but can lose this with age and weathering. They are 4–60 mm in length and 0.45–0.60 mm in diameter at the base. 0–4 spines can be produced from a single areole. Spine production is a function of habitat characteristics, where degrees of shading and lower temperatures tend to decrease spine production and increase cladode length and width. High amounts of sunlight and subsequently high temperatures have the opposite effect and increase cladode thickness (Majure and Ervin unpubl. data). However, in natural populations typically 2–3 spines are produced when plants are in full sun. Younger spines can be maroon, creamy-yellow, or pale white with yellow tips, while older spines tend to age bright white, then darken to gray and have darker (brownish) tips.

Glochids The glochids of *O. pusilla* are the same color as in *O. humifusa* and can be up to 6 mm long. They also form the same patterns and have the same varying lengths as those of *O. humifusa*.

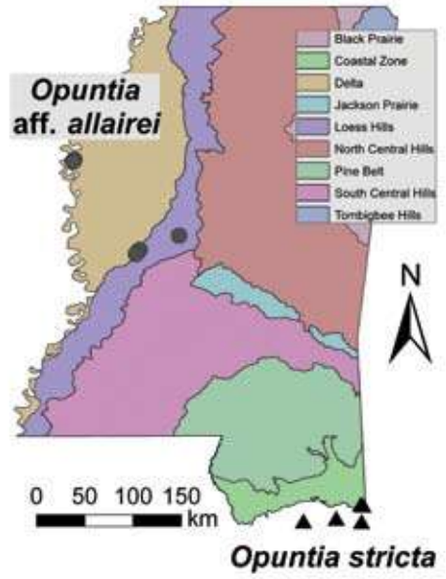
Flowers and Fruit Flowers of this species have wholly yellow inner tepals and outer tepals that are green with light colored margins. The style and stigma lobes are white. The filaments of the stamens are yellowish or cream colored and the anthers are yellow (Fig 15), as in *O. humifusa*. The fruit are pinkish to pale red, or purplish in color when mature.

Putative hybrid

Plants resembling a putative hybrid between *O. humifusa* and *O. pusilla* have frequently been found in Mississippi within the Jackson Prairie, North Central Hills, South Central Hills, and the Pine Belt physiographic regions in Mississippi. The putative hybrids are typically found farther disjunct from riparian systems than is *O. pusilla*, much like *O. humifusa*, but have overall habitat characteristics similar to both *O. humifusa* and *O. pusilla* (Majure and Ervin unpubl. data).

Other authors have also noted growth forms that appear intermediate between these two species (Benson 1944, 1982; Doyle 1990; Snow unpubl. data), but all accounts have been observational and not empirically tested. Hybridization among *Opuntia* is not uncommon (for instance, Grant and Grant 1979; Benson 1982; Rebman and Pinkava 2001; Bobich and Nobel 2001; Griffith 2004). However, until further evidence elucidates the actual relationships among these taxa, this taxon will not be treated. Molecular genetic analyses are currently underway to gain a better understanding of interrelationships among these taxa (Majure and others, unpubl. data).

Figure 16 . Distribution of *O.* aff *allairei* (gray circles) and *O. stricta* (black triangles) in Mississippi.



IV. *Opuntia* aff *allairei* Griffiths, *Rep Mo Bot Gard* 20: 81-95. 1909.

Opuntia aff *allairei* has been found in the floodplain of the Mississippi River in the Delta physiographic region and in the Loess Hills physiographic region (Fig 16). In the Delta Physiographic region it occurs in an area that was heavily impacted by the "great flood" in 1927, when levees along the Mississippi River failed following months of almost continuous

winter and spring rains (Barry 1997). There are hundreds of hectares of sandy fields in that area inhabited by this species. Hilgard (1884) mentions seeing *Opuntia* along the Dogwood Ridge in the Mississippi floodplain that occurred from Coahoma County, which is adjacent to Bolivar County, down to Holmes County. Whether it is the same species is yet to be determined, and trips to locate Dogwood Ridge and any *Opuntia* species that might occur there have been unsuccessful. The other populations have been found only in one county in the Loess Hills. Through more investigation, more populations of this species should be found in the Loess Hill physiographic region. One specimen from Wilkinson County that closely resembles this species has been examined.

This plant is unlike any other *Opuntia* species in the state with regard to growth form, although its flower color overlaps with *O. cespitosa*. It is obviously within the *O. humifusa* complex but is probably more closely related to *O. macrorhiza* than to *O. humifusa*. Due to its size, spine coverage, glochid color, and growth habit (Griffiths 1909), *Opuntia allairei* is morphologically the closest taxon to this species among those species described from the southwestern United States. (*O. allairei* was described from east Texas). Griffiths described *O. allairei* as having wholly yellow flowers; however, Britton and Rose (1920) mention yellow flowers with red centers and more numerous spines than Griffiths originally proposed. Weniger (1970, 1984) states that this taxon can have wholly yellow flowers or flowers with red centers. He also considered *O. allairei* to be a variety of *O. humifusa* (although his idea of *O. humifusa* actually corresponds to *O. cespitosa*). Morphologically *O. allairei* is quite divergent from *O. humifusa*, so here we will tentatively consider it as a separate entity closely resembling (that is, affinis) *O. allairei*. More work is needed in order to fully understand the appropriate nomenclature for this entity, as well as its relationship to the other taxa.

Ecological data for this plant is relatively limited. The populations observed in the Delta and Loess Hills were among the last found during the research on which this treatment is based, and more ecological investigation is called for. Soils in the delta area are of the dundee-askew-sharkey series. The askew soils are the main component where the *Opuntia* is found and consist of a fine, slightly acidic, silty loam. The area resembles a Midwestern grassland or sandy prairie with sparse woody vegetation among a variety of forbs and grasses. Soils in the Loess Hills area are of the morganfield-adler-convent and the dundee-dubbs-sharkey series. The morganfield-adler-convent are silty to loamy soils formed from alluvium and are nonacid and moderate to well-drained. The dundee-dubbs-sharkey soils also were formed from alluvium. Dundee soils are well-drained and neutral, whereas the other two soils are acidic and poorly drained.

Associate species for this taxon in the delta area are those generally found in sandy, slightly disturbed areas, which in some cases are the same as those found for *O. humifusa* and *O. pusilla* (for instance, *Cenchrus spinifex* and *Triplasis purpurea*). Other associate species include *Gleditsia triacanthos*, *Juniperus virginiana*, *Xanthoxylum clava-hercules*, *Ambrosia artemisiifolia*, *Ampelopsis arborea*, *Bromus arvensis*, *Brunnichia ovata*, *Chenopodium ambrosioides*, *Cocculus carolinus*, *Croptilon divaricatum*, *Croton glandulosus*, *Cynodon dactylon*, *Cyperus refractus*, *Paspalum setaceum*, and *Toxicodendron radicans*. Associate species for the Loess Hill populations are species that can occur in dry environments, for instance, *Celtis laevigata*, *Diospyros virginiana*, *Juniperus virginiana*, *Rhus copallinum*, and *Sassafras albidum*, although habitat characteristics here are more similar to those for *O. cespitosa*.

Morphological Characteristics

This plant can reach heights of 60 cm in shaded conditions, but it generally is around 30–40 cm tall with dark green to yellow-green pads. It forms large colonies of mostly ascending or occasionally slightly decumbent cladodes (Fig 17). It is the largest of the naturally occurring, inland opuntia in Mississippi.

Cladodes are generally 7.0–13.6 (–32.5) cm long, 4.0–6.8 (–8.5) cm wide and 5–25 mm thick. They tend to be more tuberculate than either *O. cespitosa* or *O. humifusa*. Younger cladodes can be slightly glaucous as well.

Spines are almost completely lacking in this species. When present they are relatively small, ranging from 15–18 mm long and about 0.6 mm in diameter at the base. Only one spine per areole has been observed, and greenhouse grown plants produced no spines, even in full light under increased temperatures.

Glochids can be up to 5 mm long and are bright yellow when young to orange-brown in age. They have the same arrangement and varying lengths as those of *O. humifusa*.

Flowers and Fruit The flowers of this species are showy, with inner yellow tepals basally tinged red (Fig 18), as in *O. cespitosa*. Flowers of this species tend to be paler that those of *O. cespitosa*. The fruit are reddish in color to dark purple when mature.

V. *Opuntia stricta* (Haw.) Haw., *Syn Pl Succ* 191. 1812.

Opuntia stricta is generally restricted to coastal areas (Benson 1982; Pinkava 2003; Wunderlin 1998). Benson (1982) places it "even in jungles along the Everglades, where the water table is only a few centimeters below the surface," implying that this species can survive in areas atypical for cacti. However, humans have transported this species throughout the mid-south, planting it in yards and flower gardens. Cladodes are often taken from coastal populations for this purpose. In Mississippi this species occurs naturally in two counties in the Coastal Zone physiographic region (Fig 16).

Records from Hancock County exist as well, but these have not been reconfirmed. It occurs on barrier islands, oyster shell middens, and weedy areas along the coast. It has been seen occasionally in wrack and could potentially be dispersed by water during meteorological events, such as hurricanes (Majure and others 2007).

Opuntia stricta is most well-known for its destructive invasion in Australia and parts of South Africa. These locations have also been stages for use of the successful biological control agent, the cactus moth, *Cactoblastis cactorum* Berg (Zimmerman and others 2000). In

Figures 17a, b. *O.* aff *allairei* demonstrating ascending habit of cladodes and large size forming long chains of cladodes up to one meter in length, Yazoo Co., MS. **Figure 18.** Flower of *O.* aff *allairei*, Yazoo Co., MS. **Figures 19a, b.** *O. stricta* growth forms, showing scalloped margined cladodes and dark purple fruit, Horn Island, Jackson Co. MS and Dauphin Island, Mobile Co., AL. All photos by LC Majure excpet where indicated.

Australia this moth was released and eventually decimated millions of hectares of invaded rangeland by the non-native *O. stricta* and other *Opuntia* spp (Mahr 2001). Unfortunately, the moth was also released into the Caribbean islands and has since found its way to the continental United States, where it has negatively affected populations of our native opuntias (Stiling 2000; Stiling and Moon 2001; Zimmerman and others 2001; Stiling and others 2004). *O. stricta* has been heavily affected in certain areas, such as Bon Secour and Dauphin Island, AL (Majure and Ervin pers. obs.). Because *O. stricta* is relatively rare in Mississippi, the cactus moth could easily eliminate entire populations of this species. The cactus moth was found early in 2008 along the barrier islands in Mississippi (Joel Floyd and Stephen Hight, USDA APHIS, pers. comm.). In order to assess threats to its continued survival in the face of this blight, *O. stricta* should be put on the Mississippi Natural Heritage Program Tracking list.

Morphological characteristics

Opuntia stricta is a frutescent prickly pear that can grow up to 1 m or more tall. It can form dense colonies in certain situations, but most often populations are composed of plants that are sparsely scattered throughout an area (Fig 19).

Cladodes range in size from 11.0–20.4 (–28.0) cm long, 6.3–11.4 (–17.0) cm wide, and 9–13 (–19) mm thick. They are light lime green to yellow-green, moderately glaucous on younger growth, and have scalloped margins (Fig 19).

Spines range in size from 20–27 mm long and 1.05–1.30 cm in diameter at the base. They are dark yellow or yellow orange and are flattened longitudinally near the base or throughout. Usually they curve and may be twisted. Spines are stout, erect, spreading, or commonly deflexed. There can be from 0–3 spines per areole, at least in material seen from Mississippi.

Glochids of this species are dark yellow to brown in age and can be 0–6 mm long. They form a tight, fascicled adaxial crescent in the areole or can have nearly the same patterns as those discussed for *O. humifusa* and the other species.

Flowers and Fruit The inner tepals are yellow and the outer tepals are green, as in *O. humifusa* and *O. pusilla*. The fruit of this species are relatively large, many seeded, and dark purple when mature (Fig 19).

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Literature Cited

Anderson EF. 2001. *The cactus family*. Timber Press, Portland, OR.

Barlow C. 2001. Ghost stories from the ice age: some plants are haunted by large mammals from another era. *Natural History* 110: 62–67.

Barry JM. 1997. *Rising tide*: *the great Mississippi flood of 1927 and how it changed America*. Simon and Schuster, New York, NY.

Benson L. 1944. A revision of some Arizona Cactaceae. *Proceedings of the California Academy of Sciences* 25: 245–268.

Benson L. 1962. *Plant taxonomy*, *methods and principles*. Ronald Press, New York, NY.

Benson L. 1969. *The native cacti of California*. Stanford University Press, Stanford, CA.

Benson L. 1982. *The cacti of the United States and Canada*. Stanford University Press, Stanford, CA.

Bobich EG, Nobel PS. 2001. Biomechanics and anatomy of cladode junctions for two *Opuntia* (Cactaceae) and their hybrid. *American Journal of Botany* 88: 391–400.

Bowden WM. 1945. A list of chromosome numbers in higher plants. I. Acanthaceae to Myrtaceae. *American Journal of Botany* 32: 81–92.

Britton NL, Rose JN. 1919. *The Cactaceae*. Carnegie Institute of Washington, Washington, DC.

Dean WRJ, Milton SJ. 2000. Directed dispersal of *Opuntia* species in the Karoo, South Africa: are crows the responsible agents? *Journal of Arid Environments* 45: 305–314.

DeFelice MS. 2004. Prickly pear cactus, *Opuntia* spp.: a spine tingling tale. *Weed Technology* 18: 869–877.

Doyle JD. 1990. Systematics of the *Opuntia humifusa* complex. PhD Dissertation. University of North Carolina, Chapel Hill, NC.

Engelmann G. 1850. Plantae Lindheimerianae. *Boston Journal of Natural History* 6: 206–240.

Engelmann G. 1856. Synopsis of the Cactaceae of the territory of the United States and adjacent regions. *Proceedings of the American Academy* 3: 259–346.

Frego KA, Staniforth RJ. 1985. Factors determining the distribution of *Opuntia fragilis* in the boreal forest of southeastern Manitoba. *Canadian Journal of Botany* 63: 2377–2382.

Gleason HA. 1952. *The New Britton and Brown illustrated flora of the northeastern United States and adjacent Canada*. Lancaster Press, Lancaster, PA.

Grant V, Grant K. 1979. Hybridization and variation in the *Opuntia phaeacantha* group in central Texas. *Botanical Gazette* 140: 208–215.

Griffith MP. 2004. The origins of an important cactus crop, *Opuntia ficus-indica* (Cactaceae): new molecular evidence. *American Journal of Botany* 91: 1915–1921.

Griffiths D. 1909. Illustrated studies in the genus *Opuntia*. II. *Reports of the Missouri Botanical Garden* 20: 81–95.

Hanselka CW, Paschal JC. 1991. Prickly pear cactus: a Texas rangeland enigma. *Rangelands* 13: 109–111.

Haworth AH. 1812. *Synopsis plantarum succulentarum*. Richard Taylor, London.

Hilgard EW. 1884. Cotton Production in the United States: Part 1, Mississippi Valley and southwestern States. Department of the Interior, Government Printing Office, Washington, DC

Hunt D. 2006. *The new cactus lexicon*. DH Books, Milbourne Port, England.

Jansen DH. 1986. Chihuahuan Desert nopaleras: defaunated big mammal vegetation. *Annual Review of Ecology and Systematics* 17: 595–636.

Kalmbacher G. 1975. New York's neglected cactus: *Opuntia* thrives despite lack of desert climate. *Garden Journal* 25: 144–147.

Leuenberger BE. 1993. Interpretation and typification of *Cactus opuntia* L., *Opuntia vulgaris* Mill., and *O. humifusa* (Rafin.) Rafin. (Cactaceae). *Taxon* 42: 419–429.

Lewis DA, Nobel PS. 1977. Thermal energy exchange model and water loss of a barrel cactus, *Ferocactus acanthodes*. *Plant Physiology* 60: 609–616.

Lundell CL. 1969. *Flora of Texas*: Vol 2. George Banta, Menasha, WI.

Mahr DL. 2001. *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in North America: a workshop of assessment and planning. *Florida Entomologist* 84: 465–473.

Majure LC. 2007. The vascular flora of the Chunky River (Mississippi). *Journal of the Botanical Research Institute of Texas* 1: 1179–1202.

Majure LC, Fitzpatrick P, Ervin GN. 2007. Storm-driven maritime dispersal of prickly pear cacti (*Opuntia* species). USDA, Animal and Plant Health Inspection Service, International *Cactoblastis cactorum* Conference, Phoenix, AZ, May 7–10.

Mann J. 1969. Cactus-feeding insects and mites. Smithsonian Institute Bulletin 256. Washington, DC

Mauseth JD. 2006. Structure-function relationships in highly modified shoots of Cactaceae. *Annals of Botany* 98: 901–926.

Melink E, Riojas-Lopez ME. 2001. Consumption of platyopuntias by wild vertebrates. *In* Nobel PS, editor. *Cacti*, *biology and uses*. University of California Press, Berkeley, CA. pp 109–123.

Mitich LW. 1970. Wyoming native cacti. *Cactus and Succulent Journal* 42: 155–159.

Mohamed-Yasseen Y, Barringer SA, Splittstoesser WE. 1996. A note on the uses of *Opuntia* spp. in Central/North America. *Journal of Arid Environments* 32: 347–353.

Nefzaoui A, Salem HB. 2001. Forage, fodder, and animal nutrition. *In* Nobel PS, editor. *Cacti*, *biology and uses*. University of California Press, Berkeley, CA. pp 199–210.

Nobel PS. 1978. Surface temperatures of cacti-influences of environmental and morphological factors. *Ecology* 59: 986–996.

Nobel PS. 1983. Spine influences on PAR interception, stem temperature, and nocturnal acid accumulation by cacti. *Plant*, *Cell and Environment* 6: 153–159.

Perez-Sandi M. 2001. Addressing the threat of *Cactoblastis cactorum* (Lepidoptera: Pyralidae), to *Opuntia* in Mexico. *Florida Entomologist* 84: 499–502.

Pimienta-Barrios E. 1997. El nopal en México y el mundo. *In* Septíen and Pérez, editors. *Suculentas Mexicanas*, *Cactáceas*. CVS Publicaciones. pp 87–95.

Pinkava DJ. 2003. *Opuntia*. *In* Flora of North America Editorial Committee, editors. 1993+. *Flora of North America north of Mexico*. 12+ vols. New York and Oxford. Vol 4. pp 123–148.

Powell AM, Weedin JF. 2004. *Cacti of the Trans-Pecos and adjacent areas*. Texas Tech University Press, Lubbock, TX.

Radford AE, Ahles HE, Bell CR. 1968. *Manual of the vascular flora of the Carolinas*. University of North Carolina Press, Chapel Hill, NC.

Rafinesque CS. 1820. *Annals of nature*, Annual synopsis of new genera and species of animals, plants, etc discovered in North America.

Rafinesque CS. 1830. *Bulletin Botanique*, ou Collection de notices originales et d'extraits des ouvrages botaniques, souvent accompagne's de gravures repre'sentant des analyses d'organes importants de la fleur ou du fruit, etc. Gene've,

Paris 2: pp 215–216.
Rafinesque CS. 1830. *Medical flora of the United States*. SC Atkinson, Philadelphia, PA. Vol 2, p 247.
Rebman JP, Pinkava DJ. 2001. *Opuntia* cacti of North America: an overview. *Florida Entomologist* 84(4): 474–483.
Small JK. 1903. *Flora of the southeastern United States*. Privately Printed, New York, NY.
Small JK. 1913. *Flora of the southeastern United States*. Privately Printed, New York, NY.
Small JK. 1933. *Manual of the southeastern Flora*. Privately Printed, New York, NY.
Stevens PF. (2001 onwards). Angiosperm Phylogeny Website. Version 7, May 2006. http://www.mobot.org/MOBOT/research/APweb/.
Stiling P. 2000. A worm that turned. *Natural History* 109: 40–43.
Stiling P, Moon D. 2001. Protecting rare Florida cacti from attack by the exotic cactus moth, *Cactoblastis cactorum* (Lepidoptera: Pyralidae). *Florida Entomologist* 84: 506–509.
Stiling P, Moon D, Gordon D. 2004. Endangered cactus restoration: mitigating the non-target effects of a biological control agent (*Cactoblastis cactorum*) in Florida. *Restoration Ecology* 12: 605–610.
Timmons FL. 1941. The dissemination of prickly pear seed by jack rabbits. *Journal of the American Society of Agronomy* 33: 513–520.
USDA, NRCS. 2007. The PLANTS Database (http://plants.usda.gov, accessed 18 August 2007). National Plant Data Center, Baton Rouge, LA 70874–4490 USA.
Vigueras AL, Portillo L. 1997. Cultivo de la grana o cochinilla del nopal. *In* Septíen and Pérez, editors. *Suculentas mexicanas*, *Cactáceas*. CVS Publicaciones. pp 96–99.
Wallace RS, Fairbrothers DE. 1987. The New England distribution of *Opuntia humifusa* (Raf.) Raf. *Rhodora*: *Journal of the New England Botanical Club* 89(859): 327–331.
Weakley AS. 2003. Flora of the Carolinas and Virginia: Dicotyledons. Working draft of July 2003. University of North Carolina, Chapel Hill.
Weniger D. 1970. *Cacti of the southwest*: *Texas*, *New Mexico*, *Oklahoma*, *Arkansas*, *and Louisiana*. University of Texas Press, Austin.
Weniger D. 1984. *Cacti of Texas and neighboring states*. University of Texas Press, Austin.
Wunderlin RP. 1998. *Guide to the vascular plants of Florida*. University Press of Florida. Gainesville, FL.
Zimmerman HG, Moran VC, Hoffman JH. 2000. The renowned cactus moth, *Cactoblastis cactorum*: its natural history and threat to native *Opuntia* floras in Mexico and the United States of America. *Diversity and Distributions* 6: 259–269.