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Taxonomic revision of the *Opuntia humifusa* complex (Opuntieae: Cactaceae) of the eastern United States

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Abstract

The *Humifusa* clade represents a recent radiation that originated in the late Pliocene or early Pleistocene and consists of about 10 species widely distributed in North America from northern Mexico north to Ontario, Canada, and south to the Florida Keys. This clade likely originated in the edaphically subxeric regions of northern Mexico and the southwestern United States, and from there it later spread to the southeastern United States and ultimately produced a small radiation in the eastern United States. Hybridization among evolutionarily divergent diploid species of the southeastern (SE) and southwestern (SW) United States subclades led to the origin of many polyploid taxa, which today occupy about 75% of the distribution of the clade. Here we present a taxonomic revision of the SE subclade of the *Humifusa* clade and polyploid derivatives that commonly occur in the eastern United States (i.e., the *O. humifusa* complex). We recognize eight taxa: *Opuntia abjecta*, *O. austrina*, *O. cespitosa*, *O. drummondii*, *O. humifusa*, *O. mesacantha* subsp. *mesacantha*, *O. mesacantha* subsp. *lata*, and *O. nemoralis*, as well as the interclade allopolyploid, *Opuntia ochrocentra*, derived, in part, from a member of the *O. humifusa* complex. Diagnostic keys, descriptions, original photos, and distribution maps are provided for each taxon. Neotypes are designated for the names *O. austrina* (NY) and *O. youngii* (USF), and *O. drummondii* and *O. tracyi* are lectotypified from an illustration in Maund & Henslow and a specimen at NY, respectively.

Key words: cacti, hybridization, morphology, polyploidy, prickly pears, taxonomy

Introduction

Opuntia Miller (1754) (tribe Opuntieae DC.) is a genus native to the Americas and it is distributed from southern Argentina to Canada (Anderson 2001). Members of the clade occupy many habitats, from seasonally dry tropical and subtropical deciduous forests and scrub, to moderate desert environments, temperate prairies, coastlines, and forest openings (Britton & Rose 1919, Benson 1982, Anderson 2001, Pinkava 2003).

Opuntia displays a peculiar set of morphological characters including longitudinally flattened, determinate stem segments, or cladodes, that take over the photosynthetic function of the small and ephemeral long shoot leaves, which are produced as the cladode develops. Cladodes may be glabrous or pubescent (see Majure & Puente 2014), ranging in color from dark-green to purple. All species of *Opuntia* (and subfamily Opuntioideae K.Schum., tribes Cylindropuntieae Doweld, Opuntieae and Tephrocacteae Doweld) have glochids (Fig. 1A), or retrorsely barbed [with the exception of *Micropuntia* Daston (1946: 661) that has antrorsely-barbed glochids] and deciduous hair-like spines that are produced from specialized short shoots (areoles), which are mostly included within the stem tissue (see Mauseth 2006). These spines often become exserted and conspicuous as the cladode develops and form an impressive armament against herbivores. Glochids have also been shown to aid in water uptake in *O. microdasys* (Lehmann 1827: 16) Lehmann ex Pfeiffer (1837: 154); the retrorse barbs force water droplets from the apex to the base of the glochid where they are absorbed by the trichomes of the areole and then presumably by the apical meristem within each areole (Ju *et al.* 2012), aiding in water uptake in arid environments. Long spines are also produced in most species and can be strongly retrorsely barbed or smooth to the touch (although all spines produce overlapping cells that develop a small degree of "barbedness"; see Fig. 1B-C). Some species form only one type of spine, whereas others may develop both central (those produced from the center of the areole) and radial spines (those produced from the periphery of the areole; see Parfitt 1991, Pinkava 2003). The spine development pattern from the areole can be a useful taxonomic character. Spine color changes through time but can also be diagnostic at the species level.

Opuntia species produce high quantities of betalain pigments (see Brockington *et al.* 2011, 2015) under stressful conditions, and water- or cold-stressed plants often become reddish, pinkish, or purplish, especially around the areoles, and certain members of specific clades always are purplish (i.e., the *Macrocentra* clade; Majure & Puente 2014).

Species of *Opuntia* can form spreading to erect shrubs or even trees. Most tree-like taxa are found in tropical or subtropical areas (e.g., certain members of the *Nopalea* clade and species in the Galapagos Islands; see Britton & Rose 1919, Anderson 2001, Majure *et al.* 2012a). In temperate areas, smaller shrubby taxa, which commonly sprawl or trail along the ground, are more frequently found, such as *O. macrorhiza* Engelman (1850: 206) and *O. humifusa* (Rafinesque 1820: 15) Rafinesque (1830: 247).

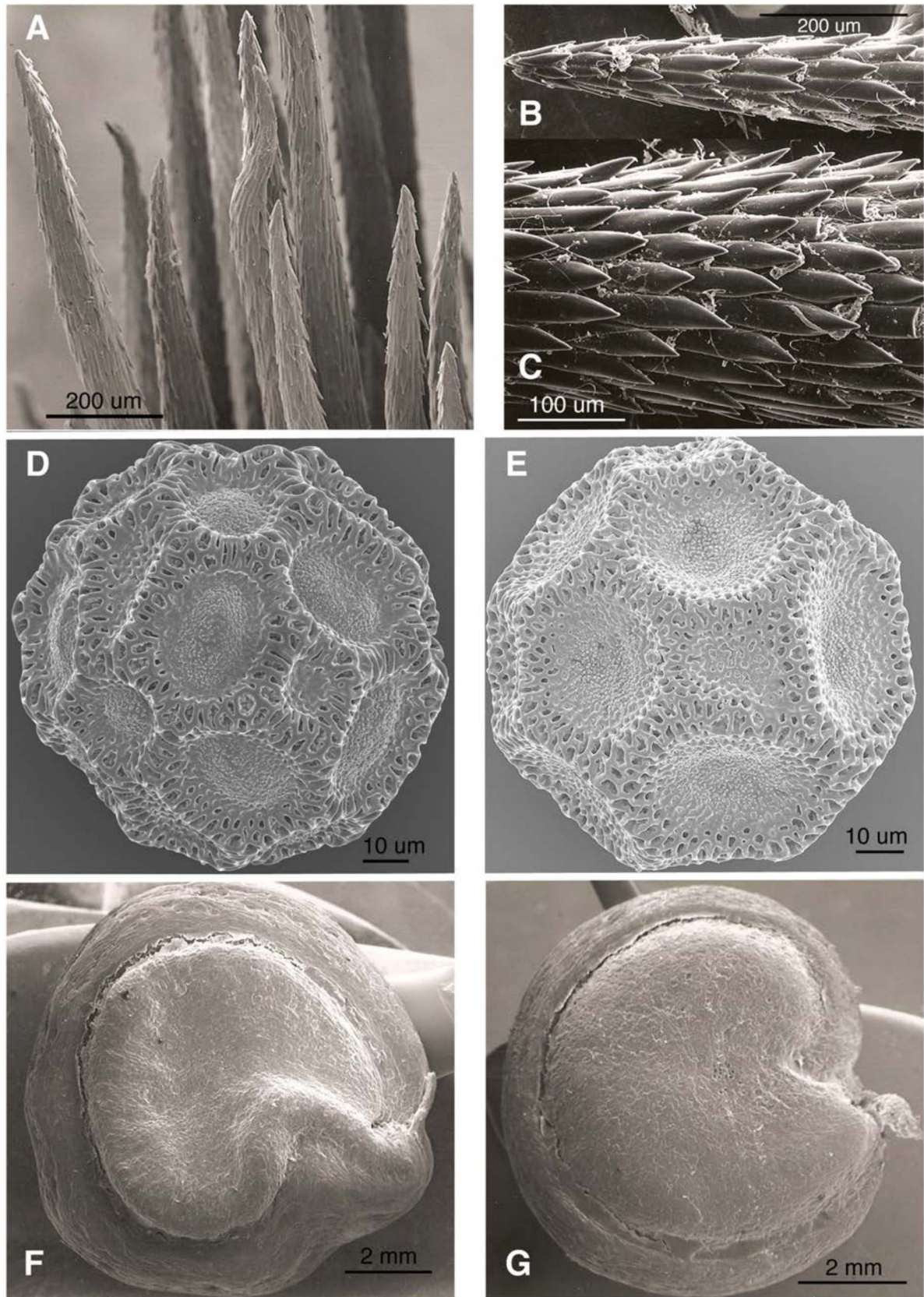


FIGURE 1. SEM micrographs of characters of *Opuntia* from the *O. humifusa* complex. A) close-up of glochids of *O. cespitosa* at 106x (Majure 736), B-C) close-up of spine surfaces showing overlapping cells creating retrorse barbs in *O. drummondii* (Majure 843), B) spine tip at 200x, C) mid-section of spine at 289x, D) pollen grain of *O. cespitosa* (Majure 736) at 850x, E) pollen grain of *O. mesacantha* subsp. *lata* at 900x (Ervin s.n.), F) seed of *O. cespitosa* at 16x (Majure 736), G) seed of *O. drummondii* at 20x (Majure 843). All photos taken by L.C. Majure.

Most of the species exhibit open, insect-pollinated flowers with thigmonastic stamens (not to be confused with thigmotropic stamens that move in the direction of a stimulus), which move toward the stigma upon stimulation suggesting a bias towards oligolectic pollinators (see Schlindwein & Whittman 1997, Diaz & Cocucci 2003). However, bird pollination and the loss of stamen movement have evolved numerous times in the group (Majure & Puente 2014). Most species of “strictly” insect-pollinated *Opuntia* have pollen with a reticulate exine (see Majure & Puente 2014), and Majure and Ervin (2007) noted an increase in pore number in certain individuals—from 12–14 (Fig. 1D–E)—and those species were subsequently discovered to be tetraploid [see *O. cespitosa* Rafinesque (1830: 216); Majure *et al.* 2012b]. The same increase in pore number can be seen in the hexaploid *O. megarrhiza* Rose (1906: 126) versus the diploid relative *O. pachyrrhiza* Hernández, Gómez-Honostrosa, Bárcenas (2001: 309) (see Fig. 3 K–L in Majure & Puente 2014). Although not a synapomorphy of *Opuntia* (but rather Opuntioideae), the seeds are characteristic in having a bony funicular girdle that surrounds a bony funicular envelope (Fig. 1F–G), which covers the embryo (Stuppy 2002). The latter may be glabrous or pubescent (Stuppy 2002, Majure & Puente 2014), and the surface features of the funicular envelope may be taxonomically useful in species delimitation. Putative synapomorphies of *Opuntia* s.str. are pollen with a reticulate exine, although this character was equivocal in some analyses (Majure & Puente unpubl. data), and has mostly been lost in certain bird-pollinated members of the clade (see Majure & Puente 2014), and spirally enrolled embryos [as shown in Stuppy (2002) and Majure *et al.* (2013)]. However, morphological synapomorphies are still being investigated in the group (Majure unpubl. data).

The *Opuntia* clade likely originated in the late Miocene (Arakaki *et al.* 2011, Majure *et al.* 2012a) in southern South America and from there it dispersed north into the North American desert region [modern-day central and northern Mexico and southwestern United States (US)], where the clade diversified and expanded through to the Caribbean Islands and throughout the rest of the continental US. A small group, the *Humifusa* clade, eventually migrated to the eastern US (Majure *et al.* 2012a), where it experienced an additional, small radiation.

The *Humifusa* clade consists of two subclades (Fig. 2), a southwestern subclade (SW) including the widespread and morphologically highly variable taxon, *O. macrorrhiza* s.lat. (Fig. 3) and close relatives, e.g., *O. pottsii* Salm-Dyck (1849: 236.), and the southeastern subclade (SE), which includes *O. austrina* and several other species (Majure *et al.* 2012b). Diploids belonging to the SW subclade are characterized by procumbent species with yellow glochids, non-retrorsely barbed (smooth to the touch) spines, and yellow flowers with red centers. Red-centered flowers also occur in members of the sister clade to the *Humifusa* clade (i.e., the *Macrocentra* clade; Majure & Puente 2014) and may represent a retained plesiomorphy in the *Humifusa* clade (Majure *et al.* unpubl. data).

Diploids of the SE subclade are characterized by procumbent, trailing, and erect species that have stramineous glochids, retrorsely barbed spines (to the touch), and entirely yellow flowers. Numerous polyploid taxa have evolved within the *Humifusa* clade. Several of those taxa originated from hybridization between the SE and SW subclades and display characters of both subclades (Majure *et al.* 2012b; Majure *et al.* in prep.). The SE subclade and polyploid derivatives occurring in the eastern US are here referred to as the *O. humifusa* complex, as most of those taxa historically have been recognized under a broadly circumscribed *O. humifusa*.

There are multiple dispersal mechanisms in species of *Opuntia*, including via the consumption of fruit and dissemination of seeds. Vegetative dispersal is also common, wherein cladodes stick into the fur/skin on animals and are deposited later where they can then root and form clones of the parent plant. Another vegetative means of dispersal is via hydrochory [e.g. *Opuntia fragilis* (Nuttall 1818: 296) Haworth (1819: 82) was suggested to be dispersed along water courses during times of flooding (Frego & Staniforth 1985)]. Likewise, in the *O. humifusa* complex, seeds of *O. mesacantha* Rafinesque (1830: 216) subsp. *mesacantha* and *O. austrina* Small (1903: 816) have been found in rabbit dung, and fruit are commonly eaten by rodents, as well as other larger mammals (Majure pers. obsv.). Seeds of *O. drummondii* Graham (1841: 246) have been found in harvester ant [*Pogonomyrmex badius* (Latreille) (1802: 238)] nests [MacGown *et al.* 2008, as *O. pusilla* (Haworth 1803: 188) Haworth (1812: 195)]. Entire plants of *O. nemoralis* Griffiths (1913: 133) have been observed uprooted by feral hogs and partially eaten in Louisiana (Majure pers. obsv.). After Hurricane Katrina made landfall on the coastline of the southeastern US in the fall of 2005, cladodes of *Opuntia mesacantha* subsp. *mesacantha*, as well as the distantly related *O. stricta*, were found in wrack all along the coast of Jackson Co., Mississippi, and entire plants of *O. mesacantha* subsp. *mesacantha* were found uprooted and even stranded in trees on Horn Island, a barrier island off of the Mississippi coast (Majure pers. obsv.; Majure *et al.* 2007). Likewise, after Hurricane Sandy hit the Atlantic coast in 2012, cladodes presumably of *O. humifusa* were encountered washed up along the shore of Rhode Island (H.

Leeson, RI Natural History Survey, pers. comm.), a state in which *Opuntia* was only known previously from one population in a different location. Thus, it is likely that species of the *O. humifusa* complex that occur along the coast also could be dispersed widely during meteorological events. This may also account for the widespread occurrence of *O. drummondii*, a species that easily spreads vegetatively, along watercourses in Mississippi (Majure 2007b, Majure & Ervin 2008, as *O. pusilla*) and along the Gulf and Atlantic coasts.

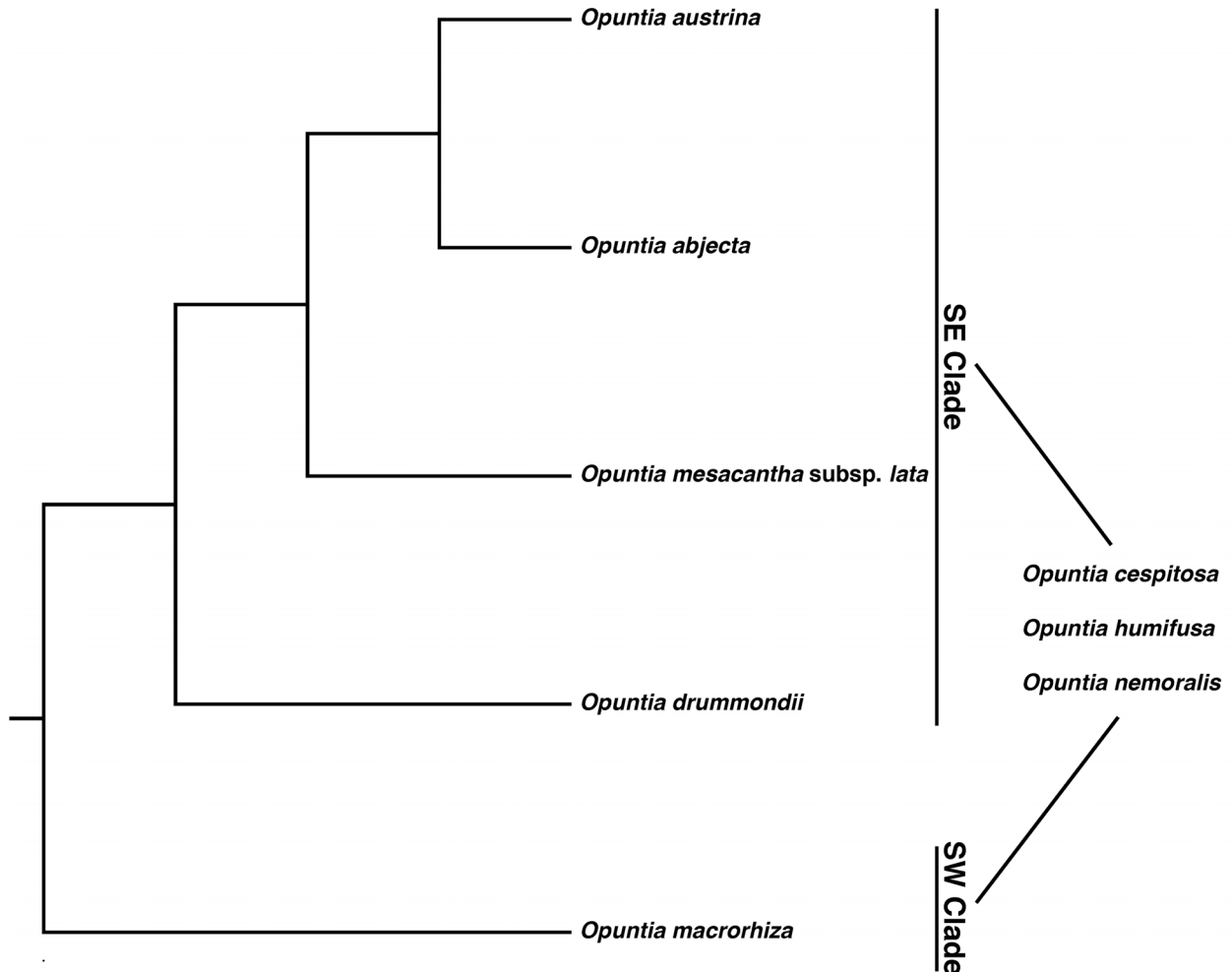


FIGURE 2. Phylogeny of the *O. humifusa* complex. This is a phylogeny of the diploid members of the *Humifusa* clade, which consists of a SE and SW subclade. The *O. humifusa* complex is represented by the SE clade, as well as the reticulate taxa shown here (*O. cespitosa*, *O. humifusa*, and *O. nemoralis*) and the putative autotetraploid *Opuntia mesacantha* subsp. *mesacantha* (not shown here).

Hybridization, polyploidy, and morphological variability

Hybridization in *Opuntia* is common and plays a major role in polyploid formation and the origin of new species (Parfitt 1980, Griffith 2001, Pinkava 2002, Hernández *et al.* 2003, Puente & Hamann 2005, Majure *et al.* 2012a-b, Majure *et al.* 2014). The ability for taxa to readily hybridize and produce nearly fertile offspring would suggest the breakdown of species boundaries by those biologists following a strict biological species concept (Mayr 1942). Hybridization in *Opuntia* occurs even among members of widely divergent clades within *Opuntia* s.str. and with other closely related genera within the Opuntieae, such as *Consolea* Lemaire (1862: 174) (Majure *et al.* 2012a). Hence, as in many plant groups, the ability to hybridize and form viable offspring is common and may or may not represent qualities relating to perceived species boundaries (Soltis and Soltis 2009).

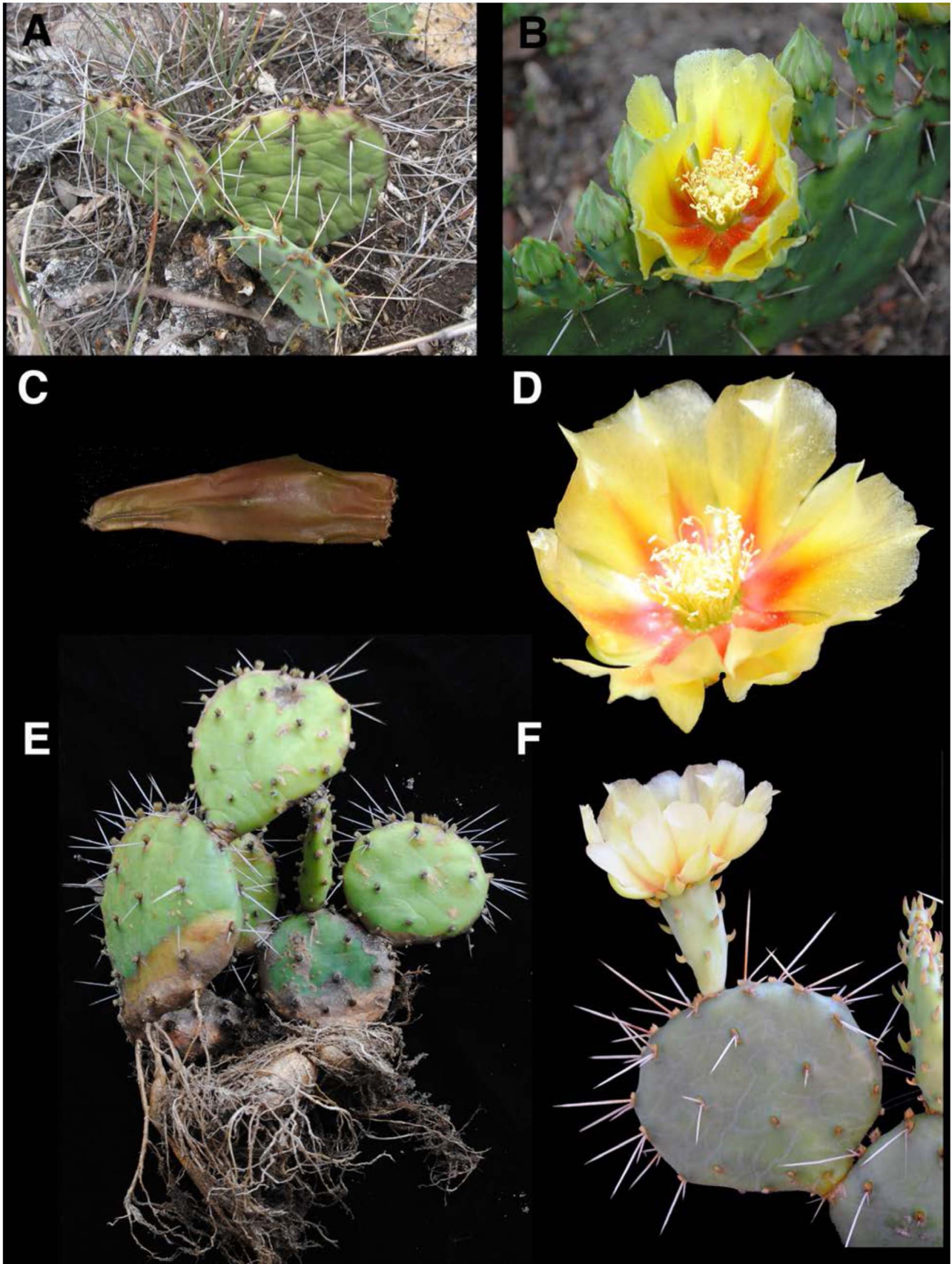


FIGURE 3. Morphological features of *O. macrorhiza* s.s. A) plant in habitat, B) close-up of flower and floral buds, C) mature fruit, D) flower, E) entire plant in vegetative state showing tuber formation, F) side view of cladode in flower. All from *Majure 3510* (Kerr Co., TX; FLAS). All photos taken by L.C. Majure.

In *Opuntia*, hybridization between different species is frequently associated with polyploidization (i.e., allopolyploidy; see Majure *et al.* 2012a-b, Majure & Puente 2014), so reproductive barriers likely exist among divergent diploid species. Of those taxa in *Opuntia* with chromosome counts or ploidy inferred through flow cytometry, 30.4% are diploid, 55.8% are polyploid, and 13.8% have been recorded as both diploid and polyploid (Majure & Puente 2014). Polyploidization of hybrid derivatives (i.e., allopolyploids), presumably aids in overcoming sterility barriers (Stebbins 1950, 1971; Grant 1981, Levin 1983). The actual mechanisms behind polyploidization in this group need further study, although unreduced gametes are commonly observed in *Opuntia* and may be the primary cause for the formation of polyploids (Pinkava 2002), both within (i.e., autopolyploidy) and between (allopolyploidy) species. Homoploid hybrid species are also known but are presumed to be relatively rare, e.g., *O. × carstenii* R.Puente & Hamann (2005: 231) (Puente & Hamann 2005, Majure & Puente 2014).

Although allopolyploidy appears to be the more common type of polyploidy in *Opuntia*, autopolyploidy may also be frequent. Certain species of *Opuntia* have been suggested to include autopolyploids based on morphological and some genetic work [e.g., *O. abjecta* Small ex Britton & Rose (1923: 257), *O. drummondii*, *O. mesacantha*, *O. macrocentra* Engelman (1856: 292), and *O. strigil* Engelman (1856: 34); Powell & Weedon 2004, Majure *et al.* 2012a, 2012b; Majure *et al.* in prep.]. However, ploidal type has not been intensively investigated in the prickly pears. As Stebbins (1971) noted, in perennial herbs taxa with efficient vegetative reproduction are more likely to show higher levels of polyploidy than sexual species. *Opuntia*, although mostly shrubs or small trees, shows high rates of vegetative reproduction and dispersal, which likely influence the incidence of polyploidy and the maintenance of those polyploid derivatives over time.

Polyploidy serves as a bridge for species formation and, in many cases, the combination of different genomes, which may facilitate adaptation to extreme environmental conditions (Stebbins 1950), as in northern temperate members of the *Humifusa* (Nobel and Bobich 2002, Majure and Ribbens 2012, Majure *et al.* 2012b, 2012c) and *Polyacantha* clades (e.g., Parfitt 1991, Nobel and Bobich 2002, Pinkava 2002, Majure and Ribbens 2012), which are all polyploid [see the hexaploid *O. fragilis* (Parfitt (1991), Pinkava (2003), Majure & Ribbens (2012)]. Although the common correlation between polyploidization and the successful invasion of harsh environmental conditions needs to be explored further, it is clear that polyploids have been more successful at invading cooler climates with harsher winters than the more restricted, southern diploids in the *Humifusa* clade (Majure *et al.* 2012b).

Opuntia species can be highly variable morphologically, in which cladode size, spine production, tuberous root production, among other features, are in many instances phenotypically plastic (Britton and Rose 1920, Benson 1982, Rebman & Pinkava 2001, Majure 2007, Majure & Ervin 2008). This variability, in addition to hybridization and polyploidy, makes species delimitation in the group difficult, as populations of a species may show polymorphisms that result from growth under heterogeneous environmental conditions (Majure 2007, Majure & Ervin 2008). Also, because of their succulence and spine production, opuntias are rarely collected, or the resulting specimens are often improperly processed leading to very poor representation in herbaria (Reyes-Agüero *et al.* 2007). Likewise, the use of herbarium specimens for taxonomic studies is problematic without very detailed morphological descriptions and measurements of the living plants on which the specimens were based, data that most often are lacking in collections.

Another phenomenon that is occasionally observed in *Opuntia*, but poorly understood, is the production of morphotypes that appear closely related to, or even conspecific with, other morphologically similar species but that are not closely related to those species. The result of character combinations through hybridization between two different species can coincidentally produce morphotypes that appear to be species with which they have no actual phylogenetic relationship. One example of this phenomenon can be seen in *O. pinkavae* Parfitt. Vegetatively, the species superficially resembles *O. macrorhiza* to the point that Parfitt (1997) even compared the species with *O. macrorhiza* in the description. However, there is no phylogenetic evidence to suggest any actual relationship to *O. macrorhiza* (see Majure *et al.* 2012a), and taking the totality of morphological characters, chromosome number, and distribution into account provides substantial evidence for the recognition of the species. Understanding the distribution and knowing the geographic origin of individuals of *Opuntia* can oftentimes be crucial for the proper identification of taxa.

Species of *Opuntia* within the *Humifusa* complex are highly variable in flowering time, which seems to be directly related to changes in temperature regimes. For example, *O. austrina* may begin to flower in south Florida in mid-March but in the same year may bloom in north Florida at the end of March or beginning of April. The same

individual, if moved to cooler climates, will further change its flowering time. Material of *O. austrina* from central Florida, which typically blooms around the beginning of April, may flower around the first or second week of May in central Mississippi (Majure, pers. obs.). The same phenomenon can be seen in *O. cespitosa*, *O. humifusa*, and *O. mesacantha*. Southern populations start to flower before more northerly populations. Individuals taken from northern populations and transplanted to more southerly locations often alter their flowering times within one or two growing seasons to nearly match those of local populations (Majure, pers. obs.), at least within the same species.

Members of the *O. humifusa* complex have been introduced into numerous countries, including Bulgaria (Tashev 2012), Croatia, France, Germany (Essl & Kobler 2008), Italy (Guiggi 2010, 2014), South Africa (Patterson *et al.* 2011, H.G. Zimmermann, pers. comm.), Spain (López 2001, Cuchillo Sastriques & Gimeno López 2006), and Switzerland (Desfayes 2008). In Korea, *O. humifusa* is even known by the common name Cheonnyuncho and is commonly used for its medicinal properties (Lee *et al.* 2005, Yang *et al.* 2016).

Material and methods

The present work is based on the examination of about 1200 herbarium specimens collected in eastern North America from the following herbaria: ALU, ASU, EKY, FSU, GA, ILL, ILLS, LSU, MICH, MISS, MISSA, MMNS, MO, MOAR, MU, NY, TENN, TROY, UNA, UNC, US, USF, USMS, WISC. Extensive fieldwork was carried out by L. C. Majure from Fall 2004–Spring 2012, where more than 200 specimens were collected. Specimens are deposited in DES, FLAS, MISSA and MMNS (acromyn according to Thiers 2016+).

The diagnostic key was generated mainly by the examination of living plants, supplemented by herbarium material, so it is most useful to identify living individuals. The knowledge of the range of morphological variation within a population is often necessary to correctly identify species, since individuals within a population may or may not display characters essential for the identification of a given taxon (as a result of phenotypic plasticity, age of the plant, or other factors). Therefore, this dichotomous key is best used to identify a species when there are data about morphological variation within a given population and also when the entire plant, in living condition, is available for observation. *Opuntia macrorhiza* is also included in the key to aid in the separation of that species from members of the *O. humifusa* complex.

Taxonomic treatment

Opuntia humifusa complex

Description:—Small to large shrubs, erect and forming a single, well-defined trunk and branching above, or decumbent, or trailing and branching from the base, 0.1–2 m tall, branching profusely or sparingly; with tuberous and/or fibrous roots. Cladodes elliptical, rotund, oblong, or obovate, 0.8–29.5 cm long, 0.6–11.3 cm wide, 4.0–19.9 mm thick, dark or yellow-green, or glaucous, gray-green, margins smooth or scalloped, remaining turgid or cross-wrinkling during the winter. Leaves green or glaucous, gray-green, 2.2–13.8 mm long, ascending parallel to the cladode or spreading, apices reflexed or not. Glochids conspicuous, exerted, or inconspicuous, included within the areole, red, reddish-brown, yellow, or stramineous when young, aging dark brown, light brown, or amber. Spines 0–18 per areole, 0.9–10.3 cm long, 0.2–1.3 mm in diameter, dark brown, reddish brown, yellow, brown and white or brown, white, and yellow mottled during development, turning white with age and later gray, cylindrical, flattened, or twisted at the base, only central spines present or radial and central spines present, retrorsely barbed or smooth to the touch. Flowers: outer tepals green, yellow green, or red with light green margins, ovate, triangular, or triangular subulate, inner tepals yellow, yellow with red bases, or yellow with yellow-green bases, 7–10, obovate or obtriangular to emarginate, 2.2–5.5 cm long, generally with a mucronate apex, staminal filaments yellow or yellow with yellow-green or reddish bases, stamens thigmonastic, anthers yellow or yellowish-white; stigmas white, cream, or green, 3–10 lobed. Berries clavate or barrel-shaped, 1.8–5.0 cm long, pink, purple, red, orange-red, green, or greenish-yellow at maturity. Seeds 3.1–5.9 mm long, the funicular envelope glabrous, smooth, or only moderately elevated by the cotyledons and hypocotyl of the embryo, or bumpy, greatly elevated by the cotyledons

and hypocotyl of the embryo, funicular girdle 0.4–1.3 mm wide, regular, smooth, or irregular, bumpy and/or with undulating margin.

Historical background:—Rafinesque (1820: 15) first described *Cactus humifusus* [\equiv *Opuntia humifusa* (Raf.) Rafinesque 1830: 247] as a low-growing, yellow-flowered, and spineless species occurring in an area ranging from New York to Kentucky and west to Missouri. The majority of the distribution given for *O. humifusa* by Rafinesque (Kentucky west to Missouri) actually is inhabited by an *Opuntia* with flowers with red centers (see *O. cespitosa* below), so it is apparent that Rafinesque did not have a clear idea of the distribution or morphological variation of the species he was describing. Rafinesque (1820, 1830) noted the confusion of *Opuntia humifusa* Rafinesque (1830: 247) with that of *Cactus opuntia* Linnaeus (1753: 468) [basonym of *O. opuntia* (Linnaeus) Karsten, (1882: 888) nom. illeg.; see Leuenberger 1993] of the Atlantic Coast (note: Leuenberger (1993) showed *O. opuntia* to be synonymous with *O. ficus-indica* (Linnaeus 1753: 468) Miller (1768: without pagination) and not *O. humifusa*). Nonetheless, *O. humifusa* was again synonymized in later treatments under the tautonym *Opuntia opuntia* (see Britton and Rose 1920, Leuenberger 1993) or treated as a synonym of *O. compressa* (Salisbury 1796: 348) Macbride (1922: 41), an illegitimate name aimed at replacing *Opuntia opuntia* (see discussion by Leuenberger 1993 and Crook & Mottram 1996).

Rafinesque (1830) described two more species, *O. cespitosa* from Kentucky and Tennessee (Rafinesque 1832) and *O. mesacantha* from west Kentucky to Louisiana (Rafinesque 1832), which also were later placed in synonymy with *O. austrina* by some authors (e.g., Britton and Rose 1920). Engelmann (1856) proposed *O. rafinesquii* Engelmann (1856: 136), in honor of Rafinesque to replace the three previously described species, *O. cespitosa*, *O. humifusa*, and *O. mesacantha*. At that time, *O. vulgaris* Miller (1768) was the accepted name for the yellow-flowered Atlantic Coast species, while *O. rafinesquii* was the accepted name for the species occurring from the Mississippi Valley from Kentucky to Missouri and north to Minnesota (Engelmann 1856). Only recently (Leuenberger 1993), the name *Opuntia vulgaris* was synonymized with *O. ficus-indica* (Linnaeus 1753: 468) Miller (1768), a domesticated species originating from Mexico and commonly cultivated throughout the world for agricultural products (Casas & Barbera 2002, Inglese *et al.* 2002, Ervin 2012); however, the species is absent from most of the eastern US except for where it has been introduced in the warmer portions of Florida (Majure pers. obs.).

The name *Opuntia vulgaris* was also misapplied to the South American *O. monacantha* (Willdenow 1814: 33) Haworth (1819: 81). Notably, although Rafinesque (1820) gave nearly the same distribution as Engelmann (1856) for *O. humifusa*, he described the flowers as entirely yellow, while Engelmann (1856) described them as being mostly yellow with red centers, demonstrating that Engelmann at least had a clear idea of the morphology of the species that grew throughout the range given with his description of *O. rafinesquii*. *Opuntia macrarthra* Gibbes (1859: 273) was later described by Gibbes (1859) for low-growing, yellow-flowered material from South Carolina.

Britton and Rose (1908) described a further species of low-growing, yellow-flowered, spiny *Opuntia*, *O. pollardii* Britton & Rose (1908: 523) from the coast of Biloxi, Mississippi. Wherry (1926) described the yellow-flowered *O. calcicola* Wherry (1926: 12) from West Virginia, a species apparently restricted to circumneutral soils, and Nelson (1919) described *O. youngii* from material sent to him from Tampa, Florida.

John Kunkel Small, a botanist from the New York Botanical Garden, began his exploration of Florida in the early 1900s, where he described 12 species from the *O. humifusa* complex, *O. abjecta* Small (1923: 257), *O. austrina* Small (1903: 816), *O. ammophila* Small (Small 1919: 29), *O. lata* Small (1919: 26), *O. eburnispina* Small ex Britton & Rose (1923: 260), *O. impedita* Small ex Britton & Rose (1923: 257), *O. pisciformis* Small ex Britton & Rose (1923: 258), *O. turgida* Small ex Britton & Rose (1923: 265), *O. atrocapersis* Small (1933: 905), *O. cumulicola* Small (1933: 907), *O. nitens* Small (1933: 906), and *O. polycarpa* Small (1933: 906). Benson (1982) later placed most of Small's taxa in synonymy with *O. humifusa* or considered them (except for *O. abjecta*) hybrids between *O. stricta* (Haw.) Haw. (1812: 191) and *O. humifusa*. *Opuntia abjecta* was recognized by Benson (1982) as a synonym of the Caribbean species *O. triacantha* (Willdenow) Sweet (1826: 172).

Benson (1982) recognized three varieties of *O. humifusa*, var. *ammophila* (Small) L.D. Benson (1976: 59), var. *austrina* (Small) Dress (1975: 164), and var. *humifusa*. Subsequent researchers have mostly followed Benson's treatment (Wallace & Fairbrothers 1986, 1987; Doyle 1990, Pinkava 2003), although Pinkava (2003) did not recognize *O. humifusa* var. *austrina*, Ward (2009) recognized *O. austrina*, *O. ammophila*, and *O. pollardii* in Florida (excluding *O. humifusa*), while Wunderlin and Hansen (2003, 2011) did not recognize any varieties within *O. humifusa*.

Oddly, Benson (1982) concluded that *O. humifusa* is strictly a yellow-flowered species, as further demonstrated in his key, although his figure no. 438 of *O. humifusa* (Benson 1982: 439) represents a typical specimen, albeit vegetative, of what Majure and Ervin (2008) referred to as *O. cespitosa*, which has yellow flowers with red centers. It is thus apparent that Benson (l.c.) did not have a clear idea of the delimitation of *O. humifusa*, a problem that likely developed from his use of herbarium specimens to interpret morphological variability across such a large range, and the fact that many such specimens lose diagnostic features once processed.

Pinkava (2003) likewise suggested that *O. humifusa* has completely yellow flowers and used red-centered flowers to separate *O. macrorhiza* from *O. humifusa*. However, the majority of the distribution given for *O. humifusa* by both Benson (1982) and Pinkava (2003) is of the red-centered taxon referred to here as the allotetraploid, *O. cespitosa* (Majure & Ervin 2008, Majure *et al.* 2012b, Majure *et al.* unpubl. data; see below), which was recognized previously based on taxonomic work carried out on the genus in Mississippi (Majure & Ervin 2008). Leuenberger (1993) recognized that *O. humifusa*, although now widely accepted as the correct name (Kalmbacher 1976) of a widely distributed species in eastern North America, had not been formally typified. Thus, he neotypified *O. humifusa* based on material from Berks County, Pennsylvania, as no type specimens for the species described by Rafinesque exist (Leuenberger 1993). This was based on the assumption that Benson's (1982) suggestion that only one taxon occurred in the area was actually correct.

Although in the present treatment more than one taxon is suggested to occur in what was previously considered to be the range of only *O. humifusa*, fortunately the specimen selected by Leuenberger (1993) does in fact represent what we consider to be *O. humifusa* s.str. We have adopted the earlier names *O. cespitosa* and *O. mesacantha* and applied those to two other taxa that occur throughout the range of what was previously recognized as *O. humifusa* s.lat. (Benson 1982, Wallace and Fairbrothers 1986, 1987; Pinkava 2003). Majure (2014) neotypified both *O. cespitosa* and *O. mesacantha*, as no type specimens of those two taxa by Rafinesque have ever been found. Although there is some ambiguity surrounding these two names (e.g., Rafinesque's brief descriptions and lack of type specimens), they in a number of ways correspond to the morphology and distribution of the two taxa that we consider separate from *O. humifusa* and likewise are the oldest names available for those taxa in the eastern US. Thus, they have priority over other names that could be used for the same taxa (see treatment below). The range of *O. humifusa* is often extended to parts of the western US, i.e., west of the Mississippi River (Benson 1982, Pinkava 2003, Powell *et al.* 2008), although those populations typically correspond to members of the *O. macrorhiza* complex, except for *O. cespitosa* in AR and MO, *O. mesacantha* in LA, and *O. nemoralis* in AR, LA, MO, and TX. Cytological (Majure *et al.* 2012b) and phylogenetic (Majure *et al.* 2012a, Majure *et al.* in prep.) work has provided further evidence, clearly indicating that *O. humifusa* s.l. is polyphyletic and actually consists of several, although somewhat cryptic, taxa.

Opuntia drummondii Graham was described from Appalachicola, Florida (Maund & Henslow 1846). Subsequent researchers described numerous taxa for the same type of material from the Atlantic and Gulf Coasts, i.e., *O. pes-corvi* LeConte ex Engelm (1857: 346), *O. frustulenta* Gibbes (1859: 273), and *O. tracyi* Britton (1911: 152). Benson (1982) later placed all of these taxa in synonymy under an ambiguous species of unknown origin and with no known type specimen, *O. pusilla* (Haworth 1803: 188) Haworth (1812: 195). The name has since been accepted by subsequent authors (Doyle 1990, Pinkava 2003, Wunderlin and Hansen 2003, 2011); however, we have elected and justified the use of the name *O. drummondii* (see treatment below), which was originally described from the southeastern US.

Opuntia nemoralis Griffiths was described from Longview, Texas, by Griffiths (1913) and it was placed in synonymy with both *O. drummondii* (Weniger 1967, 1970) and *O. humifusa* (Benson 1982). Phylogenetic, cytological (Majure *et al.* 2012b), and morphological work suggests that this species actually should be maintained as separate from both *O. drummondii* and *O. humifusa*.

Opuntia ochrocentra Small ex Britton & Rose (1923: 262) was described by J.K. Small from material collected on Big Pine Key in the Florida Keys (see Britton & Rose 1923). Benson (1982) concluded that this material was synonymous with *O. cubensis* Britton & Rose (1912: 14) from Guantánamo, Cuba. However, Majure *et al.* (2012b) showed that *O. cubensis* and *O. ochrocentra* were allopolyploids derived from different progenitors and thus not synonymous.

Hanks and Fairbrothers (1969a-b) performed morphological and ecological studies on populations of *O. humifusa* s.lat. in New Jersey, but despite many morphological differences among those populations, including populations with red-centered flowers (i.e., *O. cespitosa*), they concluded that one highly variable species occurs

in that area. No significant differences were found for habitat types among populations (Hanks & Fairbrothers 1969a). Wallace and Fairbrothers (1986) used seed proteins to determine if a genetic difference was evident among 15 populations of "*O. humifusa*" over a very small portion of the species' range (DE, FL, NC, NJ). Variation among those populations was discovered, with certain populations showing geographic cohesion often based on habitat type, with hybridization potentially responsible for some of the seed protein variation discovered. Wallace and Fairbrothers (1986) concluded, however, that only one species occurred throughout the range of *O. humifusa* s.lat., but they did not carry out any morphological or cytological work and based their taxonomic conclusions mostly on previous work from that limited geographic area (Hanks & Fairbrothers 1969a-b).

Doyle (1990) carried out a biosystematic study on the *O. humifusa* complex, wherein he analyzed herbarium specimens from throughout most of the range of the group and included morphological comparisons, as well as some chromosome counts over a limited distribution of the group (mostly along the eastern coast). His taxonomic conclusions were mostly in line with Benson (1982), although he did mention that northwesterly populations of *O. humifusa* s.lat. were more similar to *O. macrorhiza* than to *O. humifusa*, those populations that we here regard as *O. cespitosa*. Doyle (1990) also included *O. stricta* (Haw.) Haw. in the *O. humifusa* complex; however, that species has been shown phylogenetically to be in an entirely different group, the *Scheerianae* clade (sensu Majure *et al.* 2012a).

Many taxa which Benson (1982) previously recognized as infraspecific taxa are currently accepted at the species level [e.g., *O. curvispina* Griffiths (1916: 88), *O. gosseliniana* F.A.C. Weber (1902: 83), *O. macrocentra*, *O. martiniana* (Benson) Parfitt (1980: 416), *O. pottsii*, *O. santa-rita* (Griffiths & Hare) Rose (1909: 195), *O. spinosibacca* Anthony (1956: 246)] after detailed taxonomic work further clarified species boundaries (see Parfitt 1980, Pinkava 2003, Powell & Weedon 2004). Likewise, work on the *O. humifusa* complex has further clarified species boundaries, and certain taxa are recognized at the species level, which were previously recognized at the infraspecific level (i.e., *O. austrina*).

Eight species are recognized in this treatment of the *O. humifusa* complex: *Opuntia abjecta* Small, *O. austrina* Small, *O. cespitosa* Raf., *O. drummondii* Graham, *O. humifusa* (Raf.) Raf., *O. mesacantha* Raf., *O. nemoralis* Griffiths, and *O. ochrocentra* Small. Two subspecies of *O. mesacantha* are recognized: *O. mesacantha* subsp. *mesacantha* and *O. mesacantha* subsp. *lata* (Small) Majure. *O. cespitosa*, *O. humifusa*, and *O. nemoralis* are allopolyploid derivatives of the SE and SW subclades of the *Humifusa* clade. *O. mesacantha* subsp. *mesacantha* is a tetraploid but was apparently derived solely from the SE clade, while *O. mesacantha* subsp. *lata* is a diploid member of the SE clade (Majure 2012, Majure *et al.* 2012b, in prep.). *O. ochrocentra* is an interclade allopolyploid (pentaploid) derived from a member of the SE subclade (*O. abjecta*) and *O. dillenii* (Ker-Gawl) Haw. of the *Scheerianae* clade (Majure *et al.* 2012a, Majure *et al.* 2014).

Species concept:—We apply a combined approach using phylogenetic, evolutionary, ecological, and morphological species concepts to delimit species in the *Humifusa* clade (Donoghue 1985, de Queiroz 2007). Species relationships and boundaries in *Opuntia* are obscured by the paucity of morphological characters and frequently also by the inadvertent loss of the few characters that exist in the process of preparing herbarium specimens (although with effort, taxonomically useful specimens can be prepared; see Reyes-Agüero *et al.* 2007). In addition, the succulence and spininess of these plants inhibits collectors, and the resulting lack of herbarium material, and especially those with useful habitat and morphological data, make specific and infraspecific delineation—exclusively through the use of herbarium specimens—virtually impossible in many instances. Thus, the time-consuming process of collecting and growing plants for use in assessing morphological variability (and correlating this variability with geography, chromosome number, and phylogenetic knowledge) is the only means to study the group in a relatively unbiased manner.

The scarcity of detailed biological data, especially regarding variation in chromosome number and the lack of an understanding of phylogenetic relationships, has also long impeded proper species delimitation in this clade (Majure *et al.* 2014, Majure and Puente 2014). Those data coupled with observations based on live material greatly enhance the ability to make accurate estimates of species boundaries. Undoubtedly, some researchers may find the species circumscription employed here to be too finely drawn, while others may wish that even more species had been recognized. We have taken a relatively conservative approach to species delimitation, underscoring the evolutionary history of these organisms, as well as their morphological cohesiveness and ploidal levels. The taxa here recognized are believed to be both biologically meaningful (reflecting the complex evolutionary history of the group) and diagnosable using accepted/traditional systematics methods and are thus appropriate for recognition in floras (e.g., Majure 2015, 2017, Naczi 2016) and use in ecological investigations.

Diagnostic key:—Key to the members of the *Humifusa* Complex and *O. macrorhiza* follows:

1. Radial spines numerous, flattened at base, spines clear yellow to dark-yellow when young, strongly retrorsely barbed, flower buds red or green; Florida Keys..... *O. ochrocentra*
- Radial spines 0–1, cylindrical or flattened at base, spines red, brown and white banded, or dark-yellow when young, ± strongly retrorsely barbed, flower buds green; widespread US and northern Mexico..... 2
2. Plants forming treelets, large shrubs, or sub-shrubs; stems strongly ascending or erect, 0.3–2 m tall; inner tepals entirely yellow, restricted to FL..... 3
- Plants forming small shrubs in clumps or mats; stems weakly ascending, decumbent or trailing, 0.1–0.5 m tall; inner tepals entirely yellow or yellow with red bases, widespread..... 4
3. Plants developing from a single flat or terete stem (i.e., trunk), usually erect or strongly ascending, cladodes not easily disarticulating, spines ± barbed to the touch, outer tepals ascending, incurved, or recurved in bud; peninsular FL *O. austrina*
- Plants branching from the base, thus forming clumps, stems strongly ascending, cladodes easily disarticulating, spines strongly retrorsely barbed to the touch, outer tepals incurved in bud; Florida Keys *O. abjecta*
4. Cladodes easily disarticulating, flat or cylindrical, spines strongly retrorsely barbed to the touch..... 5
- Cladodes not easily disarticulating, flat, spines ± retrorsely barbed..... 6
5. Cladodes glaucous, gray-green, developing spines yellow or bright white, glochids yellow or dull brown, inner tepals yellow or rarely yellow with pinkish bases..... *O. nemoralis*
- Cladodes not glaucous, dark-green, developing spines dark reddish-brown, or brown and white mottled, glochids stramineous, inner tepals entirely yellow, never with colored bases..... 7
6. Cladodes not noticeably glaucous, dark green, roots fibrous or merely forming root thickenings proximal to the point of origin, inner tepals entirely yellow..... 8
- Cladodes glaucous, gray-green or lead-green, roots fibrous or tuberous, thickened distally to the point of origin, inner tepals entirely yellow, or yellow with reddish or brownish bases..... 9
7. Plants small, sometimes even diminutive, cladodes 0.8–11.1 × 0.6–3.4 cm, 5.3–14.8 mm thick, elliptical, oblong, or rounded in shape, terminal cladodes often cylindrical in cross section, with 1–2 areoles per diagonal row at midstem; coastal southeastern US..... *O. drummondii*
- Plants larger, never diminutive, cladodes 3.2–13.5 × 2.4–6.7 cm and 6.5–15.8 mm thick, elliptical, or rotund, terminal cladodes not cylindrical in cross section, with 2–3 areoles per diagonal row at midstem; Florida Keys..... *O. abjecta*
8. Cladodes spineless, mostly rotund or elliptical in outline, cladode margins smooth, not easily disarticulating, areoles generally 4 (5) per diagonal row at midstem, glochids mostly included within the areole, plants mostly (but not exclusively) in heavier soils (e.g., clays), slate, or limestone..... *O. humifusa*
- Cladodes generally with spines, mostly obovate, rotund, or elliptical in outline, cladode margins smooth or scalloped, ± easily disarticulating, areoles generally 3 (4) per diagonal row at midstem, glochids mostly exerted from the areole, plants most commonly in deep sandy soils or granite of the coastal plain..... *O. mesacantha* (in part)
9. Spines mostly 0–3 per areole, when two or three, generally the lower spines reflexed and the upper spine porrect, occasionally with two types of spines, smaller hair-like radial spines and larger central spines; N MX, SW US, Midwest US, AR, LA, MO..... *O. macrorhiza*
- Spines mostly 0–2, generally both spines in the same plane (i.e., both reflexed, both erect), only one type of spine produced; widespread eastern US, AR, MO, TX 10
10. Plants small, cladodes 4.5–8.4 cm × 2.8–5.8 cm, 8.1–14.2 mm thick, oblong, elliptical, or obovate, ± easily disarticulating, spines ± barbed to the touch, 1.4–3.0 cm long, inner tepals almost always yellow, rarely faintly pink at the base; W of the Mississippi River, AR, LA, MO, TX *O. nemoralis*
- Plants larger, cladodes 3.8–18.7 cm × 3.2–11.3 cm, 4–19.2 mm thick, mostly elliptical, obovate, or more commonly rotund, not disarticulating, spines smooth to the touch, 1.5–4.3 cm long, inner tepals basally tinged crimson red, orange-red, reddish brown, or pinkish-red; widespread, eastern US mostly E of the Mississippi River, AR, IA, MO, TX..... *O. cespitosa*

1. *Opuntia abjecta* Small ex Britton & Rose (1923: 257) (Fig. 4). Type:—UNITED STATES. **Florida:** Monroe Co., hammock, southeastern tip of Big Pine Key, 12 April 1921, *Small & Matthaus s.n.* (holotype NY-385967!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=200894)

Description:—Shrubs to 0.3 m tall, usually with multiple stems arising from the base, stems strongly ascending and rigid; roots commonly forming tubers in older individuals. Cladodes disposed mostly with margins parallel to the soil surface, thus the cladode disposed with the broad (flat) side perpendicular to soil surface, not becoming cross-wrinkled during the winter (as in other non-erect species, such as *O. drummondii* and *O. humifusa*). Cladodes easily disarticulating from the upper nodes, generally dark green, not glaucous, and with slightly raised podaria, cladodes round to obovate (or more typically elliptical in tetraploids) in outline with 2–3 areoles per diagonal row

at midsection of cladode, cladodes 3.2–13.5 cm × 2.4–6.7 cm, and 6.5–15.8 mm thick. Leaves dark green, ascending, parallel to the cladode surface, 3.5–7.0 mm long. Glochids straw yellow (stramineous), areolar trichomes white. Spines mostly 2 per areole, but oftentimes 3 on terminal cladodes, and generally more on basal cladodes (up to 6), which continue to produce new spines, when 3 spines on terminal cladodes, 2 long and 1 short, the spines dark reddish-brown when young, turning white when mature and gray in age, strongly retrorsely barbed, twisted to cylindrical in cross section, most spines twisted at least at the base, 2.5–5.6 cm long × 0.3–1 mm in diameter. Flowers: outer tepals dark green, ovate, tepal apices erect to incurved in bud, apex of bud rounded to acute (Fig. 4E), inner tepals 8, dark yellow (Fig. 4G–H), 21–26 mm long, stamens with yellow filaments turning orange-red as flower ages (Fig. 4G), stigma cream colored with 6 lobes. The diploid population at Big Pine Key produces mutant flowers with inner tepals producing anthers at their tips and finally with normal stamens in the center of the flower surrounding the gynoecium; the stamens are not thigmonastic (Fig. 4G; this aberrant flower type has also been seen in *O. austrina* and *O. drummondii*). The two tetraploid populations have completely normal flowers (Fig. 4H.) Berries barrel shaped, dark purple or yellow-green (Fig. 4I), 2.1–3 cm long. (Tetraploids only produce sterile fruit unless the flowers are outcrossed; Majure pers. obs.). Seeds 3.1–3.6 mm long, funicular girdle 0.66–0.88 mm wide, funicular envelope smooth, i.e., with no impression of the embryo apparent on seed surface.

Phylogenetic placement:—*Opuntia abjecta* is sister to *O. austrina* (Majure *et al.* 2012a; Fig. 2).

Chromosome number:— $2n = 22$ (diploid), $2n = 44$ (tetraploid) (Majure *et al.* 2012b). The diploid population occurs at the type locality of the species (Majure *et al.* 2012b). There are cryptic morphological differences among the diploid and tetraploid populations (cladode shape, spine length), although, these minor differences are not suggestive of species boundaries. Based on phylogenetic studies (Majure *et al.* unpubl. data) and morphological similarity, it appears most likely that the tetraploid populations are autopolyploid in origin.

Phenology:—Flowering late March–mid April, fruiting May–February.

Distribution and habitat:—As far as is known, *Opuntia abjecta* is restricted to the Florida Keys, Monroe Co. (Fig. 5) and has only been recorded from three populations. One specimen has been seen that was collected from Buena Vista, Miami (*Moldenke 373a*, MO), which undoubtedly originated from cultivated material from the Florida Keys. J.K. Small cultivated nearly all of the species of *Opuntia* that he collected in the southeastern US at Buena Vista (see Britton & Rose 1923). *Opuntia abjecta* is restricted to Key Largo limestone of the lower Florida Keys where it can be found growing in depressions in the limestone containing enough humus to support root establishment. It can be found growing with *Acanthocereus tetragonus* (Linnaeus 1753: 466) Hummelink (1938: 165), *Agave decipiens* Baker (1892: 184), *Batis maritima* Linnaeus (1759: 1289), *Borrchia frutescens* (Linnaeus 1753: 903) De Candolle (1836: 489), *Bursera simaruba* (Linnaeus 1753: 1026) Sargent (1890: 260), *Capparis cynophallophora* Linnaeus (1753: 504), *Conocarpus erectus* Linnaeus (1753: 176), *Harrisia simpsonii* Small ex Britton and Rose (1920: 152), *Maytenus phyllanthoides* Benth (1844: 54), *Mosiera longipes* (Berg 1856: 150) Small (1933: 937), *Opuntia stricta* var. *dillenii* (Ker Gawler 1817: 255) Benson (1969: 126), *Pilosocereus robinii* (Lemaire 1864: 74) Byles & Rowley (1957: 67), and *Pithecellobium unguis-cati* (Linnaeus 1753: 517) Benth (1844: 200).

Conservation status:—*Opuntia abjecta*, as evaluated by the IUCN, is considered to be critically endangered, CE (Majure & Griffith 2013). The species is restricted to the Florida Keys, where only three populations are known, and one of those populations is negatively affected by Key Deer, *Odocoileus virginianus* Zimmermann (1780) subsp. *clavium* Barbour & Allen (1922), invasive plant species, as well as the cactus moth, *Cactoblastis cactorum* Berg (1885) (Majure 2010, Majure & Griffith 2013). Those populations also are nearly at sea level and will easily be inundated with slight increases in ocean depths resulting from climate change.

Notes:—Benson (1982) considered this species to be synonymous with the Caribbean taxa, *O. triacantha* and *O. militaris* Britton & Rose (1919: 104). However, it is clear from morphology and DNA sequence data that *O. triacantha* is more closely related to other Caribbean taxa, such as *O. caracassana* Salm-Dyck (1849: 238), *O. jamaicensis* Britton & Harris (1911: 130), and *O. repens* Bello (1881: 277) (Majure *et al.* 2012b, Majure *et al.* 2014) rather than members of the *Humifusa* clade. Britton and Rose (1920) also considered *O. triacantha* to be more closely related to other Caribbean taxa, and even included the species in *Opuntia* Series *Tunae*, which includes *O. caracassana* and *O. jamaicensis*. *Opuntia militaris* is closely related to *O. caracassana*, *O. jamaicensis*, and *O. triacantha* but is likely not conspecific with *O. triacantha* (Majure *et al.* 2014).

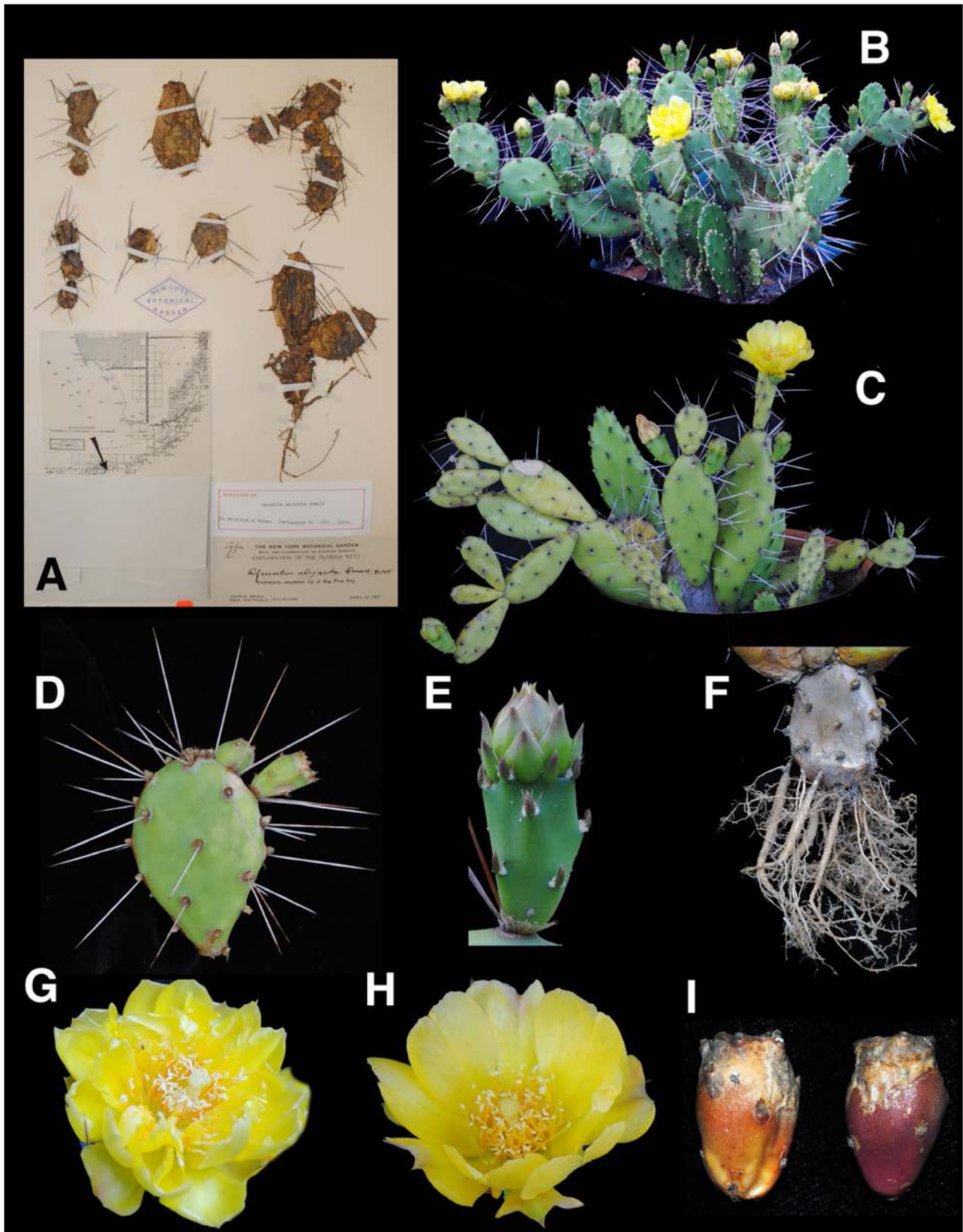


FIGURE 4. Morphological features of *O. abjecta*. A) type specimen, *J.K. Small s.n.*, Monroe Co., Florida (NY), B) growth form of diploid (*L.C. Majure 3908*), and C) tetraploid material (*L.C. Majure 3318*), D) spine development of a terminal cladode of diploid *O. abjecta* showing 1–3 spines produced per areole (*L.C. Majure 3908*), E) flower bud of *O. abjecta* (*L.C. Majure 3908*), F) slightly thickened roots developing on a specimen planted for almost 2 years (*L.C. Majure 3908*), G) flowers of diploid (*L.C. Majure 3908*), and H) tetraploid *O. abjecta* (*L.C. Majure 3318*), and I) barrel-shaped fruit of diploid *O. abjecta* (*L.C. Majure 3908*). All photos taken by L.C. Majure.

Although Crook & Mottram (2004) state that Benson (1982) neotypified *O. triacantha* using material from Big Pine Key, Florida (Benson 15367, POM 285314, 317654), Benson merely (and mistakenly) used that specimen of *O. abjecta* as a “representative specimen” of *O. triacantha* but never explicitly neotypified it using that collection. Likewise, they do not say “designated here” in their evaluation of the species, which leaves their suggestion that Benson neotypified *O. triacantha* irrelevant (see Art. 7.10). *Opuntia triacantha* was explicitly neotypified by Majure *et al.* (2014) with material from Antigua (*Smith 10442*, US). Regardless, the material used by Benson (1982) is of *O. abjecta* and does not represent true *O. triacantha* and thus should be dismissed as such (see Majure *et al.* 2014).

Opuntia triacantha is typically erect or sprawling with a single, well-defined trunk, whereas *O. abjecta* has numerous ascending stems produced from the base of the plant but never produces an erect main trunk. *Opuntia triacantha* produces chalky yellow spines when immature, which mature chalky white. The spines of *O. abjecta* are darker, reddish-brown when immature and mature bright white, not chalky white. Cladodes of *O. triacantha* are oblong to obovate or narrowly elliptic, while cladodes of *O. abjecta* are mostly rounded, obovate or broadly elliptic. *Opuntia triacantha* also has large tufts of yellow glochids associated with yellowish-clear trichomes, which are more pronounced than the stramineous glochids and white-clear trichomes of *O. abjecta*.

Material collected by *Small & Matthaus*, 12 April, 1921 was designated by Benson as the lectotype for *O. abjecta*, as the putative holotype could not be relocated (Benson 1982: p. 922). As this was a different date than the actual putative collection date given by Britton and Rose (1923), then that specimen should have been neotypified. However, it appears that Britton and Rose (1923) mistakenly suggested that the type of *O. abjecta* was collected in May of 1921 rather than when it actually was collected in April, as J.K. Small, in his handwriting, wrote “*Opuntia abjecta*, sp. nov.” on the sheet of material collected on 12 April, 1921. Thus, the material lectotypified by Benson (1982) should actually be considered the holotype of *O. abjecta*, as the only extant material of this specimen is at NYBG, the place of specimen deposition of the type of *O. abjecta*, according to Britton and Rose (1923).

Flowering times adjusts for this species depending on where it is grown. For example the species flowers late March to mid-April in Florida and Phoenix, AZ but may bloom later (late April-early May) in central Mississippi (Majure pers. obs.), demonstrating the plasticity in blooming time relative to local climate regimes.

Additional specimens examined:—UNITED STATES. **Florida:** Miami-Dade Co., Buena Vista, 1 Feb 1930, *Moldenke 373a* (MO)—[Note: likely cultivated by Small]; Monroe Co., Big Pine Key, 12 May 1919, *Barrtsch s.n.* (US); Long Key, rocky, open, low ground, 23 Apr 1966, *Byrd s.n.* (FLAS); Big Pine Key, 4 May 1951, *Killip 41332* (US); *ibid.*, 10 Jan 1952, *Killip 41708* (US); Cultivated at Montgomery Botanical Center, originally collected from Ann Williams yard on Big Pine Key, 6 Jul 2008, *Majure 3318* (DES, FLAS); SE end of Big Pine Key, Cactus Hammock, National Key Deer Refuge, 6 Mar 2010, *Majure 3908* (DES, FLAS); Big Pine Key, 22 Feb 1935, *Miller, Jr. 1710* (US); Crawl Key, Jul 2008, *Sauby s.n.* (FLAS); Big Pine Key, 17 May 1922, *Small s.n.* (NY, US).

2. *Opuntia ochrocentra* Small ex Britton & Rose (1923: 262) (Fig. 6). Type:—UNITED STATES. **Florida:** Monroe Co., Big Pine Key, hammock, southern end of Big Pine Key, 11 Dec 1921, *J.K. Small, G.K. Small et Matthews s.n.* (holotype NY-385996!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=77962; isotype US-00117014!, image available at <http://collections.nmnh.si.edu/search/botany/>)

Description:—Large, scrambling to slightly erect shrub from 0.4–0.5 m tall, usually with one main trunk, although, branching heavily above; roots fibrous. Cladodes mostly elliptical or rarely obovate in outline, with slightly scalloped margins, terminal cladodes disarticulating with only slight force, cladodes light green, 11.6–19 cm × 5.9–8.9 cm, 13.2–16.2 mm thick, with 3–4 areoles per diagonal row. Leaves light to dark green, small, 3.2–3.9 mm long. Glochids bright yellow (as in *O. dillenii*), conspicuous. Spines developing from the areoles in a stellate pattern (as in *O. dillenii*), 1–5 spines per areole, central spines delicate, 4.7–5.8 cm long × 0.86–1.3 mm in diameter, cylindrical in cross section or basally twisted, radial spines flattened at the base and deflexed along the face of the cladode in age, immature spines yellow aging white or mottled cream and brown and then gray. Flowers: outer tepals broadly ovate or triangular-ovate, yellow-green or reddish with light green margins, inner tepals 8, entirely yellow or yellow green, obovate or emarginate, with a mucronate tip, the abaxial surface often reddish down the center, 2.8–3.7 cm long, stamens with yellow filaments, stigma white or light yellow-green, 6-lobed. Berries clavate or barrel-shaped, 2.5–3.6 cm long, red to reddish-purple. [Fertile fruit are only produced when the flowers are outcrossed (Majure pers. obsv.), and this was observed in material from both populations.] Seeds 2.5–3 mm long, funicular girdle 0.85–1.25 mm wide, funicular envelope smooth.

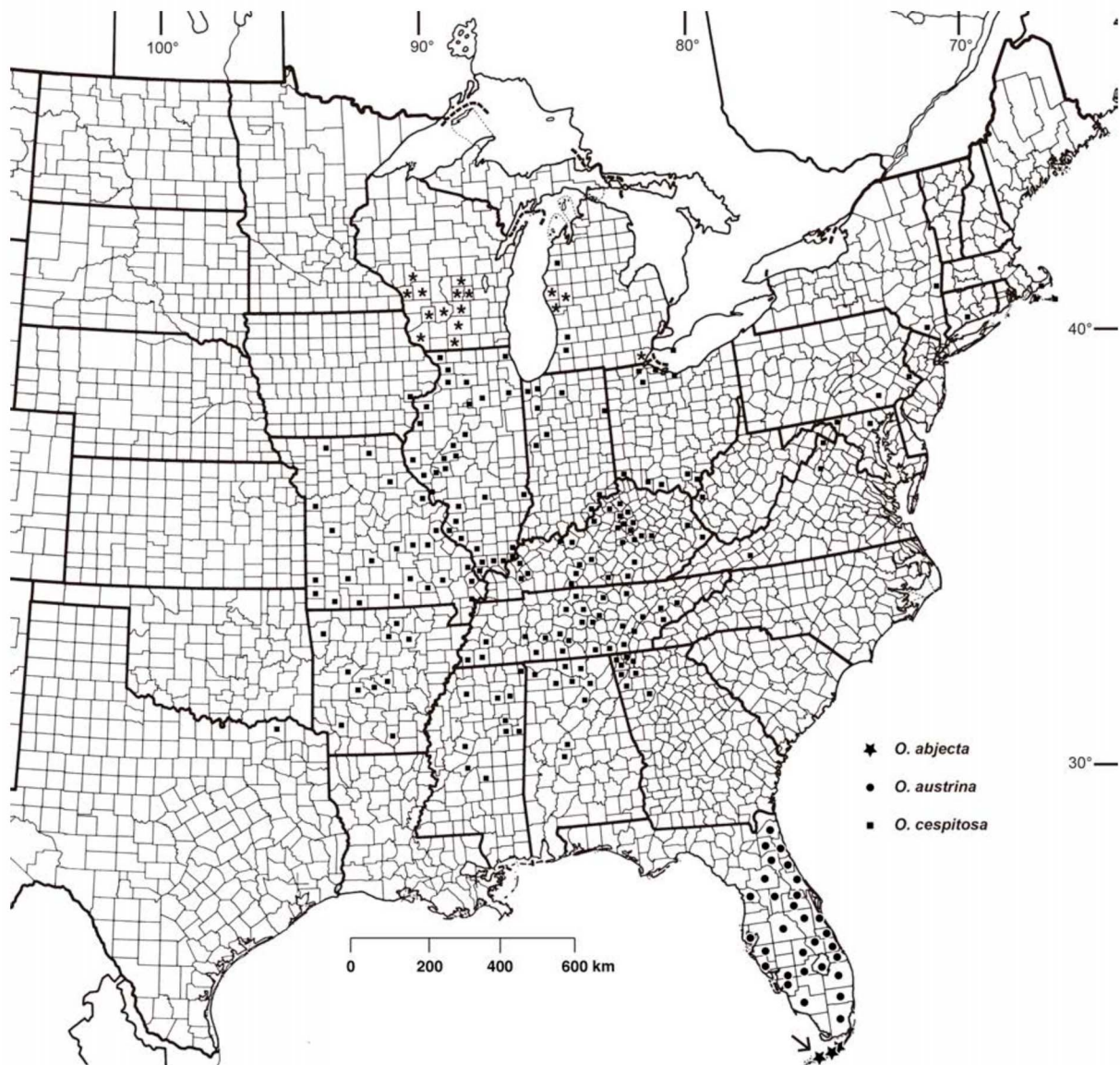


FIGURE 5. Geographic distribution of *O. abjecta* (stars), *O. austrina* (closed circles), *O. cespitosa* (squares), and *O. ochrocentra* (arrow). Putative introgressive forms of *O. cespitosa* in MI and WI are denoted with an asterisk.

Phylogenetic Placement:—This species is an allopolyploid (Majure *et al.* 2012b) of interclade hybrid origin most likely between *O. abjecta* and *O. dillenii* (Ker-Gawl.) Haw. of the *Scheerianae* clade (Majure *et al.* 2012a, Majure *et al.* 2014) with which it is largely sympatric on Big Pine Key.

Chromosome number:— $2n=55$ (pentaploid) (Majure *et al.* 2012b). *Opuntia ochrocentra* was reported as pentaploid from three individuals that have been analyzed (Majure *et al.* 2012b).

Phenology:—Flowering early April–May fruiting August–February.

Distribution and habitat:—*Opuntia ochrocentra* is only known from the lower Florida Keys and co-occurs with *O. abjecta* on Big Pine Key (Fig. 5; arrow), where it has nearly been extirpated through attack by *Cactoblastis cactorum* (Majure 2010, Majure pers. obs.) and anthropogenic disturbance (Benson 1982, Majure pers. obs.), as well as destruction by the high density Key Deer population. It is also known from Big Munson Island, just west of Big Pine Key (see collections *L.C. Majure 3968–69*, FLAS), where it has also been seen under attack by *C. cactorum* (Majure pers. obs.). It has been reported from Cape Romano as well (Small 1933), but no specimens have been seen from that locality (Benson 1982; Majure pers. obs.). *Opuntia ochrocentra* occurs essentially in the same habitat as *O. abjecta*, one of its putative parents (Majure *et al.* 2012b), on Key Largo limestone.

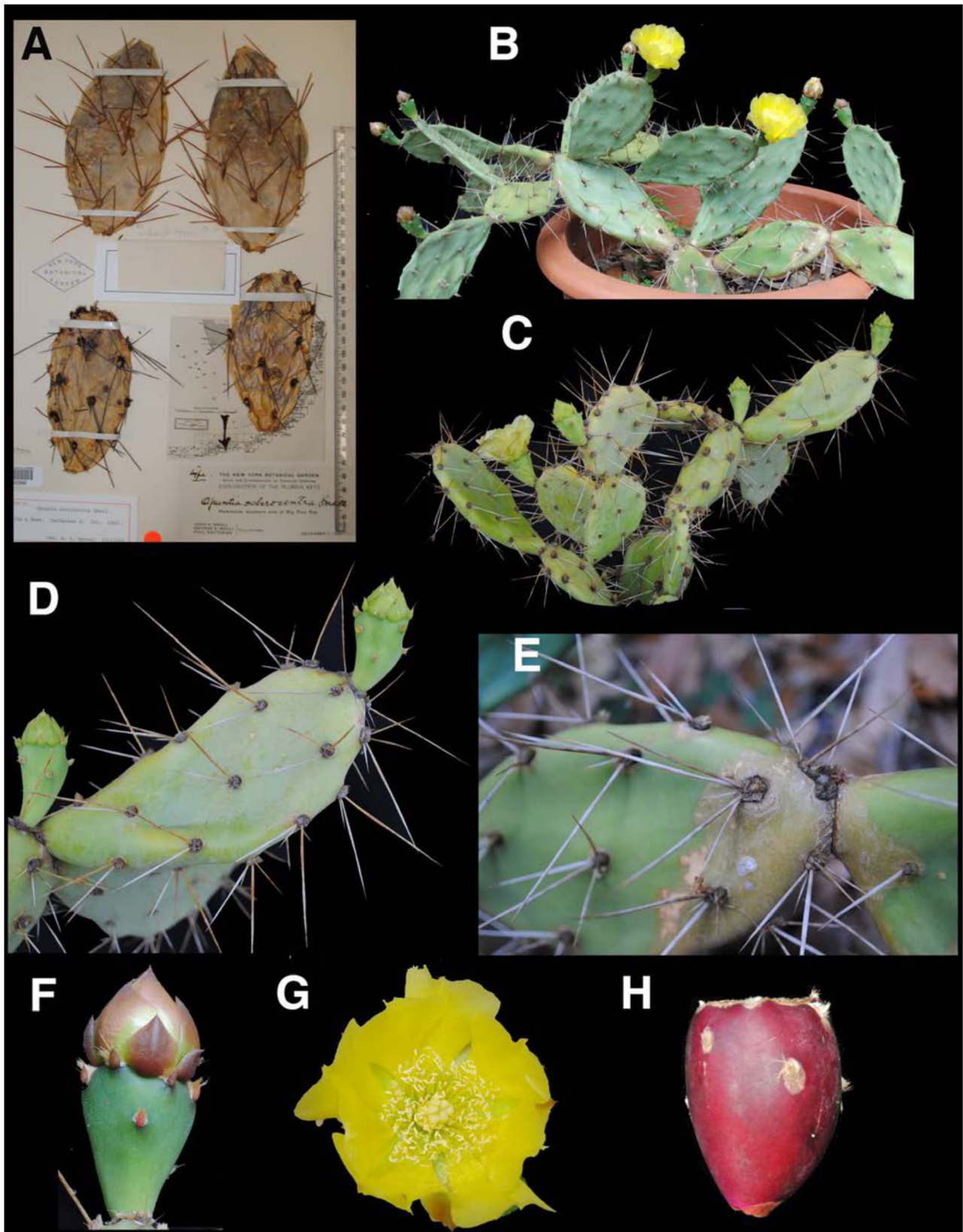


FIGURE 6. Morphological features of *O. ochrocentra*. A) type specimen of *O. ochrocentra*, J.K. Small s.n., Monroe Co., Florida (NY), B-C) growth forms of *O. ochrocentra* from B) Big Pine Key, L.C. Majure 3907, and C) Big Munson Island, L.C. Majure 3968, D) spine characters and flower buds of L.C. Majure 3968, E) spine characters of L.C. Majure 3907 showing numerous radial spines flattened at the base and several central spines twisted or cylindrical at the base, F) flower bud, G) flower, and (H) mature fruit of L.C. Majure 3907. All photos taken by L.C. Majure.

Conservation status:—At the time of the IUCN evaluation of cactus species, *O. ochrocentra* was still considered synonymous with *O. cubensis* (Benson 1982, Pinkava 2003), which was shown to be in error (Majure *et al.* 2014). Thus, *O. ochrocentra* has not been formally evaluated. That only two very small populations of this species exist and in close proximity to one another, one on Big Pine Key and the other on Big Munson Island, and both populations are threatened by a large population of key deer, invasive plant species, and *Cactoblastic cactorum*, *O. ochrocentra* should be considered critically endangered.

Notes:—This species was placed in synonymy with *O. cubensis* Britton and Rose by Benson (1982) and had since been treated likewise in other treatments (Pinkava 2003, Wunderlin & Hansen 2011). Molecular, morphological, and cytological data show that *O. ochrocentra* is not conspecific with *O. cubensis* and thus should not be considered synonymous with that species (Majure *et al.* 2014). As noted by Britton and Rose (1923), *Opuntia ochrocentra* most closely resembles *O. dillenii*, one of its putative progenitors, although, its spines are more delicate and age gray as in *O. abjecta* (its other putative progenitor; Majure *et al.* 2012a, Majure *et al.* 2014). *Opuntia ochrocentra* also forms a smaller, more delicate shrub compared to the more erect and robust growth form of *O. dillenii*. Benson's photo of *O. cubensis* (Benson 1982; Fig. 429) actually is of the South American species, *O. sulphurea* G.Don, apparently received from cultivated material (see Majure *et al.* 2014) and is still being grown at Desert Botanical Garden in Phoenix, Arizona (DBG 1994 0034: <http://livingcollections.org/dbg/Home.aspx>).

Although Benson (1982) lectotypified *O. ochrocentra* using material from US, as apparently material from NY could not be found, type material from NY does in fact exist and should be considered the holotype material, as originally cited in the protologue (Britton and Rose 1923).

Additional specimens examined. UNITED STATES. **Florida:** Monroe Co., Big Munson Island, 8 Mar 2010, Majure 3968 (DES, FLAS); [ibid.] Majure 3969 (DES, FLAS); Big Pine Key, 12–18 Feb 1935, Killip 31423 (US); Big Pine Key, hammock, 2 Mar 1936, Killip 31712 (US); Big Pine Key, SE hammock, 19 Mar 1952, Killip 42026 (US); S end of Big Pine Key, 6 Mar 2010, Majure 3907 (DES, FLAS); hammock, S front of Big Pine Key, 17 May 1922, *Small s.n.* (US).

3. *Opuntia austrina* Small (1903: 816) ≡ *Opuntia compressa* (Salisbury 1796: 348) Macbride (1922: 41) var. *austrina* (Small) Benson (1969: 125) ≡ *Opuntia humifusa* (Rafinesque 1820: 15) Rafinesque (1830: 2) var. *austrina* (Small) Dress (1975: 164) (Figs. 7–8). Neotype (designated here):—UNITED STATES. **Florida:** [Miami-Dade Co.] Miami, in pinelands, 28 October–28 November 1903, *Small 1216* (US-00292755!, image available at <http://collections.nmnh.si.edu/search/botany/>; isoneotype NY!; see below for discussion regarding the incorrect typification of *O. austrina* by Benson (1982))

= *Opuntia ammophila* Small (1919: 29) ≡ *Opuntia compressa* (Salisb.) J.F.Macbride var. *ammophila* (Small) L.D.Benson (1969: 124) ≡ *Opuntia humifusa* (Raf.) Raf. var. *ammophila* (Small) L.D.Benson (1976: 59). Type:—UNITED STATES.

Florida: [St. Lucie Co.] hammock on sand dune, St. Lucie Sound, 6 mi S of Ft. Pierce, 20 Dec 1917, *Small s.n.* (holotype NY-385970!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=228706; isotype NY-385969!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=228707).

= *Opuntia pisciformis* Small ex Britton & Rose (1923: 258). Type:—UNITED STATES. **Florida:** [Duval Co.] dunes, Pilot Island, 26 April 1921, *Small s.n.* (holotype NY-385997!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=527468).

= *Opuntia turgida* Small ex Britton & Rose (1923: 265). Type:—UNITED STATES. **Florida:** [Volusia Co.] about 5 mi S of Daytona, 30 Nov 1919, *Small, Britton et DeWinkler s.n.* (holotype NY-386005!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=535674; isotypes NY-386006!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=535675; US-00240564!, image available at <http://collections.nmnh.si.edu/search/botany/>).

= *Opuntia atrocapersis* Small (1933: 905), *syn. nov.* Type (neotype designated by Majure 2014: 1):—UNITED STATES. **Florida:** Monroe Co., sand dunes; Middle Cape Sable, 28 Nov 1916, *Small s.n.* (US-00292754!, image available at <http://collections.nmnh.si.edu/search/botany/>).

= *Opuntia cumulicola* Small (1933: 907). Type:—UNITED STATES. **Florida:** [Miami-Dade Co.] Bull Key, opposite Lemon City, 6 Nov. 1903, *Small et Carter 970* (holotype NY-385978!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=703225; isotypes NY!, US!).

= *Opuntia nitens* Small (1933: 906). Type:—UNITED STATES. **Florida:** [Volusia Co.] hammock, 5 mi S of Daytona, Florida, 23 Aug 1922, *Small, Small et DeWinkler s.n.* (holotype NY!; isotype US!).

= *Opuntia polycarpa* Small (1933: 905). Type:—UNITED STATES. **Florida:** [Collier Co.] sand-dunes, Caxambas Island, 11 May 1922, *Small s.n.* (holotype NY-386000!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=96416; isotypes NY-386001!, image available at <http://sweetgum.nybg.org/science/vh/>

Description:—Small to large shrubs, 0.2–1.2 (–2) m tall, usually erect but in some cases merely ascending, but with a central trunk, which may be cylindrical or flattened (Fig. 5B, D-E), but plants damaged at the base of the trunk (e.g., burned, cut off, scarred, damaged by insects) often producing numerous branches from the base, and in age basal-most cladodes often strongly fused and appearing as a single unit (Fig. 5D; instead of several stem segments), the plants typically heavily branched towards the apex and frequently semaphore-like; roots commonly tuberous (Fig. 5C) or fibrous, the tubers more commonly produced in very well drained, deep sands. Cladodes highly variable, generally elliptic, but commonly obovate or rarely completely round, dark or light green, sometimes slightly glaucous, never cross wrinkling unless under severe drought stress, 6.5–29.5 cm × 3.7–9.5 cm, 6.4–10.9 mm thick, mostly with slightly scalloped margins, but margins sometimes non-scalloped, from 2–6 (mostly 4) areoles per diagonal row, cladodes occasionally easily disarticulating during winter months (in the *polycarpa* entity, see below), but generally with cladodes not easily detaching (the *ammophila* entity, see also below). Leaves dark green or sometimes glaucous, 6.7–13.8 mm long, ascending (parallel to the cladode surface; Fig. 5F) or commonly spreading with the tips recurved. Glochids conspicuous, exerted from the areole, stramineous, forming adaxial crescent in older cladodes from the compression of the areole, trichomes mostly clear or appearing clear-white. Spines mostly 1–2 per areole on terminal cladodes, although up to 3, or plants occasionally spineless, the trunks occasionally with up to 18 spines per areole, round in cross section or commonly twisted longitudinally, the spines highly variable in length, 2–10.3 cm long, 0.6–1.2 mm in diameter, strongly retrorsely barbed or relatively smooth to the touch, developing spines dark reddish-brown or mottled (banded) brown-yellow and white, turning white after maturity and finally gray in age, often deflexed upon maturation. Flowers: outer tepals dark green, triangular or triangular-subulate, tips ascending, incurved or commonly recurved in bud (Fig. 5G), inner tepals 8, dark yellow to light sulfur yellow (Fig. 5H-I), obovate 3.4–4.2 cm long, with a mucronate tip, staminal filaments yellow or greenish yellow, stigmas white with generally 6 lobes. Berries clavate or barrel shaped (Fig. 5J-K), dark purple, red, pink, or yellow-green when mature, 2.8–5.0 cm long. Seeds 3.9–4.7 mm long, funicular girdle 0.67–1.26 mm wide, funicular envelope smooth with the cotyledon and hypocotyl region of the embryo only moderately raised.

Phylogenetic placement:—*Opuntia austrina* is sister to *O. abjecta*, as shown in Majure *et al.* (2012b) (Fig. 2).

Chromosome number:— $2n=22$ (diploid) (Majure *et al.* 2012b).

Phenology:—Flowering late March–early May, fruiting July–January (rarely through to February).

Distribution and habitat:—*Opuntia austrina* is mostly restricted to the central Florida peninsula east to the Atlantic Coast (Fig. 4) or west to the Gulf Coast in parts of the southern peninsula and is mostly surrounded by populations of *O. mesacantha* subsp. *lata*, although both species have been seen growing together in Polk and Highlands cos. (Majure pers. obs., e.g., *L.C. Majure 3977*). One specimen from Gadsden Co., Florida (*L.C. Anderson 25542*; FSU) was tentatively identified as *O. austrina* by Majure (2012) but upon closer inspection the specimen conforms most closely to *O. mesacantha* subsp. *mesacantha*, which also has been seen (rarely) to form ascending stem segments of up to 3–4 pads high (*L.C. Majure 1082*, *L.C. Majure 767*; MISSA). One specimen from Lowndes Co., Georgia, *K. Strickland s.n.* (GA, UNC), was described with essentially the same growth form as *O. austrina*, but the specimen is insufficient to unequivocally place within *O. austrina* and otherwise exhibits characters more suggestive of *O. mesacantha* subsp. *lata*. Attempts to find the population from which this specimen is based have been unsuccessful (Majure pers. obs.).

Opuntia austrina is most common in peninsular Florida scrub habitat dominated by scrub oaks, *Quercus chapmanii* Sargent (1895: 93), *Q. geminata* Small (1897: 438), *Q. myrtifolia* Willdenow (1805: 424) and sand pine, *Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sargent (1880: 199), as well as sandhills dominated by *Pinus palustris* Miller (1768) or *Pinus elliottii* Engelman in Sargent (1880: 186). It also is commonly associated with *Aristida stricta* Muhlenberg (1817: 174), *Asimina incana* Exell (1927: 69), *A. pygmaea* Dunal (1817), *Ceratiola ericoides* Michaux (1803: 222), *Dichantheium aciculare* (Desvaux ex Poiret 1816: 274) Gould & Clark (1979: 1116), *Licania michauxii* Prance (1970: 526), *Lyonia ferruginea* Nuttall (1818: 266), *Sabal etonia* Swingle ex Nash (1896: 99), *Serenoa repens* (Bartram 1791: 61) Small (1922: 62), *Smilax auriculata* Walter (1788: 245), *Ximenia americana* Linnaeus (1753: 1193), among many other species.

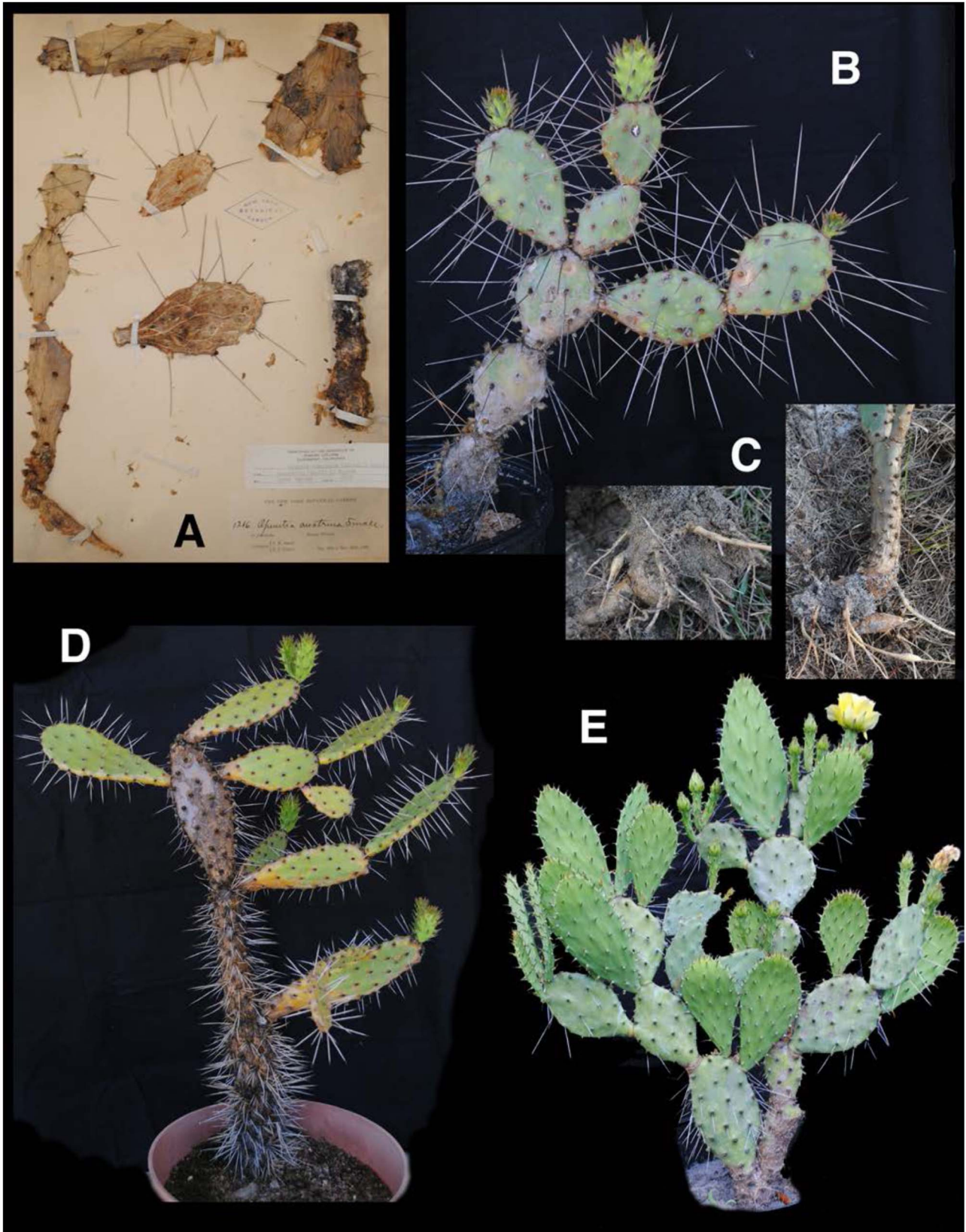


FIGURE 7. Morphological features of *O. austrina*. A) isotype specimen of *O. austrina*, *J.K. Small s.n.*, Miami-Dade Co., Florida (US), B) example of *O. austrina*, entity *polycarpa* from Highlands Co., FL, with spines up to 10 cm long (*L.C. Majure 3975*), C) tuberous roots of *O. austrina* (*L.C. Majure 4184* (left)) and *L.C. Majure 4189* (right)), D-E) growth forms of *O. austrina*, D) *ammobila* entity from Marion Co., Florida (*L.C. Majure 2754*), E) and Indian River Co., Florida (*L.C. Majure 4182*). All photos taken by L.C. Majure.

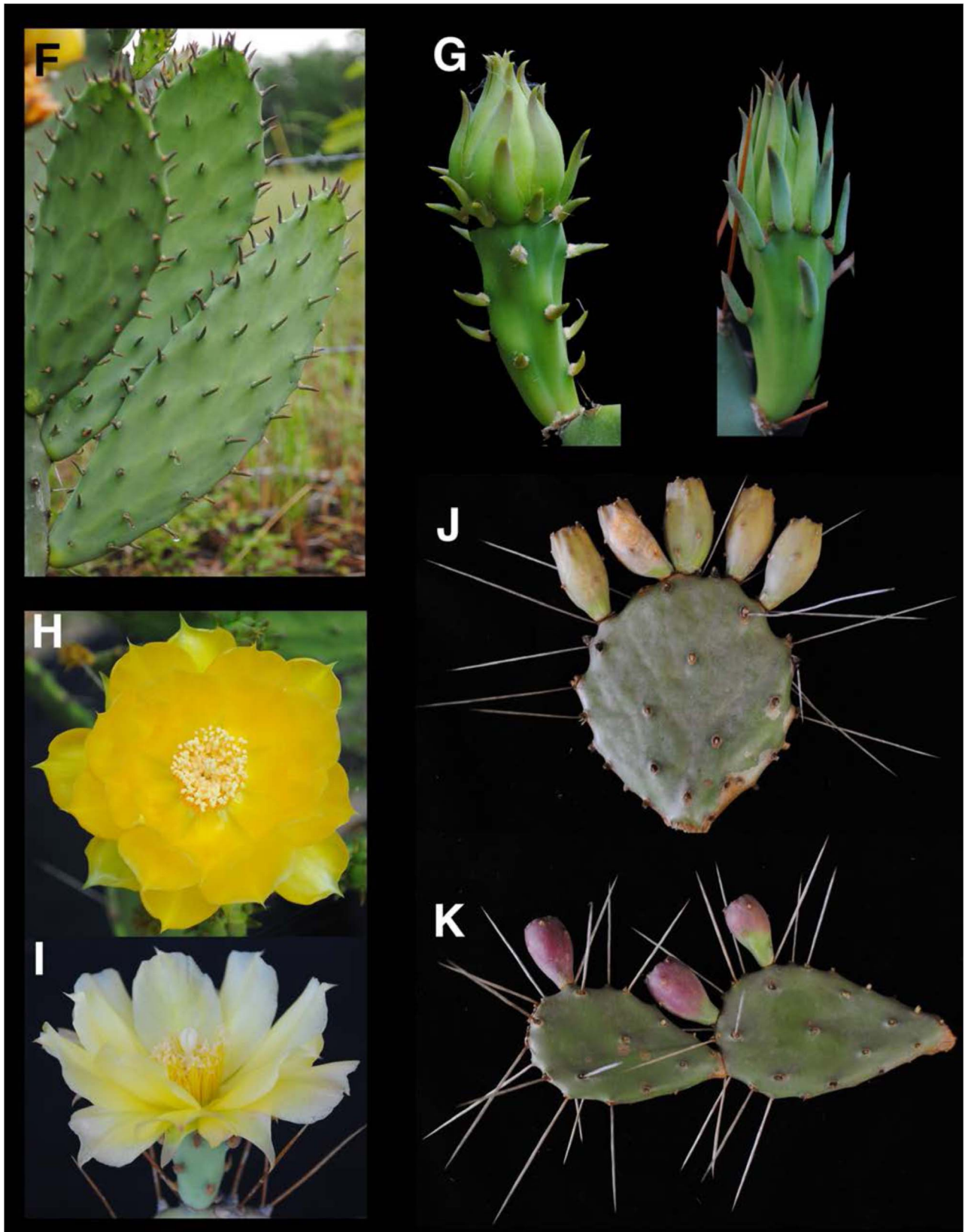


FIGURE 8. Morphological features of *O. austrina*, continued. A) long-shoot leaves of *O. austrina* from Marion Co., Florida (*Majure 5930*), B) flower buds of *O. austrina*, from Indian River Co., Florida (*Majure 4182* (left)) and Okeechobee Co., Florida (*Majure 4185* (right)), C-D) color variation in flowers of *O. austrina*, (C from *Majure 4182* and D from *Majure 3450*), and E-F) fruit color and shape variation of *O. austrina* from Highlands and Polk cos., Florida (*Majure 4226, 4227*, respectively). All photos taken by L.C. Majure.

Conservation status:—*Opuntia austrina* was evaluated to be of least concern by Majure and Griffith (2013b) and did not at that time include *O. ammophila*, also considered to be of least concern (Majure 2013a). *Opuntia austrina*, although restricted to Florida, occurs over a very broad distribution in the Florida Peninsula and populations of the species are numerous. Although *Cactoblastis cactorum* has been recorded on *O. austrina* (see Majure 2010, Sauby *et al.* 2012) and anthropogenic disturbance is a threat, this species appears to be stable with high numbers of mature, reproductive individuals throughout populations of the distribution of the species.

Notes:—*Opuntia austrina* is the one of the most common species in the Florida peninsula and is most often found in remnant scrub habitats. *Opuntia austrina* is a highly polymorphic species and has by some workers been divided into a number of other taxa that are here placed in synonymy: *O. ammophila*, *O. atrocapersis*, *O. cumulicola*, *O. nitens*, *O. polycarpa*, and *O. turgida*. Of those six taxa, *O. ammophila* and *O. polycarpa* are quite distinctive and easily recognizable in parts of their ranges and are here informally referred to as “entities” of *O. austrina*. The *O. ammophila* entity is most common from the Ocala National Forest in Lake, Marion, and Putnam counties south to St. Lucie Co., where it was first described (Small 1919). *Opuntia ammophila* can form relatively large, erect shrubs or treelets up to 1.2 m tall with a large diameter, cylindrical trunk (up to 40 cm in circumference). John K. Small recorded individuals up to nearly 2 m tall (Small 1919, 1933) but no such individuals have been found since. The *O. polycarpa* entity is primarily found in Highlands and Polk counties along the Lake Wales’ Ridge but individuals have also been seen from Collier (the type) and Lee counties. The *O. polycarpa* entity is recognized by its extremely long spines, sometimes up to 10 cm long that are strongly retrorsely barbed (see Figs. 7B & 8I-K), oftentimes easily disarticulating cladodes, and generally strongly recurved tips of the outer tepals when in bud. The *O. polycarpa* entity may form relatively large shrubs or even small treelets to 1 m tall. Although, both the *O. ammophila* and *O. polycarpa* entities are strikingly distinct in certain populations, they form a gradation of morphological characters that overlap with other populations of *O. austrina* including growth form, spine production and color of spines, the degree of spine barbedness, cladode shape and size, and tepal shape. Hence, morphological variation within most populations of both of these entities directly overlaps with those characters seen in typical *O. austrina* and for this reason, as well as the lack of phylogenetic structure, these taxa are treated as part of *O. austrina*.

Another entity of *O. austrina*, which in contrast to the *O. polycarpa* and *O. ammophila* entities has not been formally named, is noteworthy because it forms erect shrubs, which are basically miniature forms of the *O. ammophila* entity, ranging in height from 20-30 cm tall. This entity produces copious spines and in certain specimens resembles an erect form of *O. drummondii* (see below). The spines are usually strongly barbed, tuberous roots are produced, and a cylindrical trunk is also a common feature of this entity. It has been collected in Osceola (L.C. Majure 3702, 4181; FLAS), Orange (L.C. Majure 2086; MISSA), and Lee (Moldenke 956; NY) counties.

Typical *Opuntia austrina* forms erect shrubs from 40-60 cm tall, although, with a relatively flat trunk. Plants may or may not be heavily covered with spines, and the spines are slightly retrorsely barbed to the touch or oftentimes smooth. Cladodes do not disarticulate easily and plants are generally smaller and less robust than the *O. ammophila* and *O. polycarpa* entities.

Benson (1982) included *O. austrina*, at the infraspecific level, in his broad concept of *O. humifusa*, however, phylogenetic and cytological analyses have shown that *O. austrina* and *O. humifusa* are not synonymous (Majure *et al.* 2012a, Majure *et al.* in prep.). Benson (1982) cited *O. humifusa* var. *austrina* (here *O. austrina*) from Big Pine Key, although, the photo presented (p. 442; Fig. 443) is actually of *O. abjecta*, not *O. austrina*. Benson (1982) also concluded that *O. pisciformis* (included here under synonymy with *O. austrina*) was of hybrid origin between *O. humifusa* and *O. stricta*. However, characters possessed by the type specimen of *O. pisciformis* fall completely within the bounds of *O. austrina*, as circumscribed here—a hybrid origin of *O. pisciformis* appears dubious. Benson (1982) also considered *O. cumulicola* to be of hybrid origin, as the type material of *O. cumulicola* contains a large cladode that fits within the range of something like *O. stricta*. However, it is clearly *O. austrina* based on the spine color and shape and glochid color. Majure (pers. obsv.) has seen numerous large-padded specimens of *O. austrina* throughout its range that are equal to or larger than the size cladodes seen on the type material of *O. cumulicola*.

Pinkava (2003) recognized *O. austrina*, as circumscribed here, as *O. humifusa* var. *ammophila*, and suggested that the upright growth form was owed to a high number of frost-free days where the species is normally found. He did, however, qualify that the taxon needed more ecological research to be fully understood. Majure (pers. obsv.) has grown seeds of *O. austrina* and also planted the species at higher latitudes under colder winter temperatures

(central Mississippi) where the upright growth form is always maintained. So it is clear that growth form is under genetic control in *O. austrina* and not merely an artifact of local environmental conditions. Germinated seeds of *O. austrina* produced 60 cm tall, reproductively mature individuals, within three years of germination in one case (seeds germinated from *Majure 2754*).

Typification:—Benson (1982) designated the specimen *Small & Carter s.n.* as the lectotype for *O. austrina* (this was followed by *Majure 2012*), although the original material cited by Small (1903: 1335) was of *Small & Nash 198*. Thus, the specimen cited by Benson (l.c.) as “*Small & Carter s.n.*” cannot serve as the lectotype and has been selected as the neotype here, because *Small & Nash 198* has not been found. All material from the *O. humifusa* complex growing in that area from where *O. austrina* was described or specimens that have been seen from that area are of *O. austrina*, thus, the neotype material selected is morphologically identical to that described by Small for *O. austrina*.

Additional specimens examined. UNITED STATES. **Florida:** Brevard Co., 2 km N of Sebastian Inlet State Park, E side of Hwy. A1A, 7 Apr 1984, *Brunton 4895* (MICH); Malabar Cape, S of Melbourne Beach, dunes and hammock between US 1A1 and Indian River, 22 May 1965, *Lakela 28682* (UGA); off of A1A SW of Jetty Park, Cape Canaveral; 17 0539480N 3141126E, 16 Mar 2007, *Majure 2087* (MISSA); Hammock on old shell mound at side of road, shaded area, Rockledge, 12 Apr 1939, *Young 24* (FLAS). Charlotte Co., Port Charlotte Beach State Recreation Area, N portion of park, bayside, Manasota Key, 7 Mar 1991, *Erickson PC0031* (USF). Citrus Co., Florida 491, ca. 1 mi E of Holder, 26 Mar 1965, *Beckner 662* (FLAS); Lecanto, 4 mi E of US 19 on Rt. 484, 11 May 1983, *Schmid A-233* (USF). Clay Co., Camp Blanding, along N side of Ft. Lauderdale St., 3 May 2014, *Frank s.n.* (FLAS). Collier Co., 1 mi E of North Naples on Florida 846, 7 Aug 1967, *Lakela 30902B* (USF). Duval Co., Florida Beach, 17 Nov 1929, *Moldenke 5233* (NY). Flagler Co., Flagler Beach: off of Hwy. A1A S, just E of Silver Lake, 17 May 2008, *Majure 3222* (FLAS). Glades Co., 7.4 km E of Charlotte Co. line, 9.7 km S of Highlands Co. line, NE corner of C-731 and Florida 74, 8 May 2010, *Franck 2131* (USF). Highlands Co., Josephine Creek, 2 Apr 1945, *Brass 14942* (US); Lake Annie, 24 May 1945, *Brass 15216* (US); off of Hwy. 27N, ca. 21 km S of the town of Lake Placid; lower portion of Lake Wales Ridge, 20 Jul 2008, *Majure 3450* (DES, FLAS); Just N of Polandale off of Hwy. 27N, 11 March 2010, *Majure 3974* (FLAS); Just N of Venus off of Hwy. 27N, 11 Mar 2010, *Majure 3975* (DES, FLAS); off of Hwy. 27N at the town of Seabring along the Lake Wales Ridge, 11 Mar 2010, *Majure 3976* (DES, FLAS); Off of Hwy. 64W, just E of Avalon Park, corner of Dodd's Rd., empty lot, 11 Mar 2010, *Majure 3978* (DES, FLAS); off of Hwy. 64W at the corner of Bermuda Rd., 0.5 km NW of Hwy. 64W, 27.60035 81.53280, 6 Sept 2010, *Majure 4114* (DES, FLAS); town of Avon Park, ca. 1.5 mi N of Hwy. 64 W, along Olivia Rd. at junction with Laredo Rd., 25 Nov 2011, *Majure 4226* (FLAS). Indian River Co., off of Hwy. 1S, jct. of 65th St. and Old Dixie Hwy. at Winter Beach, 11 Feb 2011, *Majure 4182* (DES, FLAS); ca. 0.1 km from junction of Hwy. 1S and 65th St. off of Hwy. 1S along roadside 11 Feb 2011, *Majure 4183* (FLAS); from Hwy. 1S just S of Vero Beach off of Hwy. 606 (Oslo Rd.) and intersection of 11 lane, 11 Feb 2011, *Majure 4184* (FLAS). Lake Co., W side of Rt. Florida 19, ca. 0.3 mi S of junct. w/ S US Business 441 (Florida 500-A) in Tavares (0.2 mi N of Dora Canal; S29, T19S, R26E, 20 Sept 1979, *Judd 2462* (FLAS); Ocala National Forest, off of Hwy. 40 W ca. 4 km W of Aster Park and 2 km E of jct. with Hwy. 19; along roadside; 24 May 2008, *Majure 3246* (FLAS); in dry sandy woods near Astatula, 5 Dec 1929, *Moldenke 5369* (NY). Lee Co., Wulfert, western Sanibel, 28 Mar 1973, *Brumbach 8290* (FLAS). Manatee Co., South Fork State Park, 4 Apr 1992, *Owens SF0050* (USF); Marion Co., Ocala National Forest, Salt Springs Island, near Rt. 314. S34, T13S, R25E, 13 May 1980, *Judd 2638* (FLAS); Ocala National Forest, Jan 1942, *Kurz 282* (MICH); Ocala National Forest, just N of rt. 40 4 km W of Rt. 19, 29deg 10'N, 81deg 40'W, 24 Feb 1994, *Loconte 875* (NY); Lynn: corner of Hwy. 40 E and SE 179 Ave.; 13 Oct 2007, *Majure 2753* (FLAS); W side of Hwy. 19N & NE 77 St., 13 Oct 2007, *Majure 2754* (FLAS); Ocala National Forest, ca. 1 km S of Lake Kerr, off of FR 88-3, 9 Feb 2008, *Majure 2826* (FLAS); Ocala National Forest, Salt Springs off of Hwy. 19S at jct. with Hwy. 314, 24 May 2008, *Majure 3244* (FLAS); Ocala National Forest, Big Scrub, off of Hwy. 40., 24 May 2008, *Majure 3247* (FLAS); Co. rd. 314, 13.1 mi ENE of junct. with state Hwy. 40, ca. 6.5 mi from Salt Spring, 25 Apr 1993, *Parfitt 5171* (ASU); *ibid*, *Parfitt 5172* (ASU); scrub, 15 mi E of Ocala, 11 Mar 1939, *Young 12* (FLAS). Miami-Dade Co., Miami, 4 Jan 1909, *Griffiths 9899* (US); Miami, 28 Oct - 28 Nov 1903, *Small s.n.* (NY); Miami, 1 Feb 1911, *Small s.n.* (NY). Okeechobee Co., 0.25 km S of the Okeechobee County line, off of Hwy. 441W, 11 Feb 2011, *Majure 4185* (FLAS); ca. 0.6 km N of Hwy. 718 and 4 km N of town of Okeechobee at Whispering Pines; roadside of Hwy. 441S, 11 Feb 2011, *Majure 4186* (FLAS). Orange Co., abundant in deep sand along RR tracks to the W, in Oakland, 10 Apr 1977, *Harriman 13342* (NY); 3.5 mi SE of

Hwy. 528 along Hwy. 520 under powerline; 17 0504805N 3142822E, 16 Mar 2007, *Majure 2086* (MISSA); Orlando, at the corner of Conroy-Windmere and Hiwasee Rd., 6 Mar 2010, *Majure 3962* (DES, FLAS); Orlando, Shadow Bay Park off of Turkey Lake Rd., 6 Mar 2010, *Majure 3963* (FLAS); roadside ca. 3 mi SW of Apopka, SW 1/4 of S18, T21S, R28E, 25 Apr 1966, *Schudder 4123* (FLAS). Osceola Co., St. Cloud, Jan 1913, *Bearss s.n.* (NY, US); off of Hwy. 441S (192), S of St. Cloud at Harmony, 28 Mar 2009, *Majure 3702* (FLAS); Ashton, off of Hwy. 192 W, ca. 0.25 km E of intersection with Narcoosee Rd., 11 Feb 2011, *Majure 4181* (FLAS). Palm Beach Co., Near Boca Raton Airport, E of Interstate 95; NW 40th St. & 6th Way, 9 Mar 2010, *Majure 3970* (DES, FLAS); *ibid*, *Majure 3971* (FLAS); Boca Raton, Intersection of SW 18th St. and Sw 17th Ave. along railroad tracks, 9 Mar 2010, *Majure 3973* (FLAS). Pinellas Co., Ross Island, ca. 120 yards inshore, 12 Mar 1963, Croley 126 (USF); sand dunes, Long Key, 28 Nov 1921, *Small s.n.* (NY). Polk Co., S of Frostproof along Rt. 27 ca. 3.6 mi N of Highlands Co. line, 1 Nov 1980, *Judd 2841* (NY); off of Hwy. 27N, 9.6 km N of Avon Park, 11 Mar 2010, *Majure 3979* (DES, FLAS); ca. 0.2 km S of intersection with Hwy. 98N and Hwy. 27N. ca. 2.8 mi SW of Frostproof, 25 Nov 2011, *Majure 4227* (FLAS); Vicinity of Crooked Lake, 2 Jun 1931, *McFarlin 5610* (MICH). Putnam Co., Ocala National Forest, Delancy Lake, along FR-75-2, just W of Hwy. 19, 24 May 2008, *Majure 3248* (FLAS); Ocala National Forest, 2.4 mi on FS Rd. 75, just N of Lake Delancy, off Hwy. 314, junct. of 75 & 46, 29°26'14"N, 81°46'30"W, 17 May 2007, *Meyer 89* (FLAS). Seminole Co., 0.5 mi N of Chuluota from Hwy. 419, vcnty. of Taintsville; 17 0487346N 3169164E, 16 Mar 2007, *Majure 2084* (MISSA); off of Hwy. 419S, W of Mills Lake Park; 17 0487398N 3166757E, 16 Mar 2007, *Majure 2085* (MISSA). St. Johns Co., North-most public beach access at South Ponte Vedra Beach, ca. 3 mi S of Guana River SP, 18 Jun 1996, *Christy 2781* (ASU); Porte Vedra, Jan 1942, *Kurz 277* (MICH); Crescent Beach, Jan 1942, *Kurz 279* (MICH). St. Lucie Co., Ancient Dunes, near Ft. Pierce, 6 Sep 1922, *Small s.n.* (NY); St. Lucie Co., off of Hwy. A1A, ca. 8.5 km E of Lakewood Park along Atlantic Coast at Avalon St. Park, 28 Mar 2009, *Majure 3704* (FLAS); vicinity of Ft. Pierce, off of Hwy. A1A, E of Jack Island, 28 Mar 2009, *Majure 3705* (FLAS); E of US 1, 0.5 mi N of Taylor Cr. Bridge, N edge of Ft. Pierce, S33, T34S, R40E, 7 Aug 1965, Ward 4924 (FLAS); along Florida 707, ca. 6.5 mi S of Ft. Pierce city limit, S19, T36S, R41E, 8 Aug 1965, *Ward 5039* (FLAS); *ibid*, *Ward 5040* (FLAS). Volusia Co., Daytona, Jan 1942, *Kurz 276* (MICH); Daytona Beach: Just S of town off of the E side of A1A S remnant sand dunes between the road and the beach, 17 May 2008, *Majure 3224* (DES, FLAS); off of A1A S at New Smyrna Beach at junction with Sylvania Dr., 17 May 2008, *Majure 3227* (DES, FLAS); at the corner of Hwy. 11N and SR 40, 18 May 2008, *Majure 3231* (FLAS); off of SR 40 ca. 3 km W of jct. with Hwy. 11N, 18 May 2008, *Majure 3232* (FLAS); sand dunes E of Bulow, 21 Mar 1936, *West & Evers s.n.* (FLAS).

4. *Opuntia cespitosa* Rafinesque (1830: 216) (Fig. 9). Neotype (designated by Majure 2014):—UNITED STATES. **Kentucky:** Woodford County, Hwy. 60 N at jct. of Hwy. 62; just N of Versailles, 09 Jun 2008, *Majure et Patenge 3275* (FLAS-235446!, available online at <https://www.flmnh.ufl.edu/herbarium/cat/search.asp?accno=235446>; isoneotype US!)

= *Opuntia rafinesqueii* Engelm. (1856: 136) var. *microsperma* Engelman (1856: 295). ≡ *Opuntia mesacantha* Raf. var. *microsperma* (Engelm.) Coulter (1896: 429) ≡ *Opuntia humifusa* (Raf.) Raf. var. *microsperma* (Engelm.) Heller (1900: 8) ≡ *Opuntia compressa* (Salisb.) MacBride var. *microsperma* (Engelm.) Benson (1944: 250). Lectotype (designated by Coulter 1896: 429):—UNITED STATES. **Missouri:** Cultivated in Missouri Botanical Garden, April 1854, *s.c.* (MO-178291!, image available at <http://www.tropicos.org/Image/20166>).

= *Opuntia rafinesqueii* Engelm. var. *minor* Engelm. (1856: 295) ≡ *Opuntia mesacantha* Raf. var. *parva* Coulter (1896: 429), *nom. superfl. et illeg.* (Art. 52.1 of ICN) ≡ *Opuntia humifusa* (Raf.) Raf. var. *parva* (Coul.) Heller (1900: 8), ≡ *Opuntia humifusa* (Raf.) Raf. subsp. *minor* (Engelm.) Crook & Mottram (1998: 135). Lectotype (designated by Benson 1982: 924):—UNITED STATES. **Missouri:** Naked Sandstone ledges at Mine La Motte, Missouri, November 1845, *Engelmann s.n.* (MO-178293!, image available at <http://www.tropicos.org/Image/20175>).

Description:—Sprawling shrub, to 0.3 m tall, with chains of up to 2–6 cladodes, the cladodes generally produced with the flat (broad) surface parallel to the ground surface; roots fibrous or tuberous, apparently depending on the substrate. Cladodes mostly obovate, rotund, or elliptical in outline, margins not scalloped, with 4–6 (generally 5) areoles per diagonal row, cladodes strongly glaucous-green (gray-green) when developing, aging dark green or light gray-green, cross-wrinkling during the winter months, 3.8–18.7 cm × 3.2–11.3 cm, 4–19.2 mm thick. Leaves glaucous, gray-green, ascending parallel to the cladode surface or slightly spreading, 5.5–6.8 mm long. Glochids dark red, crimson red, or dark amber, aging light to dark brown. Spines robust or delicate, smooth to the touch, 1–2

(3) per areole (most commonly 1), 1.5–4.3 cm long, 0.78–0.87 mm in diameter, these castaneous at the base during development but maturing bony-white, and finally dark gray in age, typically spreading in one plain from the areoles (i.e., in line with one another) with primarily 1 spine, or occasionally 2 of roughly the same length or 1 long and 1 short and slightly deflexed (these characters can be seen in individuals in the same population or even on the same plant), rarely 3 spines produced from the areoles, but in this case the central spine typically not correct (as in *O. macrorhiza*); in age the mid-cladode and especially the basal cladode spines tend to deflex. Flowers: outer tepals triangular to ovate, inner tepals 9–10, 2.5–5.5 cm long, basally tinged dark red, crimson, orange-red, or reddish-pink, obovate with a mucronate tip, staminal filaments yellow, reddish basally, stigmas white to cream, lobes 6–10. Berries dark red, or orange-red, 2.7–4.5 cm long. Seeds 4.9–5.4 mm long, funicular girdle 0.95–1.3 mm wide, funicular envelope bumpy from the enlargement of the cotyledons and hypocotyl, the funicular girdle also tends to be slightly irregular or bumpy.

Phylogenetic placement:—*Opuntia cespitosa* is an allopolyploid derivative of the southwestern *O. macrorhiza* species complex (SW clade) and the *O. humifusa* species complex (SE clade) of the southeastern US. The southeastern progenitor of *O. cespitosa* was most likely the tetraploid, *O. mesacantha* subsp. *mesacantha*, or an ancestor thereof, which was derived solely from the SE clade (Majure in prep.).

Phenology:—Flowering early May–early July, fruiting August–May.

Distribution and habitat:—*Opuntia cespitosa* is the most common species in the eastern US occurring mostly west of the Appalachian Mountains west to Wisconsin, Iowa, Missouri, Arkansas, and eastern Texas, south to Mississippi and Alabama, and north to Michigan, in the US, and also in southeastern Ontario, Canada. Populations are occasionally found in the eastern Appalachians as well (Fig. 4). *Opuntia cespitosa* is most commonly found in sandy or blackland prairies, juniper glades, or on rock outcrops (generally limestone or sandstone). It also grows with *Campanulastrum americanum* Small (1903: 1338), *Carex cherokeensis* Schweinitz (1824: 71), *Dichantheium linearifolium* (Scribner in Britton & Brown 1898: 500) Gould (1974: 60), *D. oligosanthes* (Schultes 1824: 256) Gould (1974: 60), (esp. *D. oligosanthes* subsp. *scribnerianum* (Nash 1895: 421) Freckmann & Lelong (2002: 170)), *Juglans nigra* L. (1753: 997), *Juniperus virginiana* L. (1753: 1039), *Quercus muehlenbergii* Engelm (1877: 391), *Q. prinus* Linnaeus (1753: 995), *Ratibida pinnata* Barnhart (1897: 410), *Rhus aromatica* Aiton (1789: 367), *Xanthoxylum clava-herculis* Linnaeus (1753: 270) among many other species.

Conservation status:—*Opuntia cespitosa* has not formally been evaluated by the IUCN. At the time of the last evaluation of Cactaceae (Goettsch *et al.* 2015), *O. cespitosa* was still considered synonymous with *O. humifusa*. Although, *O. cespitosa* is the most widespread taxon in the eastern US, reduced and fragmented habits throughout the east result in relatively small population sizes that tend to be highly disjunct from one another. So local extinction of the species is highly probable. Thus, we consider the species to be vulnerable to habitat loss, and it should like be placed on most state watch lists for rare species.

Chromosome number:— $2n=44$ (tetraploid) (Majure *et al.* 2012b).

Notes:—Engelmann (1856) was the first to truly recognize the difference between *O. cespitosa* and *O. humifusa*, although, he recognized *O. cespitosa* under the superfluous name, *O. rafinesquei*, apparently in an attempt to reconcile the taxonomic confusion surrounding the eastern US' material. *Opuntia humifusa* at the time was recognized as *Opuntia vulgaris*. Although we have only recorded *O. cespitosa* from nine counties in Ohio, Noelle and Blackwell (1972) recorded what at the time was called *O. compressa* (= *O. humifusa*) from 15 counties in Ohio and from a total of 19 populations. Although, they did not provide enough information to distinguish this species from close relatives, based on geography (this area falls completely within the range of *O. cespitosa*) and populations seen by the first author in the state, more populations of *O. cespitosa* must surely occur in Ohio than what is recorded in this treatment.

Central US populations (in Arkansas, Iowa, Illinois, Michigan, Missouri, and nearly all populations in Wisconsin) often show evidence of putative introgression with the eastern flank of *O. macrorhiza* and *O. cymochila*, as they have spreading spines in more than one plain and occasionally one or more, small, bristle-like radial spines produced at the base of the areole [e.g., MI, Musekegon Co., L.C. Majure 3259 (FLAS), WI, Dane Co., *D. Ugent 60–11J* (WISC)]. These populations are currently under further study (Majure in prep.; see asterisks in Fig. 4). There also is apparent introgression with *O. humifusa* at the eastern boundary of the two species (e.g., eastern NY, Orange Co., *H.M. Dunslow s.n.*, Nantucket Island, MA), and populations in Bibb County, Alabama along the Cahaba River (e.g., L.C. Majure 2042; MISSA) are nearly identical to *O. mesacantha* subsp. *mesacantha*, except for the red-centered flowers, lack of strong barbs on the spines, and the typical rotund cladodes of *O.*

cespitosa. Those populations also occasionally occur in long leaf pine forest barrens, a habitat more typical for *O. mesacantha*; however, those populations in Bibb County occur on uncommon dolomite soils.

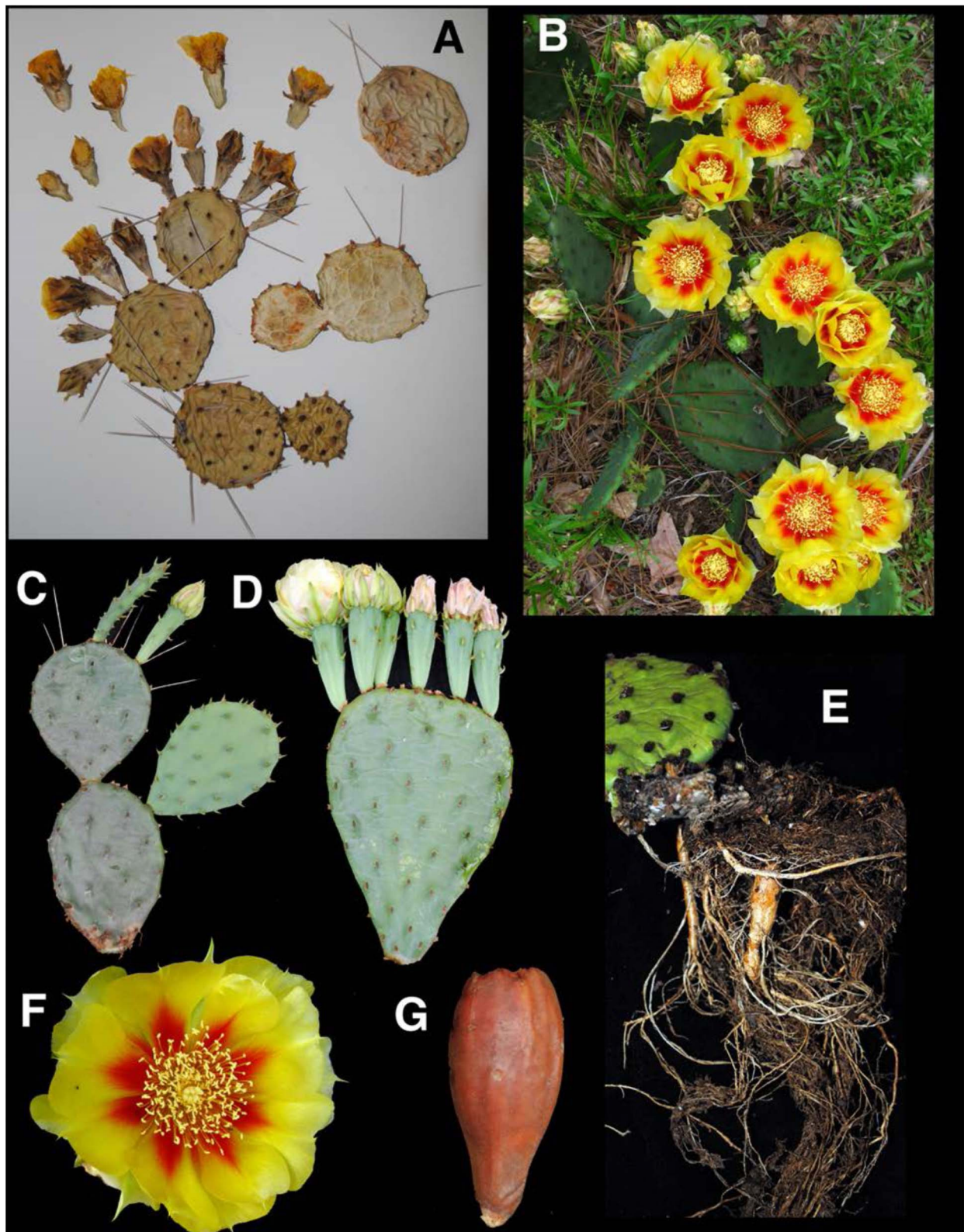


FIGURE 9. Morphological features of *O. cespitosa*. A) neotype specimen of *O. cespitosa* (Majure 3275, Woodford Co., KY), B) spreading growth form of *O. cespitosa* (Majure 1380, Oktibehe Co., MS), C-D) pad shape variation showing glaucous color and cladodes either spiny or spineless (Majure 1380), E) occasional tuberous roots of *O. cespitosa* (Majure 2609, Lawrence Co., AL), F) flower (Majure 1380) and G) fruit of *O. cespitosa* (Majure 1380). Photos A and E taken by L.C. Majure, B-D, F, and G taken by M. Pajuelo.

Although no specimens have been seen confirming the species in New Jersey, Hanks and Fairbrothers (1969b) noted that some northern populations in their study had red-centered flowers, thus, *O. cespitosa* likely occurs in New Jersey as well. Unfortunately, no specimens were cited in their study, so those identities have not been confirmed.

Additional specimens examined. CANADA. **Ontario:** Essex Co., Pt. Pelee, Lake Erie, 18 Sept 1884, *Macoun s.n.* (NY); Pelee Island, W side of Fish Point, near N end, 9 May 1981, *Reznicek 6230* (MICH); Point Pelee, Jan 1913, *Taverner s.n.* (MICH). Kent Co., Harwich Township, Bethel Cemetery, UTM 107042, map 40J/8, square 17MT10, 6 Sep 1986, *Oldham 6867* (note: most likely planted, originating from Pelee Island) (MICH). UNITED STATES. **Alabama:** Bibb Co., off of Hwy. 219N from Hwy. 5 N at jct. with Schultz Cr. Rd.; 16 0486461E 3653643N, 7 Mar 2007, *Majure 2042* (MISSA); dolomite glade btwn. Pratt Creek and Cahaba River; 33.0494°N, 87.0929°W, 30 Apr 2007, *Majure 2293* (MISSA). Colbert Co., Leighton, 14 Jul 1913, *Holt 13-63* (NY); off of Natchez Trace, just S of jct. with Hwy. 72, 34.7525N 88.0269W, 25 Jul 2007, *Majure 2610* (MISSA). Franklin Co., along Spruce Pine Hwy., ca. 4 mi S of Russelville, 30 Aug 1966, *Clark 8004* (UNC). Jackson Co., Hwy. 79 0.2 mi N of jct. with US Hwy. 72, 8 Jul 1966, *Clark 4582* (UNC). Lawrence Co., Prairie Grove Glades, 3.6 km NE of Mt. Hope, 34.4859N 87.5005W, 25 Jul 2007, *Majure 2609* (MISSA). Limestone Co., Elkmont, 14 Jul 1913, *Holt 13-64* (NY). Madison Co., Huntsville, Monte Sano State Park, E flank of mountain, 30 July 1996, *Zebryk 3059* (GA). Marshall Co., 7 mi W of Guntersville on Georgia Mt., 9 Apr 1966, *Brown 7* (UNA). Morgan Co., off CR-55 in Massey east of Emmanuel Church, Moulton Valley district of the Highland Rim section; 34°22'12"N 87°01'12"W, 6 Jul 2003, *Spaulding 11977* (TROY, UNA). Perry Co., Uniontown, 1 Jan 1912, *Howell 12-47* (NY, US). **Arkansas:** Bradley Co., Warren, 21 May 1937, *Demaree 15046* (MO, NY). Garland Co., Above Lake Hamilton, 25 Feb 1967, *Demaree 57519* (ASU); Ouachita Nat'l Forest, N of FS rd. 130 and Cedar Fourche Landing of Lake Ouachita; 34.6660°N, 93.2834°W, 6 Apr 2007, *Majure 2198* (MISSA). Grant Co., 5 Jun 1940, *Demaree 21180* (MO); Mt. Riante, S of Lake Hamilton, 23 Jul 1990, *Parfitt 4479* (ASU), *ibid*, *Parfitt 4480* (ASU). Hempstead Co., near Tokis, 22 Oct 1932, *Demaree 10024* (US). Hot Springs, rocky, dry ridges; P.O. - Bismarck, 14 Mar 1937, *Demaree 14291* (MO, NY); igneous intrusive area, rocky ridges, Magnet Cove, 25 Mar 1942, *Demaree 16493* (MO, NY). Independence Co., along Pine Hollow Rd. where it crosses Lafferty Creek, 3.5 mi W of Cushman, Sec. 14, T14N, R8W, 6 Jun 1968, *Thomas 8023* (TENN). IZARD Co., Guion, 16 Aug 1913, *Emig 187a* (MO). Marion Co., opposite Cotter (in Baxter Co.), 15 Sep 1960, *Jones 31045* (ILL). Miller Co., Stateline Rd., S of jct. with Hwy. 134 on W side of Miller County Sandhills Natural Area, 33° 11.137N, 94° 2.569W, 2 Oct 2008, *Snow 2062* (FLAS). Pulaski Co., Levy, 4 Nov 1931, *Demaree 8849* (MO, NY); dry rocky ridges, Fourche Mt., 6 Jun 1940, *Demaree 21150* (MO, NY). Saline Co., Alum Fork of Saline River, Dierks Forest, 12 May 1968, *Demaree 57621* (ASU); Just N of Detonti; E of Bauxite Cutoff Rd.; 34.5300°N, 92.5043°W, 6 Apr 2007, *Majure 2194* (MISSA); Middle Fork Shell Barren along Middle Fork Saline River, NW of Owensville; 34.6390°N, 92.8404°W, 6 Apr 2007, *Majure 2195* (MISSA). Stone Co., Mountain View, *Demaree 57932* (ASU; note, mixed collection with *O. nemoralis*). Washington Co., White River, Fayetteville, *Engelmann 931*, 1 Jun 1835 (MO). Yell Co., 1 mi W of Dardanelle Rock, 19 Apr 1969, *Demaree 85281* (ASU); 1.95km NNW of Dardanelle, just W of Arkansas River, 1 Oct 2011, *Johnson s.n.* (FLAS). **Connecticut:** New Haven Co., near New Haven, [no date], *Beardslee s.n.* (MU); Milford, exposed ledges, 8 July 1892, *Eames s.n.* (ILL). **Georgia:** Catoosa Co., Chicamauga Battlefield, N side of trail off of Reeds Bridge Rd., NW of Rock Haven Lane, 25 Mar 2016, *Adanick & Medley s.n.* (DES). Chatooga Co., Taylor Ridge, trailhead off of Hwy. 100 & N of City Rd. 22, 26 Mar 2016, *Adanick & Medley s.n.* (DES). Cobb Co., Kennesaw Mt. over mafic gneiss, 29 March 2016, *Adanick & Medley s.n.* (DES). Dade Co., SE of Rising Fawn, Cumberland Province, 10 Jun 1940, *Duncan 2601* (GA). Floyd Co., Cunningham Rd., directly across rd. from Flatrock Baptist Church, 26 Mar 2016, *Adanick & Medley s.n.* (DES). Gordon Co., on E side of Pine Chapel Rd., across from Moss Memorial church, 25 Mar 2016, *Adanick & Medley s.n.* (DES). Walker Co., near intersection of Hwy. 136 & Kensington Rd., 25 Mar 2016, *Adanick & Medley s.n.* (DES). Whitfield Co., Rocky Face Mountain, near Crow Valley Rd., 25 Mar 2016, *Adanick & Medley s.n.* (DES). **Illinois:** Adams Co., Mississippi Bottom SE of Quincy, 15 Jul 1943, *Brinker 2824* (ILLS); Bluff Hall: on south facing sandy slope of J. Gunseth's farm (Sec. 20 T 3S R8W), 23 Aug 1940, *Evers 186* (ILLS, NY); along roadside in a sand ridge, Sec. 20, T3S, R8W, 22 Jun 1943, *Evers 1205* (ILLS); in the sand ridge south of Bluff Hall, 25 Sept 1948, *Evers 15129* (ILLS). Calhoun Co., rocky bank, Golden Eagle Ferry Landing, 22 Jul 1948, *Evers 12095* (ILLS); Prairie opening, Cap au Gris bluff south of Batchtown, 10 Jul 1957, *Evers 54095* (ILLS); Cap au Gris Hill Prairie, 2.5 mi SE of Batchtown, T15N, R2W, Sec. 29, 4 Jun 1987, *Robertson 4514* (ILLS). Cass Co., sandy bank along

roadside, 5 mi E of Beardstown, 31 May 1947, *Evers 3413* (ILLS); Chandlerville 7.5 min topo map, 6 Jul 1994, *Phillipe 24911* (ILLS); Aruizville, 15 Aug 1910, *Steele 10-250* (NY). Crawford Co., SE of Palestine, 26 Nov 1949, *Evers 22044* (ILLS). Fayette Co., bluffs of Dismal Creek NE of Laclede, 23 Jul 1947, *Evers 5587* (ILLS); 38.85315°N 89.08837°W; Rt. 51 Project Area, 9 Jul 2008, *Murphy 3001* (ILLS). Gallatin Co., sandstone outcrop NE of The Pounda, SW of Gibsonia, 24 Sep 1947, *Evers 8550* (ILLS); on sandstone, Buzzards Point, S of Kedron, 14 May 1964, *Evers 79393* (ILLS). Hardin Co., above Ohio River, 1 mi E of Rosiclare, 29 May 1949, *G.S. Winterringer 1963* (ILL). Henderson Co., N of Oquawka, *Evers 14786*, 18 Sep 1948 (ILLS). Jackson Co., cliff summits in Giant City State Park, SE Jackson Co., 1 Oct 1931, *Pepoon s.n.* (ILLS); Devil's Bake Oven, NW of Grant Tower, 1 Jun 1988, *Ulaszek 1341* (ILLS). Jersey Co., Riehl Station, *A.H. Horrell 09-168*, 30 May 1909 (US). Jo Daviess Co., in the sand area near Blanding, 18 Jun 1948, *Evers 10526* (ILLS); Savanna Army Depot, Green Island 7.5 min quad E of Building D-107, 18 Jul 1996, *Phillipe 27862* (ILLS); xeric sand prairie W of Hanover, 23 Jun 1968, *Sheviak 248* (ILLS). Johnson Co., rock outcrop at Cedar Hills, SE of Ozark, 21 Aug 1948, *Evers 13300* (ILLS); rock ledges at Ferne Cliffe, SW of Goreville, 14 Jun 1949, *Evers 17540* (ILLS); rock outcrop, NE of Simpson, 23 Apr 1953, *Evers 36736* (ILLS). Marion quad, R2E T11S, 1.75 mi S of Goreville, E of Dunntown school, 27 Jul 1931, *Schopf 858* (ILLS). La Salle Co., on St. Peter Sandstone outcrops W of Ottawa, 29 Apr 1948, *Evers 9327* (ILLS); SW of Naplate, 30 Aug 1974, *Evers 113834* (ILLS); 41°19'1.1"N 88°53'8.6"W; 0.45 mi W of W 2401 St. (Deer Park Rd.), north side of IL Rt. 71, just W of Covell Creek, ca. 320 m S-SW of mi 237 of Illinois River, W of S Ottawa, 20 Jun 2003, *Hill 35277* (ILLS, MU). Lake Co., N of Waukegan and E of the glacial Glenwood Ridge, 1 Jul 1908, *Gates 2802* (ILL); sand dunes, Waukegan Dunes, Dead River, 29 Sept 1951, *Lane 502* (ILL); Beauli St. Park, 8 Jul 1961, *Laskowski 270* (MICH); near Waukegan, 13 Jun 1911, *Traeviehir s.n.* (NY). Lee Co., near Amboy, 8 Jul 1956, *Long 293* (ILL). Mason Co., Manito, 1 Oct 1979, *Cull s.n.* (ILLS); found along roadside 1.5 km W of Forest City near Chautauqua National Wildlife Refuge, *DeShurko 119* (MU); in scrubby woods along rt. 10, 5 mi NW of Easton, 19 Nov 1941, *Evers s.n.* (ILLS); sand prairie 5 mi W of Easton, 28 Jun 1955, *Evers 47033* (ILLS); sand prairie, NW of Forest City, 27 Jun 1973, *Evers 110585* (ILLS); 1.6 mi E of 1130E on 600N, 7 Jun 2007, *Majure 2522* (MISSA); 0.2mi S of Batts, on St. Rt. 78 on 600N heading W turn on 1400E, 7 Jun 2007, *Majure 2523* (MISSA); Long Branch Sand Prairie, Topo Kilbourne, Located just W of the Mid State Dragway and about 2.5 mi E of the Illinois River, 13 Jun 1988, *Phillipe 13326* (ILLS); 40.38217°N 89.901°W; Sand Ridge State Forest, Illinois River Sec. of the Illinois River and Mississippi River Sand Areas Natural Division; Duck Island Quad; Burns Prairie, 1 Jun 2004, *Phillipe 36755* (ILLS). Menard Co., Athens, *Hall s.n.*, 1 Jan 1862 (NY). Mercer Co., roadside, S of Keithsburg, 18 Sept 1948, *Evers 14785* (ILLS); SE of Keithsburg, 2 Jul 1964, *Evers 80855* (ILLS). Monroe Co., rock ledges, 3 mi S of Valmeyer, 24 May 1950, *Evers 23057* (ILLS); Hill Prairie, Vic. Of Fults, 30 Oct 1965, *Neill 16801* (ILLS). Morgan Co., S of Meredosia, 31 May 1947, *Evers 3521* (ILLS). Perry Co., N of Pinckneyville, 24 Sep 1953, *Evers 41629* (ILLS). Pike Co., rock ledge of Kinderhook, 7 Sep 1949, *Evers 20829* (ILLS). Pope Co., at the summit of War Bluff 7 mi of Golconda, 16 Jul 1947, *Evers 5111* (ILLS); Brownfield Quad R5E, T12S, on top of northern bluffs of hollow N of Rising Sun Cemetery, 14 Aug 1941, *Schopf 1248* (ILLS); Brownfield Quad R5E, T12S, Pine Hollow 2.5 mi E of Dixon Springs, 18 Aug 1931, *Schopf 1360* (ILLS); Belle Smith Springs, Eddyville, 19 Oct 1968, *Sheviak 433* (ILLS); Jackson Hollow Natural Area, T11S R5E Sec. 31, 2 Jul 1985, *Smith 186* (ILLS). Putnam Co., 1 mi S of Hennepin, 15 Jul 1955, *Evers 7661* (ILLS). Randolph Co., between Rockwood and Chester, 4 Jun 1952, *Ahles 6165* (ILL); rock ledges, 1 mi N of Prairie du Rocher, 24 May 1950, *Evers 23137* (ILLS); Limestone ledge, SE of Prairie du Rocher, 25 Jul 1973, *Evers 110935* (ILLS). Scott Co., Sandy bottomland 0.5 mi N of Naples, 31 May 1947, *Evers 3486* (ILLS); Sand terrace, west of Glasgow, 23 Jun 1961, *Evers 69588* (ILLS); sandy roadside W of Winchester, 3 Jul 1973, *Evers 110680* (ILLS); 3.5 mi W of Winchester, T14N R13W Sec. 27 NW 1/4, 23 Jun 1981, *Robertson 2607* (ILLS). St. Clair Co., Stony hills, 20 Jun 1878, *Eggert s.n.* (ILL, MU); on bluff top 2.5 mi S of Falling Springs near Dupo, 31 Aug 1947, *Neill 1427* (ILLS); rocky sloping soil, vic. 3 forks, 19 Jun 1961, *Neill 15678* (ILLS). Tazewell Co., Sand Prairie, SW of Powerton, 12 Jun 1952, *Evers 33743* (ILLS); SW of Spring Lake State Park, 27 Jun 1973, *Evers 110590* (ILLS); near Spring Lake, 10 mi SW of Pekin, 6 Jun 1948, *Hoehn s.n.* (ILL); Sand prairie, 28 Mar 1968, *Sheviak 242* (ILLS). Union Co., rocky slopes of Pine Hills, SE of Aldridge, 2 Oct 1948, *Evers 15475* (ILLS); T11S R1E Sec. 3 NW4 NE4, Crab Orchard National Wildlife Refuge, Devil's Kitchen Lake Research Natural Area, 4 Jul 1983, *Ulaszek 391* (ILLS). Whiteside Co., along CB&Q & CMSP&P RRs, N of Fulton, 29 Jan 1968, *C.J. Sheviak 206* (ILL). Will Co., prairie W of Wilmington, 14 Jun 1966, *Evers 87390* (ILLS); 41°24.19'N 88°10.62'W; Channahon Quad, Channahon, ca. 1.5 mi SE of Des Plaine River, E of active RR, S of old E-W RR

spur; SW of Midewin gate, W of perimeter rd., Drummond Dolomite Prairie, 28 Aug 2001, *Hill 33058* (ILLS, NY); Kankakee River Watershed, Sand Ridge Savanna Nature Preserve, 2.7 mi E of Braidwood (jct. of Rt. 53 and 113) along Rt. 113, in the Kankakee Sand Area Section of the Grand Prairie Natural Division, 41.26025°N 88.1662°W, 13 Aug 2007, *Phillipe 40000* (ILLS); dunes, SE of Braidwood, 29 Jun 1968, *Sheviak 245* (ILLS).

Indiana: Adams Co., Sec. 20, T3S, R8W, 22 Jun 1943, *Evers 1205* (NY). Clark Co., 1 mi E of Charlestown, 9 May 1953, *Buser 3047* (ILL); sand hills, Clarke, 30 Jun 1895, *Moffatt s.n.* (ILL); Clark, 1896, *Umbach s.n.* (MICH). Fountain Co., Covington, 1 Aug 1953, *Buser 3167* (ILL). Jasper Co., Walker TP and SJ Wheatfield, 8 Jul 1924, *Welch 619* (ILL, NY). Jefferson Co., just N of Madison, 22 Jun 1913, *C.C. Deam 13412* (MO, US). Lake Co., Miller IN, sand dunes, 23 Jun 1937, *Evers 10651* (MU); Gary, 19 Jul 1907, *Greenman 2075* (MO); Dry sand hills, Whiting, IN, 15 July 1875, *Hill s.n.* (ILL); Dunes of Lake Michigan, 1 mi from the Lake - Miller's, 20 Oct 1911, *Niewlaud s.n.* (NY); 1 mi N of Miller, 23 Aug 1913, *Smith 5779* (NY); Hammond, 16 Sept 1909, *Steele 09-305* (US); Long Lake, 20 Jul 1927, *Welch 5616* (NY). Porter Co., Dunes at Tremont, 20 Jul 1924, *Lyon, Jr. s.n.* (MICH); just S of Lake Michigan off of Hwy. 12, 8 Jun 2008, *Majure 3274* (FLAS); Ogden Dunes, in sandy region at Kratz Field, Hillcrest Rd., 28 Jun 1990, *Vincent 3853* (MU). Tippecanoe Co., Lafayette, Jan 1912, *Arthur s.n.* (NY); Fairfield, 14 Jun 1898, *Cunningham 468* (NY); SW of Lafayette, 17 Jun 1941, *Ek s.n.* (NY); Lafayette, Hanover, Sept 1878, *Young s.n.* (MICH). Iowa. Muscatine Co., Bayfield, 7 Aug 1909, *Lorries 3546* (US); E of Cedar River R.R. bridge, W of Bayfield, 3 Jul 1915, *Shimek* (MO, NY).

Kentucky: Anderson Co., Kentucky River Cliffs, Lover's Leap off Lane's Mill Rd. near Ninevah, 28 Jun 1978, *Bryant 484* (EKY); *ibid*, 6 Jul 1978, *Bryant 591* (EKY); off of Hwy. 127S, ca. 1 mi S of jct. with Bluegrass Parkway, 9 Jun 2008, *Majure 3276* (FLAS); on dry, sunny limestone ledge, 12 Jun 1956, *Wharton 10072* (EKY). Boyle Co., just SW of Perryville, 27 Aug 1959, *C.F. Reed 45203* (MO). Breckinridge Co., W of Cloverport, Rt. US 60, Breckinridge, 17 Aug 1961, *C.F. Reed s.n.* (MO). Caldwell Co., North Rim of French Springs Hollow. Gorge is about 0.5 mi SE of the Beulah Hill Church, USGS topo. Princeton East 3787-17, 1 Oct 1980, *Hannah & Phillipe 5837* (EKY); Pennyryle St. Park, 22 Jun 1966, *Hunter 1676* (UNC). Clark Co., 1.5 mi SE of Indian Fields, 31 Aug 1939, *Gleason, Jr. 115* (MICH). Crittendon Co., Rt. 60, 1 mi N of Mattoon, 23 Jun 1974, *Reed 138388* (MO). Cumberland Co., ca. 0.25 mi W of KY Hwy. 704; ca. 1 mi S of Adair-Cumberland county line, 15 Apr 1999, *Clark 24276* (EKY). Edmonson Co., Mammoth Caves, 7 Jun 1949, *Reed 15304* (MO). Estill Co., Paul Goosey Farm, Intersection of Little Horns Creek Rd. and Red Lick Rd., 37.6056°N, 84.0396°W, 29 Jan 2016, *Adanick s.n.* (DES). Fayette Co., Elk Lick Falls Rd., N of entrance to Floracliff Nature Preserve, E side of rd., 37.9062°N, 84.3594°W, 30 Jan 2016, *Adanick s.n.* (DES). Franklin Co., Dad's farm, 10 Oct 1980, *Rice FR-109* (EKY). Garrard Co., W bank Paint Lick Creek, and directly W of Geo. Caldwell farm, this on KY 21, 1.7 mi E of jct. rd. and KY 52, Blue Grass Province, 5 Oct 1963, *Browne 8150* (EKY). Hancock Co., USGS Topo, Cloverport 3786-86, 450-650' Jeffry Cliff entered from US 60 on the gravel rd. 1.35 km SE of US 60 and KY 1406 jct., 18 Jun 1980, *Hannan 4259* (EKY). Hart Co., Lawler Bend Rd., E side of rd., top of ridge overlooking Green River, 36.6160°N, 85.9435°W, 26 Feb 2016, *Adanick s.n.* (DES). Henry Co., 1.4 mi SW of Lockport, 6 Jun 1962, *Gentry, Jr. 301* (NY). Jefferson Co., Goose Creek, 30 Apr 1947, *Davies s.n.* (UNC). Jessamine Co., Jessamine Cr.; Blue Grass Province, 17 Jun 1961, *Browne 4221* (EKY, TENN, UNC); 2 mi NE of Logana, between Old Railroad Lane and Mackey Rd. on roadside of KY 169, 13 Jun 1994, *Libby 359* (EKY); limestone ledges above Brooklyn Bridge, 14 Apr 1950, *Reed 18645* (MO); Camp Nelson, cliffs of Kentucky River, Jan 1923, *Wherry 23-100* (US). Johnson Co., C. Ferguson farm near Flat Gap, Mud Lick, rd. to Paintsville, 22 Jun 1949, *O. McKenzie s.n.* (MO). Lyon Co., western KY, Kuttawa, 2-18 Jun 1909, *Eggleston s.n.* (NY). Madison Co., G. Caldwell farm, 1.7 mi E of Paint Lick on KY 21, 5 Oct 1963, *Browne 8130* (EKY). Owen Co., Gilbert Tract WMA; Brown Bottom., 3 Oct 2003, *Jones 9542* (EKY). Pike Co., Old US 460, 4.6 mi E of jct. this rd. and KY 80 near Fishtrap Dam, 9 Jun 1964, *Browne 8641* (EKY, TENN). Pulaski Co., Pumpkin Hollow, Burnside Q., E of Burnside, Rte N side of Lake Cumberland in Williams Bend in Pumpkin Hollow, 11 Apr 1979, *Hannan 1190* (EKY). Scott Co., Stamping Ground, 14 Jun 1930, *Singer 282* (US). Simpson Co., Bowling Green Rd., just N of Luvata plant on roadside, 36.7984°N, 86.5611°W, 15 Dec 2015, *Adanick s.n.* (DES). Warren Co., Bowling Green, 1 Jan 1899, *Price s.n.* (MO). Wayne Co., Cooperville Rd., 15 Apr 1940, *Braun 2814* (US).

Maryland: Baltimore Co., Factory Rd., 0.5 mi N of Harford Rd., 10 Dec 1981, *Reed 121328* (MO). Washington Co., Kemps Mills N of Williamsport, 14 Jun 1952, *Reed 29115* (MO).

Massachusetts: Barnstable Co., Wellfleet, 30 Nov 1930, *Fernald s.n.* (NY, US); Dukes Co., Martha's Vineyard, ca. 0.5 km SE of Meeting House Way and 0.4 km N of peninsula of Mashacket Cove, ca. 2.8 km SW of Edgartown, 9 May 2011, *Conolly s.n.* (FLAS). Nantucket Co., Nantucket Island, Coatue Point, 1 Sep 1964, *MacKeever* (NY).

Michigan: Allegan Co., 3 mi W of Allegan,

summit of bluffs above Kalamazoo River, 15 May 1950, *McVaugh 11260* (MICH); Allegan State Game Area, 21 Jun 1987, *Thomson 3931* (MICH); near center sec. 26, Valley Tp., ca. 4 mi W of Allegan, 5 Jul 1958, *Voss 7223* (MICH). Manistee Co., S end of Maple Grove Township Cemetery immediately E of Kaleva on the N side of Nine Mile Rd; SE quarter of Sec. 21, T23N, R14W, 30 Jul 1978, *Johnsen 1596* (MICH). Monroe Co., S side of Tunnickliffe Rd., ca. 5 mi SE of Petersburg, 7 May 1992, *Reznicek 8931* (MICH). Muskegon Co., off of Hwy. 31N, 6.2 KM SE of Whitehall, 2 km NW of Lakewood, 2 Jun 2008, *Majure 3259* (FLAS); Whitehall Tp., ca. 2.5 mi SE of center of Whitehall, 27 Aug 1955, *Voss 2861* (MICH). Newaygo Co., 1 mi W of Croton Dam, 3 Nov 1930, *Bullock s.n.* (MICH); off of Hwy. 31N; ca. 8.3 km NE of Newaygo and 6.7 km SE of White Cloud, 2 Jun 2008, *Majure 3260* (FLAS); along the corner of 16th St. and Hwy. 37N, 2 Jun 2008, *Majure 3261* (FLAS); near center of W edge NW 1/4 sec. 25; Brooks Tp., ca. 5.5. mi ESE of Newaygo, 4 Jul 1958, *Voss 7207* (MICH). Oceana Co., off of Hwy. 20, W of jct. with 132 Ave., 2 Jun 2008, *Majure 3262* (FLAS; note: normal form of *O. cespitosa*); SE1/4 NE 1/4 Sec. 36, Otto Tp. Ca. 9 mi SW of Hesperia, 4 Jul 1958, *Voss 7192* (MICH). Van Buren Co., 0.03 mi N of 28th Ave. and 0.39 mi W of 77th St., 42°18'57.795N 86°17'57.904W, 14 Jul 2008, *Walters 11972* (MICH).

Mississippi: Clay Co., off of Herman-Shirley Rd., ca. 0.25 mi S of Hwy. 50, 16 May 2006, *Majure 1442* (MISSA, MMNS). Holmes Co., off of Hebron Rd., Loess Hills, 33.07420 90.15976, 15 May 2007, *Majure 2365* (MISSA). Lee Co., Tombigbee St Park, 13 Nov 1986, *Bishop 38* (MISS); Tombigbee State Park, W side of lake shore, 30 Dec 2005, *Majure 1292* (MISSA, MMNS). Lowndes Co., Old West Point Rd., ca 0.5 mi E of Catalpa Cr., 18 Dec 2004, *Majure 736* (MISSA); Wilburn Property, S of Gilmer/Wilburn Rd.; UTM 16 0350497E 3697220N, 31 Dec 2004, *Majure 755* (MISSA, MMNS); off of Old West Point Rd, ca. .25 mi E of Catalpa Cr, N side of rd, 33.51480 - 88.56680, 23 Jun 2005, *Majure 1058* (MMNS); off of Old W Pt. Rd., 33.5103°N, 88.5567°W, 6 May 2006, *Majure 1295a* (MISSA, MMNS). Madison Co., Natchez Trace Parkway, 20 May 1948, *McDougall 1651* (US). Noxubee Co., off Hwy. 14 behind St. John's Church, 25 Jun 2005, *Majure 1543* (MISSA, MMNS). Oktibbeha Co., Bardswell pasture, 33.45472 -88.78861, 16 Jun 1947, *Davis s.n.* (MISSA); Along MS Hwy 389, at bluff S of Trim Cane Creek, about 3 mi (air) NNW of jct US 82 in Starkville, 33.50583 -88.83167, 31 May 2004, *Fishbein 5044* (MISSA); T19N, R15E, S25, on Hwy 182, on the N side of the rd, Black Prairie Region, just W of the Co line, 11 Sept 1994, *Leidolf 940* (MISS); N of Starkville along bluffs and powerline S of Trim Cane Cr., E of Hwy. 389; 16 0329865E 3708912N (NAD83), 22 Feb 2005, *Majure 790* (MISSA, MMNS); N of Starkville along bluffs S of Trim Cane Cr., W of Hwy. 389; 16 0329783E 3708918N (NAD83), 22 Feb 2005, *Majure 791* (MISSA, MMNS); MSU campus, between "The Pit" and University Apts., UTM 16 0334214E 3703011N NAD83, 29 Mar 2005, *Majure 829* (MISSA, MMNS); W of Hwy. 389, ca. 6 mi N of Starkville; on Margaret Copeland Property; 33.5027°N, 88.8315°W, 6 May 2006, *Majure 1379* (MISSA, MMNS); property of Anne Daniels, just W of Hwy. 389, near Trim Cane Creek, N of Starkville, 6 May 2006, *Majure 1380* (MISSA, MMNS); roadside of Bardswell Rd. ca. 1.4 km E of MSU; 33.45465N 88.76884W, 7 May 2006, *Majure 1431* (MISSA, MMNS); Kellum property off of Reed Rd., ca. .75mi W of Hwy. 25 bypass; 33.48420N 88.86287W, 18 May 2006, *Majure 1445* (MISSA, MMNS); John Byrd property, at the end of Crumpton Rd. off of Bardswell Rd., 33.45427N 88.76114W , 18 May 2006, *Majure 1446* (MISSA, MMNS); Residence of Cathy Scruggs off of Oktoc Rd., 33.4172°N, 88.7796°W, 18 Sept 2006, *Majure 1843* (MISSA, MMNS); Property of Jovonn Hill S of Blackjack Rd. ca. 3.2 mi E of MSU campus; 33.4464°N, 88.7459°W, 4 Dec 2006, *Majure 1923* (MISSA); off of Hwy. 25; vicinity of Starkville; 33° 29.389' 88° 51.011', 19 May 2007, *Majure 2417* (MISSA); Mississippi State University Campus, frisbee golf field about "The Pit" student parking lot, UTM 16 0334214E 3703011N, 14 Oct 2015, *Majure 5924* (DES). Panola Co., NW Panola Co., Hwy. 310, E of Askew, 8 Mar 1975, *Baker s.n.* (USMS). Pontotoc Co., vicinity of Troy, off of Shannon Rd., 7 Jun 2006, *Majure 1519* (MISSA, MMNS). Scott Co., S of town of Forest off of Hwy. 501S, ca. 1km NW of Norris, 32.3000°N, 89.4448°W, 25 Jun 2007, *Majure 2563* (MISSA). Tishomingo Co., J.P. Coleman State Park, E of boat launch at end of Steel Br. Rd., 24 May 2007, *Majure 2434* (MISSA).

Missouri: Adair Co., terrace on E side of Chariton River, ca. 2.5 mi N of State Hwy. 6 on W side of dirt CR, ca. 5 mi NW of Kirksville; T63N, R16W, S15/22 boundary, 29 Jun 1994, *Ford 719* (MO). Barry Co., Eagle Rock, *Bush 614*, 25 Sep 1896 (MO). Cape Girardeau Co., South of Delta, 19 May 1926, *Woodson s.n.* (MO). Carter Co., along Hwy. 103, just W of Ozark National Scenic Riverways entrance gate, 3 May 1993, *Summers 5607* (MO). Crawford Co., Savanna Ridge Glade, T40N R2W sec. 23 NE1/4, 5 Jun 1997, *Darigo 2888* (MO). Greene Co., vicinity of Willard, 30 Aug 1912, *Standley 9634* (US). Harrison Co., T66N, R26W, S10, 7 May 1985, *Delozier 1722* (MO). Henry Co., bluffs of Grand River, 3 mi NE of Piney, near Benton Co. line, 8 Oct 1934, *Steyermark 15977* (MO). Howell Co., Tingler Lake Conservation Area, ca. 7 mi S of West Plains on S Fork of Spring River, T22N R08W S06 N1/4, 23 May

1997, *Summers 8132* (MO). Jasper Co., Joplin, barrens on Turkey Creek, 19 May 1909, *Palmer 2278* (MO); Tingle Lake Conservation Area, ca. 7 mi S of West Plains on S Fork of Spring River; prairie restoration area S of Lake; T22N R08W S06 N1/4, 23 May 1997, *Summers 8132* (MO). Jefferson Co., sandy ridge above sandy creek, parallel to Rice Rd., exposed Petersburg sandstone, 29 Jun 1978, *Lorence 291* (MO); 4 mi NW of Pevely, Joachim township (T41N R5E Sec. 4, 9 Oct 1976, *Solomon 2587* (MO); 5 mi SE of Catawissa, 22 Jun 29, *Steyermark 1279* (MO); barrens near Big River, about 5 mi W of High Ridge, 17 Jun 1928, *Steyermark 2381* (MO); [loc. non indicato], 1891, *Wislizenus 946* (MO). Laclede Co., Sweet Hollow Creek, 3 mi W of Eldridge, off Hwy. NN, T36N R17W S28, 9 Oct 1991, *Summers 4759* (MO). Lincoln Co., west of bridge on Cuivre River, 23 Oct 1982, *Crosby 14618* (MO); Brashear's farm, near Whiteside, 28 Mar 1915, *Davis s.n.* (MO); Whiteside, 29 Mar 1914, *Davis 4427* (MO). Monroe Co., near Victor, 27 Jun 1933, *Palmer 40740-A* (MO). New Madrid Co., off of I-55N at mi 61.2, S of Sikeston, 36.80077 89.53167, 25 May 2007, *Majure 2435* (MISSA). Newton Co., Reding's Mill, 12 Aug 1908, *Bush 5072* (MO, US), Near Jofoliue [sic] 8 Apr 1909, *Palmer 09-027* (US). Phelps Co., Duke, 1 Aug 1913, *Emig 187* (MO), Rolla, Sept 1917, *Daniels s.n.* (NY). Scott Co., off of I-55N beside Best Western Hotel, Miner and N Sikeston; 36.8883°N, 89.5320°W, 26 May 2007, *Majure 2441* (MISSA). Shannon Co., Ozark National Scenic Riverways, Jerktail Mt., ca. 8 mi des NE of Eminence, 37°13'30"N, 91°18'00"W, 25 Oct 1996, *Dietrich 461* (MO). Taney Co., Mark Twain National Forest, Ozark, T23N R18W, along Blair Ridge Rd., 2 Jun 1978, *Hicks 988* (MO); upland ridge slope tributary to White River, 2 mi S of Groom, sect. 1, 30 May 1938, *Steyermark 5554* (MO); grassy berm, of US Rte. 160 at Rd. 160/270 (Kimball Rd.), 31 Jul 1999, *Vincent 8706* (MO, MU). Washington Co., limestone glades, old mines, 6 Jun 1927, *Kellogg s.n.* (MO); 7 mi N of Potosi on state rd. F at Mineral Fork Creek, 38° 00'N, 90°4.9'W, 19 Apr 1990, *Miller 4879* (MO). **New York:** Columbia Co., Hudson, NY, 25 Aug 1904, *Hastings* (NY). Orange Co., Coronham, 7 Aug 1912, *Dunslow* (NY). **Ohio:** Adams Co., Sandy Springs, sandy soil 1 mi N of the Ohio river near Church Township rd. 31 off rt. 52, Green Township, 12 Aug 1973, *Bryant s.n.* (MU); Hwy. 52E along the Ohio River (N of river and Hwy. 52) in graveyard of Sand Springs Church, 1 Jun 2008, *Majure 3251* (FLAS). Brown Co., Huntington Township, above Aberdeen, Ohio - station # 1., 1 Apr 1975, *Bryant s.n.* (MU). Erie Co., Cedar Point, Sandusky, Ohio; in the sand near the new Lake Laboratory, 1 Jul 1903, *Wetzstein s.n.* (MU); near Castalia, Jan 1921, *Wherry s.n.* (NY). Gallia Co., 1.5 mi off Rt. 325 on State Rt. 141 on banks of Raccoon Creek where it crosses Rt. 141, 12 Aug 1973, *Bryant s.n.* (MU); off of Hwy. 141 E just (ca. 1 km) E of Raccoon Creek, 1 Jun 2008, *Majure 3252* (FLAS). Hamilton Co., Ft. Dennison, E of Cincinnati, 10 Sep 1922, *Wherry s.n.* (NY). Jackson Co., dry cliff 0.5 mi west of Jackson, 14 Jun 1936, *Bartley & Pontius 59* (NY). Lucas Co., Oak Openings Metropark, 0.05-0.1 mi S of Reed Rd. & 0.1-0.2 mi E of Wilkins Rd., SW 1/4, Sect. 21, Swanton Twp., Whitehouse Quad., *Cusick 27529* (MU, NY); beside Swan Creek, along Oak Openings Preserve, just E of Wilkins Rd., S of Reed Rd., and W of Berkeley Southern Rd., 1 Jun 2008, *Majure 3254* (FLAS). Ottawa Co., Lakeside, Ohio, Marblehead Lighthouse, 8 Jul 1899, *Sanger s.n.* (MU); Cedar Point, 23 Jun 1894, *Worrallo s.n.* (MU). Woods Co., west end of cemetery S of Housekeeper Rd. on Zepernick Rd., 8 mi E of Bowling Green, 1 Apr 1971, *Hart s.n.* (MU); off of Zepernick Rd. from Hwy. 6 E ca. 8 mi E of Bowling Green, 1 Jun 2008, *Majure 3253* (FLAS). **Pennsylvania:** Bucks Co., Ralph Stover State Park, 9 Mar 1986, *Rhoads s.n.* (MOAR). Lancaster Co., Peach Bottom, 26 Jun 1893, *Castez & Small s.n.* (NY). **Tennessee:** Bledsoe Co., Off of Lowes Gap Mt. Rd., vicinity of Litton, 21 Dec 2006, *Majure 1938* (MISSA). Blount Co., Cave Springs near Townsend, 14 Aug 1942, *Sharp S-4247* (TENN). Cannon Co., jct. of Poplar Bluff Rd. (TN hwy. 96) and Hurricane Cr. Rd.; 16 583120N 3980169E, 9 Mar 2007, *Majure 2072* (MISSA). Cheatam Co., just W of Nashville along Hwy. 24W, ca. 0.5km E of exit 40 (Old Hickory Blvd.), 10 Jun 2008, *Majure 3280* (FLAS). Davidson Co., Davidson County, Hermitage, Tennessee; from I-40 East take the Old Hickory Blvd/Hermitage exit, north on Old Hickory Blvd to Central Pike, west on Central Pike for about 3 miles almost to Lebanon Road; plants are located ca 100 yards east of Lebanon Road on Central Pike on north side of road on a limestone outcropping in the lawn of a business near the railroad tracks, 36.18164 -86.62797, 19 Jul 2009, *Ward 420* (DES); Hermitage, Tennessee; from I-40 East take the Old Hickory Blvd/Hermitage exit, north on Old Hickory Blvd to Central Pike, east on Central Pike for about 2 miles to S. New Hope Road, then S about .4 miles to John Hager Road, east on John Hagar Road ca .1 mile on the south side of the road in an open field (glade); houses on west side, fenced farm on east side of lot; plants are in the field which appears to have been mowed, 36.15561 -86.58456, 20 Jul 2009, *Ward 421* (DES); cedar glade area along Bryant Grove Trail; Long Hunter State Park; SE of Nashville, 25 Jul 1997, *Weckman 3682* (EKY); Knapp Farm about 500 yards E of Mills Creek, 13 Jun 1937, *Woodruff s.n.* (TENN). De Kalb Co., 36.05907°N, 85.80175°W, Edgar Evans State Park, Center Hill Dam quad. 15 Sep 2002, *Phillippe 34887* (TENN). Decatur Co., eastern shore

of TN River, 13 mi above Perryville, 22 Aug 1907, *Clark 456* (US). Fayette Co., Gordon Hill area, S of Lagrange, 4 Oct 1980, *Bates, Jr. 1925* (TENN); TN 8113, 0.5 mi S of junct., this rte. and TN 57 in LaGrange, roadside and floodplain S Fork of Wolf River, Lower Coastal Plain Province, Jun 1968, *Brown T-478* (EMY, TENN). Fentress Co., 19 Apr 1949, *Fassett 27936* (TENN). Franklin Co., along Old Stage Rd., SW of Cowan about 4 mi, 2 Jun 2001, *Rhinehart s.n.* (TENN); Cumberland Plateau, Powerline ROW, S off of Hwy. 16 on Old Rowe Gap Rd., Limestone glade in clearing; 35deg 6.702N, 86deg 7.510W, 2 Aug 2008, *Snow 2061* (FLAS). Giles Co., SW of Pulaski, on north side of Hwy. 11, 100 yards N of Circle Rd., 14 May 2001, *Estes 1626* (TENN); Pulaski, from the courthouse, on Hwy 31 go south 3.1 miles to Hwy 64S bypass, go east 3.4 mi to Pisgah Ridge Road, then southeast for 0.8 miles to a field on right side of road to an area called 'Mt. Pisgah', in an open field on rollings hills with limestone outcroppings, 35.17983 -86.91975, 10 Jul 2008, *Ward 341* (DES). Hamilton Co., Snow Hill, S of Hwy. 312E on Whiteoak Mtn., before junc. w/ Ootlewah-Georgetown Rd.; 35.1737°N, 85.0331°W, 21 Dec 2006, *Majure 1937* (MISSA). Haywood Co., SE corner of the Hillville Loop Rd., 20 Mar 1984, *Lewis 1769* (TENN). Jackson Co., Flynn Creek Rd., about 9 mi W of Rt. 56, 11 Jun 1992 *McNeilus 92-545* (TENN). Jefferson Co., Friends Station, 1 mi W of New Market, 17 Jun 1934, *Weaver 1586* (TENN). Knox Co., 4 mi from Knoxville, on old Sevierville Rd., 5 Jun 1934, *Cain 555* (TENN); Eastern State Wildlife Management Area (aka Forks fo the River WMA), 3.9 miles E of downtown Knoxville, 0.6 mi due S of the confluence of the Holston and French Broad Rivers, 35.95056 -83.85111, 1 Apr 2006, *Estes s.n.* (DES); Eastern State Wildlife Mgmt. Area, S of TN River, W of Pickel Is.; 35.9503°N, 83.8517°W, 21 Nov 2006, *Majure 1939* (MISSA); open prairie, Knoxville, May 1897, *Ruth 2711* (NY). Lewis Co., Natchez Trace Parkway, Jacks Branch pulloff; 35° 24' 50"N 87° 30' 59"W, 19 Jun 2009, *Hill s.n.* (FLAS). Marion Co., High limestone bluffs N of Lee Highway Bridge; Cedar Mtn., 1 Jan 2003, *Beck 4398* (TENN). Marshall Co., exposed, dry area along Rt. 99, about 6.0 miles west of Rt. 31A, 7 Jun 1998, *McNeilus 98-312* (TENN); just W of Henry Horton State Park, South side of Caney Springs Rd., at a point ca. 0.7 mi W of Hwy. 31A; 35°36'10"N, 86° 42'43"W, 6 Jun 2005, *Rhinehart s.n.* (TENN). Maury Co., off of I-65 N; mi marker no. 32-51, 20 Jul 2007, *Majure 2608* (MISSA). Roane Co., Pisgah Ridge, facing Watts Bar Lake at river mi 570.8 (Bacon Gap quad), 14 Jun 1984, *Wofford 84-40* (TENN). Rutherford Co., Rt. 99, between Murphreesboro and Rockvale, 11 Oct 1958, *Sharp 25493* (TENN). Shelby Co., S of Cordova, 20 Aug 1947, *Sharp 6605* (TENN). Smith Co., Caney Fork; Upchurch Rd., ca. 4.9 mi W of jct. with Horseshoe Bend Rd., due E of Carthage, TN, 8 May 1999, *Weckman 4888* (EKY). Sumner Co., 5 mi N of Gallatin, 13 Oct 1968, *Rogers 42903* (TENN); on Old Hickory Lake along west side of Cumberland River bed north of Bluegrass Boat dock, 2 Jun 1999, *Ward 001* (DES); Cottontown, TN; From Nashville take I-65 N to Highway 25, east ca 6.5-7 miles, left on Awesome Avenue to 2nd property on left, 201 Awesome Ave. Plants are on east side of driveway at the edge of the woods and into the woods, 36.46839 -86.55258, 17 Jul 2007, *Ward 309* (DES); Gallatin, TN; from Nashville, TN take I-40 east to 109 N to Nichols Lane west to Loch Four Road to Bell Road at 446 Bell Road, road side for over 35 years, never seen any flowers (pc Jim Smart, owner of property); frontage was originally grown up in shrubs; original land was farmed with corn (pc original owner who was 109 years old at time of sharing story in 1998), 36.34306 -86.46525, 12 Jul 2008, *Ward 342* (DES); Cottontown, TN; From Nashville take I-65 N to Highway 25, east ca 6.5-7 miles, left on Awesome Avenue to 2nd property on left, 201 Awesome Ave. Plants are on east side of driveway at the edge of the woods and into the woods, 36.46839 -86.55258, 12 Jun 2010, *Ward 452* (DES). Wayne Co., 2.2 mi E of Clifton Junction, N side of Hwy. 64; 35° 18.416N, 87° 54.276W, 3 Aug 2008, *Snow 2061A* (FLAS). Wilson Co., S end of Lebanon, 8 Aug 1968, *Blum 2863* (FLAS). **Virginia:** Fredrick Co., off of Hwy. 50 W at Hayfield; jct. of N Hayfield St. and Hwy. 50 W, 30 May 2009, *Majure 3806* (FLAS). Page Co., eastern foothills of the Massanutten Mt., 8 Jun 1936, *Camp 1406* (NY); Luray, 20 Sep 1926, *Wherry s.n.* (US). Wythe Co., Barren Springs, Rt. 100, *Reed 97725*, 6 Mar 1975 (MO). **West Virginia:** Cabell Co., sandy field, near Milton, 9 Oct 1935, *Williams 366* (MO). **Wisconsin:** Columbia Co., sandy roadside near Lake Wisconsin, 24 Sep 1955, *Koeppe s.n.*, Dane Co., off of Hwy. 78S just N of Mt. Horeb, (T7N, R6E, Sec. 26), 21 Jul 1960, *Ugent 60-11J* (WISC). Grant Co., sec. 5, Woodman Township, T7N, R4W; W side of Hwy. 132 N of Mt. Hope, 4 Oct 1968, *Musselman 2291* (WISC). Green Co., 1 mi off county Hwy. on Sawmill Rd. (T4N, R6E, Sec. 20), 4 Dec 1970, *Cram 27* (WISC). Green Lake Co., Granite Knobs, Marquette, 18 Sep 1929, *Fassett 9203* (WISC). Jackson Co., near Rezin Marsh, 23 mi SE of Black River; Falk (Sec. 25, T26N, R1W), 20 Aug 1947, *Grether 6618* (WISC). La Crosse Co., Trunk quad, T18N, R6E, Sec. 9; Farmington Twp., 28 Jun 1956, *Hartley 923* (WISC). Marquette Co., Budsin Corner (T17N, R10E, Sec. 28), 9 Aug 1960, *Ugent 60-16* (WISC). Monroe Co., Dalton Ave. 0.75 mi E of hwy. 71; T16N, R3W, Sec. 3, 4 Sep 1988, *Graber 310* (WISC). Richland Co., ca. 1 mi NW of Hub City, off of Hwy. 80S, 8 Jun 2008, *Majure 3273* (FLAS).

Sauk Co., vicinity of Troy (T9N, R5E, Sec. 35, SW1/4), 17 Jul 1960, *Ugent 60-8c-8a*, (WISC). Waushara Co., T18N, R9E, Sec. 30, SE of Coloma and SW of Richford W of Hwy. 22, 1 Sep 1959, *Pochmann 15152* (WISC).

5. *Opuntia drummondii* Graham in Maund & Henslow (1846: 246) (Fig. 10). Lectotype (designated here):—[Icon] Plate 246 by Graham in Maund & Henslow (1846: 246) (see Fig. 10)

- = *Opuntia pes-corvi* LeConte ex Engelmann (1856: 346). Neotype (designated by L.D. Benson 1982: 923):—UNITED STATES. **Florida**: [Franklin Co.,] Apalachicola, FL, April, July, Nov., 1860, *Chapman s.n.*; MO-178898!, image available at <http://www.tropicos.org/Image/3893>).
- = *Opuntia frustulenta* Gibbes (1859: 273). Neotype (designated by L.D. Benson 1982: 923):—UNITED STATES. **South Carolina**: Charleston Co., Folly Island, near Charleston, 15 Feb 1916, *Small s.n.*; US-00178261!, image available at <http://collections.nmnh.si.edu/search/botany/>).
- = *Opuntia tracyi* Britton (1911: 152). Type (lectotype designated here):—UNITED STATES. **Mississippi**: [Harrison Co.,] Coast, Biloxi, May 1911, *Tracy s.n.* (NY-386004!, mature cladodes at the bottom left side of the sheet, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=561903).

Description:—Small shrubs 0.2–0.3 m tall, often forming large mounds as a result of disarticulating stems coupled with a high degree of branching, typically consist of numerous (3–5 or more) radiating branches (Fig. 9B) from a thick but shallow rootstock; older stems with a thin scaly bark; roots are mostly fibrous but commonly expand in girth for a short distance proximally (Fig. 9E). Cladodes typically cylindrical, but flattened as well, especially in larger basal cladodes, dark green, or yellow-green, not glaucous, small relative to other species, 0.8–11.1 cm × 0.6–3.4 cm, 5.3–14.8 mm thick, elliptical, oblong, or rounded in shape, with 1–2 areoles per diagonal row at midstem, the terminal cladodes easily disarticulating at the nodes, leading to frequent vegetative dispersal. Leaves green, 2.3–3.5 mm long, spreading or ascending parallel to cladode. Glochids stramineous, usually exerted and conspicuous. Spines 1.5–4.9 cm long, 0.2–0.9 mm in diameter, dark brown or mottled brown and white during development, aging white and finally gray, the basal cladodes usually producing spines throughout their lifetime, with up to 5 spines per areole, the terminal cladodes usually with 2–3 spines per areole; all spines are strongly retrorsely barbed, but spines on the terminal, easily disarticulating cladodes with more pronounced barbs, presumably aiding in vegetative dispersal. Flowers: outer tepals green or yellow-green, triangular or triangular ovate, erect and generally incurved in bud, generally small, inner tepals 8, dark yellow or occasionally light sulfur yellow, obovate with a mucronate tip, 2.2–3.2 cm long, staminal filaments yellow or yellow toward the apex and greenish-yellow at the base, stigmas white, with 3–6 lobes. Berries small, barrel shaped or clavate (Fig. 9G), 1.8–3.5 cm long, purple, pink, reddish-pink, or green at maturity. Seeds 4–5.4 mm long, funicular girdle 0.4–0.9 mm wide, funicular envelope smooth (with no prominent expansion from the embryo), or occasionally bumpy.

Phylogenetic placement:—*Opuntia drummondii* is sister to the rest of the diploid species in the SE clade of the *Humifusa* clade (see Fig. 1; Majure *et al.* in prep.).

Phenology:—Flowering mid-April–mid-May (rarely also in June), fruiting August–December (rarely to February).

Distribution and habitat:—*Opuntia drummondii* is found in coastal areas from North Carolina to western coastal Mississippi and can be found substantially far inland in Alabama and Mississippi (Majure & Ervin 2008). This species is slightly disjunct from the Gulf of Mexico to the Atlantic Coast (i.e., contiguous populations have not been found stretching across the Florida peninsula to the Atlantic Coast; Fig. 11). Interestingly, disjunct mountain populations and introgressive forms produced from putative hybridization with *O. mesacantha* have been found in Georgia (Fig. 10; asterisk) and South Carolina, suggesting a distribution pattern coincident with changing sea levels during interglacial cycles with the subsequent extinction of populations of the species in parts of the outer coastal plain.

Opuntia drummondii is most commonly found in coastal strand vegetation of the Gulf of Mexico and the Atlantic Coast commonly associated with *O. mesacantha* subsp. *mesacantha* or *O. mesacantha* subsp. *lata*. It is most common in non-shifting sands behind primary dunes, although, the species is also very common in certain parts of its range along major river systems with open, sandy habitats (see Majure & Ervin 2008). *Opuntia drummondii* is occasionally found on rock outcrops, as well, almost always associated with *O. mesacantha* subsp. *mesacantha*. The species also grows with *Aristida tuberculosa* Nuttall (1818: 57), *Bulbostylis ciliatifolia* (Elliott 1816: 82) Fernald (1938: 391) var. *coarctata* (Elliott 1816: 83) Kral (1971: 96), *Carex tenax* Chapman ex Dewey (1855: 254), *Ceratiola ericoides*, *Commelina erecta* Linnaeus (1753: 41), *Dichanthelium aciculare*, *D.*

oligosanthes, *D. ovale* (Elliott 1816: 123) Gould & C.A. Clark (1979: 1114), *Hypericum gentianoides* (Linnaeus 1753: 272) Britton, Stearns & Poggenb. (1888: 9), *Paspalum setaceum* Michaux (1803: 43), *Physalis angustifolia* Nuttall (1834: 113), *Pinus elliottii*, *P. palustris*, *P. taeda* Linnaeus (1753: 1000), *Smilax bona-nox* Linnaeus (1753: 1030), *Sporobolus junceus* (Beauvois 1812: 147) Kunth (1829: 68), *Stipulicida setacea* Michaux (1803: 26), *Stylisma humistrata* Chapman (1860: 346), *Triplasis americana* Beauvois (1812: 81), *T. purpurea* (Walter 1788: 78) Chapman (1860: 560).

Conservation status:—Although evaluated as least concern by Majure (2013b; as *O. pusilla*), and occurring over a wide range from North Carolina to Mississippi, *O. drummondii* often occurs in relatively small populations along river systems (Majure 2007b, Majure & Ervin 2008) that are subject to rapid succession and competition by other vegetation coupled with the absence of the historical fire regime in most of those areas to maintain open areas for colonization by the species. Likewise, many coastal populations are often fragmented by anthropogenic disturbance and development, so we consider *O. drummondii* to be vulnerable throughout its range.

Chromosome number:— $2n=22$ (diploid), $2n=33$ (triploid) and $2n=44$ (tetraploid) (Majure *et al.* 2012a). There are very minor morphological differences associated with cytotype, however, sufficient differences have not been observed that would suggest different ploidal levels should be recognized as separate species. Phylogenetic analyses to date reveal that these ploidal levels are not distinguishable from one another, suggesting that the polyploids may be autopolyploids (Majure *et al.* in prep.). Polyploids are mostly limited to coastal areas (except for mountain populations), under presumable harsher environmental conditions, whereas diploid members of the species are more widespread. Doyle (1990) considered *O. drummondii* (as *O. pusilla*) to be a diploid species, but had only determined chromosome number from two populations (from Okaloosa, Florida and Georgetown, SC). Majure *et al.* (2012b) did not find any diploid populations from the Atlantic Coast but rather tetraploids—diploids were restricted to the Gulf Coast/Coastal Plain region of AL, Florida and MS.

Notes:—Benson (1982) placed *O. drummondii* in synonymy with *O. pusilla* with no clarification as to why he thought this southeastern US species belonged within *O. pusilla*. Benson (1982) designated the neotype of *O. pusilla* as the line drawing by Pfeiffer & Otto of *O. foliosa* (Willdenow) Salm-Dyck (1828: 471) assuming that the two taxa were synonymous (see Britton and Rose 1920, p. 106), which although somewhat conforming to the morphology of *O. drummondii*, does not show a sufficient number of diagnostic characters to be identified to the species. This line drawing also was selected as the neotype for *O. foliosa*. Thus, it is unreasonable to use this name for the southeastern US material, since no type locality was ever given for *O. pusilla* (Haworth 1803, 1812) or *O. foliosa*, and the actual identity of *O. pusilla* is ambiguous, as no type ever existed. Likewise no type material has ever been found of *O. foliosa* (Leuenberger 2004) other than the line drawing by Pfeiffer and Otto designated as the neotype by Benson (1982). Apparently *O. pusilla* was introduced into cultivation in Europe by around 1805, as Haworth (1803) mentioned, however, he also mentioned that the species flowered in cultivation in June of 1796, so it is difficult to determine exactly when his *O. pusilla* was introduced into Europe. Britton and Rose (1920) mentioned that the species was typically assigned to South America and may even belong within *Tephrocactus* Lemaire (1868: 88), another genus within subfamily Opuntioideae. The later homonym, *Opuntia pusilla* Salm-Dyck, certainly does represent a South American species, *Maihueniopsis glomerata* (Haworth) Kiesling (1984: 202) (see Crook & Mottram 2001 for a discussion), although presumably this is not the same species as *O. pusilla*. Haworth (1812) also thought that the species may have been from South America and in his monograph described it alongside *O. curassavica* Miller (1768), a species from the Lesser Antilles (Venezuelan Caribbean)—several other Caribbean species of *Opuntia* are quite similar to that of *O. curassavica*, including *O. repens*, *O. taylorii* Britton & Rose (1908: 520), sometimes considered synonymous with *O. repens* (see Hunt *et al.* 2006, and Majure & Clase (2017) for a discussion), and *O. pubescens* Wendland in Pfeiffer (1837: 149). *Opuntia pubescens* also is distributed widely throughout South America. It is also highly likely that the name *O. pusilla* could have been confused with the southeastern US material, as many European cactus collectors often traded and sold *O. drummondii* under the mistaken identity of *O. pusilla*, according to Britton and Rose (1920). As far as is currently known, however, no material closely related to the southeastern US species has been found in the West Indies or South America, although, the closely related *O. abjecta* is found in the Florida Keys, which shares some Caribbean taxa with Antillean islands (although no close relatives of the *O. humifusa* complex). *Opuntia drummondii* has never been recorded from the West Indies and was described from the southeastern US (Appalachicola, Florida; Maund & Henslow 1846), so this name should be used for the southeastern US material instead of the ambiguous and undeterminable taxon *O. pusilla*. Further study is needed to determine the correct identity and affinity of *O. pusilla*.

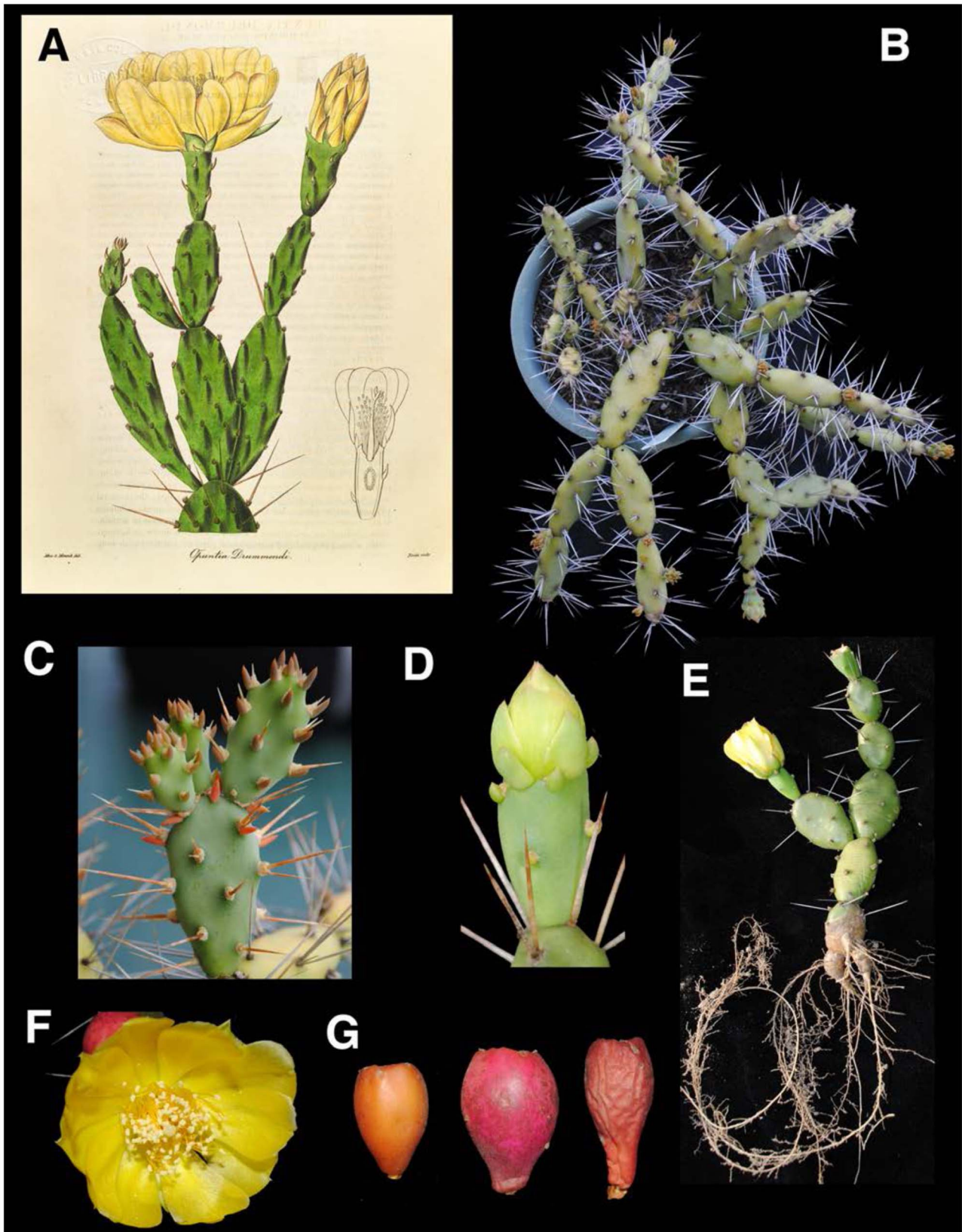


FIGURE 10. Morphological features of *O. drummondii*. A) lectotype of *O. drummondii*, from Maund & Henslow (1846), *Drummond s.n.*, Appalachicola, FL, B) spreading/trailing growth form of *O. drummondii* (*Mann s.n.*- Glynn Co., GA), C) young cladodes, showing long shoot leaves and reddish-brown developing spines from Horry Co., SC (*Majure 3833*), D) flower bud from Forrest Co., Mississippi (*Majure 756*), E) fibrous roots of *O. drummondii* showing proximal thickenings from Newton Co., MS, F) flower and G) fruit of *O. drummondii* (E-G from *Majure 4211*). Photo D taken by M. Pajuelo, and all other photos taken by L.C. Majure.

Although *O. drummondii* was described from Appalachicola, Florida (along the Gulf coast of Florida), Benson (1982) designated a neotype for the species from the Atlantic coast in St. John's County. However, he designated the neotype for *O. pes-corvi*, a synonym of *O. drummondii* described from South Carolina, from Appalachicola, Florida. Anderson (2001) placed *O. drummondii*, *O. pes-corvi*, *O. pisciformis*, and *O. tracyi* (all taxa described from the southeastern US) under synonymy with *O. pusilla*, and further stated that the species is found in the West Indies. By his placement of these other taxa in synonymy with *O. pusilla*, it is clear that Anderson (2001) understood neither where these other taxa were actually native, nor from where they were originally described. *Opuntia drummondii* is listed for Louisiana (under *O. pusilla*; USDA, NRCS, 2012), but those collections actually represent *O. nemoralis* Griffiths (see below). Benson (1982) placed *O. macateei* under synonymy with *O. pusilla*, which also conforms to *O. nemoralis*. Likewise, Weniger (1967) encountered what he identified as *O. drummondii* on Galveston Island, Texas. His collection also is *O. nemoralis* and not of *O. drummondii*, as circumscribed here. Weniger described the glaucous color of the stems, as well as a slightly reddish hue of the inner tepals, both characters exhibited by some populations of *O. nemoralis*. *Opuntia drummondii* never exhibits reddish coloring of the inner tepals, as *O. drummondii* is derived solely from the yellow-flowered southeastern subclade of the *Humifusa* clade (Majure *et al.* in prep.). Benson (1982) also reported *O. pusilla* from Anahuac, TX based on a specimen of David Griffiths (US). That specimen actually represents *Maihueniopsis ovata* (Pfeiffer) F. Ritter (1980: 399), a South American species, and must have been received by D. Griffiths from cultivated material.

Typifications:—*Opuntia drummondii*. The neotype material as designated by Benson (1982) is composed of material collected at two different times, the vegetative joints (POM-286363) in September of 1954 and then the flowers on a different sheet (POM-286363B) obviously collected at a different time of the year. *Opuntia drummondii* never flowers in September. Regardless, the neotypification by Benson (1982) is not applicable as original material exists, which is represented by the illustration in Maund & Henslow (1846: plate 246). That plate is here designated as the lectotype for the name *Opuntia drummondii*. Crook & Mottram (1996) wrongly considered the Plate 246 as the holotype.

Opuntia tracyi. Britton (1911: 152) stated "In sandy soil near the coast, Biloxi, Mississippi, *A. M. Tracy*, May, 1911; flowered at New York Botanical Garden May 12–13, 1911 (33786, type)". *Opuntia tracyi* is here lectotypified based on only the mature cladodes and excluding the flower on sheet NY-386004, as it is obvious from Britton (1911) and the sheet at NY that the flowers were collected at a later date (12–13 May) by Britton from the mature cladodes, which were originally collected by S. M. Tracy earlier in May of that same year.

Additional specimens examined. UNITED STATES. **Alabama:** Baldwin Co., sand dunes and roadsides between Gulf Shores and Ft. Morgan on Hwy. 180, 15 May 1971, *Evans 46023* (TENN); 8 air miles W of Gulf Shores. Bon Secour National Wildlife Refuge; 30°14'6"N 87°49'54"W, 26 May 2002, *Haynes 10259* (UNA); Fort Morgan Unit, Bon Secour NWR; 16 0401223E 3344351N, 29 Jun 2005, *Majure 1091* (MISSA, MMNS); Bon Secour National Wildlife Refuge, off of Mobile St., 29 May 2006, *Majure 1512* (MISSA, MMNS); 1.5 mi W of junct. of state Hwys. 182 and 161 in Orange Beach, N side of Hwy. 182, 23 Apr 1993, *Parfitt 5161* (ASU); E end of Ft. Morgan and 11.1 mi W of junct. of state Hwys. 180 & 59, S side of Hwy. 180, 23 Apr 1993, *Parfitt 5158* (ASU); *ibid*, *Parfitt 5159* (ASU). Butler Co., Hwy. 7, 2.5 mi N of Butler, Co. Hwy. 54, 31°56'50.38"N 86°51'25.19"W, 6 Sep 2007, *Diamond 18045* (TROY). Conecuh Co., US Hwy. 31 at N side of the Sepulga River, W of the rd, 31°27'16.5"N 86°47'8.5"W, 17 May 2008, *Diamond 19255* (TROY). Mobile Co., Dauphin Island, off of Hwy. 163 S; 30.2645°N, 88.1156°W, 8 Jul 2007, *Majure 2570* (MISSA); Drifting sand. Gulfshores, 27 Jul 1888, *Mohr s.n.* (UNA, US). **Florida:** Alachua Co., off of Waldo Rd., beside Gainesville Regional Airport, W side of rd., 29.69288°N, 82.28488°W, 11 Apr 2010, *Majure 4003* (FLAS). Baker Co., along Florida 2, at Breakfast Branch, 3.5 mi NW of Eddy Tower, 4.2 mi SE of Georgia St. line, 11 Jul 1984, *Hansen 9964* (USF). Bay Co., off of Hwy. 98W just W of Bay County Canal & W of Pt. St. Joe at Highland View, 6 Nov 2011, *Majure 4223* (DES, FLAS); from Hwy. 98W off of Flat Water East Rd., W of Highland View, 6 Nov 2011, *Majure 4224* (DES, FLAS). Columbia Co., off of Hwy. (CR) 246W, 7.7km E of White Springs, 15 Feb 2011, *Majure 4191* (FLAS). Duval Co., on ridge at N end of Big Talbot Island in NE corner of co., btwn. Sawpit Creek and Atlantic Ocean, 27 Dec 1965, *Blake s.n.* (UGA); Little Talbot Island State Park, N 1/2; R29E, T1N. Close to first boardwalk from 1st parking lot, 19 Apr 1990, *Easley 958* (FLAS); Jacksonville, Ft. Caroline National Monument and Timucuan Ecological and Historical Preserve, Willie Brown Trail, just E of the National Park Service building and museum, 13165 Mt. Pleasant Rd., 24 Apr 2005, *Giannasi 1385* (UGA); St. John's Bluff, Jan 1942, *Kurz 275* (MICH); at Jacksonville Beach, ca. 1.9 km S of Neptune Beach, 28 Mar 2009, *Majure 3700* (FLAS). Escambia Co., Near Pensacola, S of Navy Blvd., W of

Pace Blvd., just E of RR tracks and bridge, 3 Jun 1979, *Burkhalter 6405* (FLAS); Weedy area along railroad tracks at L St. and Barrancas Ave., Pensacola, 22 Aug 1976, *Hansen 3941* (USF). Flagler Co., off of Hwy. A1A S, just S of Sumner; roadside, 17 May 2008, *Majure 3221* (FLAS). Franklin Co., Appalachicola, 1 Aug 1922, *Kimball s.n.* (NY); St. Teresa, 28 Jul 1942, *Kurz 292* (MICH); *ibid*, *Kurz 293* (MICH); St. Vincent Island, 31 Oct 1910, *MacAtee 1775* (NY, US); jct. of NE 12th St. and Hwy. 98W at Carrabelle, 6 Nov 2011 *Majure 4222* (DES, FLAS); Carabelle Beach, off of Hwy. 98 E ca. 3 km SW of Carrabelle, 6 Nov 2011, *Majure 4225* (FLAS); High land, Appalachicola, Jan 1916, *Small s.n.* (NY); 4.8 mi. w. of Carrabel on U.S. #319, 6 Jun 1938, *Young 6* (FLAS). Gulf Co., Indian Pass, 28 Jul 1942, *Kurz 285* (MICH); *ibid*, *Kurz 286* (MICH); St. Joseph Peninsula State Park, 10 Sept 2008, *Sauby 325* (FLAS); Dunes along Gulf E of Port St. Joe., 4 Jun 1938, *Young 8* (FLAS). Hamilton Co., off of US Hwy. 6 E of Madison; 17 0285203N 3374733E, 8 Mar 2007, *Majure 2045* (MISSA); East side of Alapaha River, 6 mi W of Jasper off of Hwy. 41W, at jct. with Hwy. 6, 15 Feb 2011, *Majure 4192* (FLAS); E side of the Alapaha River, 6 mi W of Jasper off of Hwy. 41 W, close to junction with Hwy. 6, 30.528385, 83.035696; 15 Feb 2011, *Majure 4193* (DES, FLAS). Nassau Co., Fernandina, 21 Aug 1922, *Small s.n.* (NY); Shell mounds, Ft. George Island, 22 Aug 1922, *Small s.n.* (NY). Okaloosa Co., Mary Esther, Jan 1908, *Tracy 08-450* (US); just S of Botanical Facility, ca. 3 mi S of Valparaiso, 9 May 1968, *Smith 2395* (FLAS). Putnam Co., Off of Hwy. 100 in San Mateo, 4 Dec 2013, *Niles s.n.* (FLAS). St. Johns Co., dunes 5 mi S of Ponte Verde, 2 Sep 1954, *Benson 15388* (POM); Ft. Matanzas National Monument, St. Augustine Beach, N Rattlesnake Is., N of Ft. Matanzas, 28 May 2003, *Giannasi 48* (UGA); Ft. Matanzas National Monument, St. Augustine Beach, N Rattlesnake Is., SW of Ft. Matanzas, 29 Jul 2003, *Giannasi 266* (UGA); Ft. Matanzas National Monument, St. Augustine Beach, SE Anastasia Island, off Atlantic Beach Ocean beach access, E Florida A1A, 26 Sept 2003, *Giannasi 492* (UGA); Scrub just N of Matanzas Inlet (just off Rt. A1A); 16 May 1981, *Judd 2940* (FLAS); just S of St. Augustine, off of Hwy. A1A S, E side, vicinity of Anastasia Beach area; off of Magnolia Ave., 17 May 2008, *Majure 3218* (FLAS); off of Hwy. A1A S, W side of rd., vicinity of Devil's Elbow, 17 May 2008, *Majure 3219* (FLAS); Atlantic Beach, E of Jacksonville, 22 Aug 1922, *Small s.n.* (NY). Suwannee Co., Houston, 28 Oct 1910, *MacAtee 10-277* (US). Wakulla Co., Panacea Springs, 28 Jul 1942, *Kurz 290* (MICH). Walton Co., off of Hwy. 30A, Grayton Beach State Park, 25 Jun 2005, *Majure 1066* (MISSA). **Georgia:** Camden Co., Cumberland Island National Seashore, Stafford Field, central Cumberland Island, 27 Apr 2004, *Giannasi 836* (UGA); Cumberland Island National Seashore, S Cumberland Island, park service dormitory areas, 18 Jun 2004, *Giannasi 1026* (UGA); sand dunes, St. Marys, 20 Aug 1922, *Small s.n.* (NY); near lighthouse, Cumberland Is., 21 Jul 1974, *Worthington 202* (UGA). Chatham Co., Ft. Pulaski National Monument, NE end of Cockspur Island, adj. marsh lining the Savannah River, 6 Nov 1997, *T. Govus 901* (GA). Columbia Co., E side of Heggis's Rock ca. 2 mi N of GA 232, N of I-20, ca. 10.5 mi W of junct. of GA 232 and 104 in Martinez, 24 May 1996, *Christy 2762A-D* (ASU); 8 mi E of Appling, 11 Oct 1936, *Pyron 1033* (GA). DeKalb Co., off of Hwy. 124 N from exit 75 off of Interstate 285N, 27 May 2009, *Majure 3788* (DES, FLAS; note this is putative hybrid material between *O. mesacantha* and *O. drummondii*); collected on the summit of Stone Mt., 4 Jul 1893, *Small s.n.* (NY; note this is putative hybrid material between *O. mesacantha* and *O. drummondii*). Glynn Co., Jeckyll Island, Atlantic Coast side in center of the island, 1 Sep 2008, *Mann s.n.* (FLAS); St. Simon Island, sandy fields, E side of island on Sea Is. Rd., 28 Nov 1935, *Pyron 176* (UGA); NE shore of Jeckyll Is., just S of state campground. 31° 03'N, 81° 22'W, 10 Jun 1994, *Walker 767* (NY); Jeckyll Island, 1 Mar 1923, *Whargnam s.n.* (NY). Liberty Co., St. Catherines Island, N end of island, N of Seaside Creek, 13 June 1984, *Jones 24223* (GA). McIntosh Co., West central part of Sapelo Island, 16 Sept 1956, *Duncan 20518* (UGA); near the main residence of Plantation at S end of Sapelo Island, 28 Feb 1965, *Duncan 22469* (GA); Altamaha Waterfowl Management area near Butler Is., near Darien, 31 May 1959, *Harmer 641* (UGA); US 99 outside of Darien, 3 Jun 1992, *Heafner s.n.* (UGA). Toombs Co., sandy soil, 26 May 1964, *E. Daniels s.n.* (GA). Troup Co., N of McCombs Mill and store on Mountville Rd., 13 Jul 1971, *S.B. Jones s.n.* (GA). **Mississippi:** Clarke Co., Clarkco State Park, 6 May 1967, *Jones 12074* (UGA); Clarkco State Park off of Hwy 45S; N of lake under powerline; 32.10340N 88.69523W, 22 Oct 2005, *Majure 1254* (MISSA, MMNS); off of Hwy. 45, just N of jct. with Hwy. 512, 22 Oct 2005, *Majure 1270* (MISSA, MMNS); Chunky River off of Hwy. 11 brdge. Vic. Of Enterprise, 32.19220 - 88.82530, 7 Oct 2006, *Majure 1901* (MISSA). Forrest Co., Hattiesburg off of Edwards Rd., 5 Jan 2005, *Majure 756* (MISSA, MMNS); Hattiesburg Sanitary Landfill off of Jones St., 21 Jan 1976, *Snow s.n.* (USMS). George Co., Charles M. Deaton Preserve (TNC) at Merrill. West of Chickasawhay River. South of Hwy 98, 10 May 2002, *Leonard 10851* (MMNS); Charles Deaton Nature Preserve, Nature Conservancy Property off of US Hwy 98; vicinity of Merrill; Hog Island, 22 Jan 2005, *Majure 771* (MISSA, MMNS); Palestinian Gardens off of US Hwy

98; Property of James Kirkpatrick; UTM 16 0345811E 3429255N, 30.84994 -88.61472, 22 Jan 2005, *Majure 774* (MISSA). Greene Co., Charles Deaton Nature Preserve, Nature Conservancy Property off of US Hwy 98; vicinity of Merrill, 22 Jan 2005, *Majure 772* (MISSA, MMNS). Hancock Co., vicinity of Ansley, along Clairborne Rd., peninsula between tidal marshes, 9 Jun 2005, *Majure 1033* (MISSA, MMNS); Nasa-National Space Technology Laboratory, near gate WSTL, Gate 16, 23 Jan 1976, *Snow s.n.* (USMS). Harrison Co., Biloxi, 1 Aug 1896, *Pollard 1139* (NY, US). Jackson Co., Belle Fontaine Beach, W end, 18 May 2005, *Majure 955* (MISSA, MMNS); E end of Horn Island; 30.2220°N, 88.5795°W, 26 Nov 2006, *Majure 1920* (MISSA, MMNS); Middle of Horn Island at pier, 30.23650 -88.66740, 26 Nov 2006, *Majure 1922* (MMNS). Jasper Co., 7 mi NE of Montrose, 32.19598 -89.15074, 25 Aug 1955, *Ray, Jr. 5816* (MISSA); roadside of Hwy 503 S; S of Paulding; UTM 160308884 3544622, 32.03056, 9 Jan 2005, *Majure 765* (MISSA); Hwy 503 S; S of Paulding, across from Willam Chapel, 9 Jan 2005, *L.C. Majure 766* (MISSA, MMNS); vic. of Baxter along hwy. 15S, ca. 3 mi N of Montrose, S of Newton; 32.19248 89.16727, 30 Oct 2005, *Majure 1276* (MISSA, MMNS). Kemper Co., 11.1 mi N of Lauderdale-Kemper Co line N of Daleville, Hwy 39, 10 Jun 1969, *Jones 16051* (MISS); off of Hwy. 39S between Daleville and Dekalb, 32.71215N 88.66920W, 16 Jun 2007, *L.C. Majure 2555* (MISSA). Lauderdale Co., pipeline off Point Wanita Lake Rd., 9 Jan 2005, *L.C. Majure 763* (MISSA, MMNS); Chunky River, ca. 1 river km W of I-59; 32.22770 -88.83920, 28 May 2006, *Majure 1489* (MISSA, MMNS); Chunky River, ca. 2.5 km SSE of Stuckey's Bridge, 32.24280 -88.85380, 12 Jun 2006, *Majure 1533* (MISSA); Chunky River, E side of river btwn. Point Rd. and Hwy. 80, 32.31220 -88.89790, 8 Jul 2006, *Majure 1604* (MISSA); Chunky River, ca. 1km N of Hwy. 80 from boatlaunch, 32.33270 -88.90660, 16 Jul 2006, *Majure 1612* (MISSA); Chunky River, river trailside, ca. 0.3 km SW of Hwy. 80, 32.32520 -88.91160, 27 Aug 2006, *Majure 1729* (MISSA); off of pipeline ca. 1.2 km SW of Point Wanita Rd, 32.22680 -88.88030, 23 Sept 2006, *Majure 1854* (MMNS); 11.4 km SE of the town of Chunky off of Point-Wanita Rd., along pipeline, 0.5 km SE of P-W Rd., 15 May 2009, *Majure 3919* (FLAS). Lowndes Co., Chitlin corners; ca. 13 miles SE of Columbus, 33.29900 -88.31400, 10 April 1996, *MacDonald 9298* (MMNS); off of I-82, ca 0.5 mi W of Columbus, 12 Apr 2005, *Majure 843* (MISSA, MMNS). Newton Co., Chunky River, NE side of river, 32.31972 -88.91528, 21 May 2004, *Majure 309* (MMNS); Chunky River; ca. 0.75 mi SE of Hwy 80, 5 Feb 2005, *Majure 776* (MISSA); McGee Cemetery off of Buckley Rd., S of Hwy. 80, 32.484333 89.590166, 7 May 2005, *Majure 937* (MISSA); off of Buckley Rd, S of Hwy 80 along powerline, 32.48900 -89.57283, 7 May 2005, *Majure 938* (MISSA, MMNS); off of Liberty Church Rd. just S of the town of Newton, 12 Mar 2011, *Majure 4211* (FLAS). Noxubee Co., Gholson, off of Hwy. 21, 20 Aug 2005, *Majure 1155* (MISSA, MMNS). Perry Co., Mars Hill, Camp Shelby, DeSoto National Forest, 31 Dec 2004, *Majure 757* (MISSA, MMNS). Smith Co., Ainsworth property, S of Hwy 18, 29 Dec 2004, *Majure 753* (MISSA); Duckworth property along pipeline, S of Hwy. 18; UTM 16 0274759E 3537395N, 29 Dec 2004, *Majure 754* (MISSA); dirt rd. Off of Hwy. 35N, ENE of Mize; 31.8758°N, 89.5277°W, 9 Dec 2006, *Majure 1926* (MISSA, MMNS); dirt road off of Hwy. 35N ENE of Mize, 31.88330 -89.52330, 14 Feb 2006, *Majure 1931* (MMNS). **North Carolina:** Brunswick Co., Smith Island, 3 Apr 1918, *McCorm s.n.* (NY). Carteret Co., Beaufort, 14 Mar 1916, *Hatsel 16-46* (US); Ft. Macon, opposite Beaufort, 18 Aug 1922, *Small s.n.* (NY). Currituck Co., 1.9 mi S of Mamie on US 158, 25 Jun 1958, *Ahles 44470* (UNC); Church's Island, 20 Dec 1918, *MacAtee s.n.* (NY). Dare Co., Town of Kitty Hawk off of Hwy. 158 W between Wachovia Bank and The Marketplace, in front of shopping center, 2 Jun 2009, *Majure 3826* (DES, FLAS); Along Hwy. 12 S, S of the town of Kitty Hawk at junction with Palmetto St., 36.04467°N 75.67598°W, 2 Jun 2009, *Majure 3828* (FLAS); *ibid*, 2 Jun 2009, *Majure 3836* (DES, FLAS); Nag's Head; Vacant lot beside Blackman St. beach access parking area, off of S Virginia Dare Tr. (Rt. 12)., 13 Jun 2001, *Vincent 9384* (MU). Hyde Co., In between Old Hammock Creek and Shad Hole Creek, about 100 yds. S of Old Hammock Creek, on NC 12, 2 Apr 1966, *O'Briant 27* (GA); Ocracoke, 13-17 Oct 1898, *Kearney 2275* (US). New Hanover Co., 2.4 mi W of junc. of US Routes 74 and 76 on US Rt. 74, E of Wilmington, 22 Nov 1959, *Ahles 53112* (MU); near Wilmington, Sept 1922, Gross s.n. (NY); Wrightsville Beach at the end of Hwy. 76 E, 3 Jun 2009, *Majure 3830* (FLAS); 12 mi E of Wilmington, 3 Feb 1919, *Small s.n.* (NY). Onslow Co., at end of NC 210 near New River Inlet, 28 Apr 1969, *Leonard 2396* (UNA). **South Carolina:** Charleston Co., Porcher's Bluff, Christ Church Parish, 7 May 1911, *Mearees s.n.* (US); Charleston, Jan 1917, *Small s.n.* (NY); Isle of Palms, Charleston, 14 Feb 1916, *Small s.n.* (NY). Clarendon Co., Rt. 15-301, E Santee, 26 Mar 1988, *Reed 126895* (MO). Dorchester Co., terminus of NW-SE trending dirt rd. within white sand high-ground complex surrounded by bottomland ca. 1 mi S of US 17 (Harts Bluff bridge) on E side of Edisto River, MeadWestvaco forest land, 32.9192°N, 80.3983°W, 11 Oct 2004, *Nelson 25132* (USCH). Georgetown Co., Pawley's Island, 7 Jul 1959, *Godfrey 299* (US); N portion of Huntington Beach

State Park, just NW of north-side picnic shelters, S of Murrells inlet along US 17, 33.5172°N, 79.0537°W, 30 May 2003, *Nelson 23796* (USCH). Horry Co., at the S end of Folly Island County Park (Ashley Ave.), 3 Jun 2009, *Majure 3833* (DES, FLAS). York Co., ca. 3 mi NE of Clover off of Hwy. 321 N then off of Old Carriage Rd., 28 May 2009, *Majure 3792* (DES, FLAS).

6. *Opuntia humifusa* (Raf.) Rafinesque (1830: 247) ≡ *Cactus humifusus* Raf. Annals Nat. 15. 1820. Neotype (designated by Leuenberger 1993: 426):—UNITED STATES. **Pennsylvania:** Berks Co., 0.75 mi southwest of New Jerusalem, 10 July 1927, *Wherry s.n.* (US-000000!). (Fig. 12)

= *Opuntia calcicola* Wherry (1926: 12). Type:—UNITED STATES. **West Virginia:** Jefferson Co., growing on limestone edges, exact locality along B. & O. RR track about 2 mi N of Harper's Ferry RR station, 10 Jun 1925, *Wherry s.n.* (holotype US-00292854!, image available at <http://collections.nmnh.si.edu/search/botany/>; isotype NY-385974!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=740751).

Description:—Sprawling or slightly ascending shrub, during warmer months, forming large, often dense colonies, or caespitose clumps, the cladodes produced in chains of 1–4, often branching towards the tips of the plant and from the base; roots fibrous. Cladodes elliptical or rotund, dark green, not glaucous, cross-wrinkling during the winter, 9–15 × 5.7–8.3 cm, 9.6–15.7 mm thick, (3) 4–5 (mostly 4) areoles per diagonal row at midstem. Leaves dark green, 6.2–9.6 mm long, triangular-ovate, to narrowly ovate, ascending (parallel to the cladode surface). Glochids inconspicuous, generally only exerted in older, basal stems, stramineous, but turning light brown or amber in age. Spines absent. Flowers: outer tepals dark green to slightly gray-green, ovate or long triangular, erect or incurved, inner tepals 8–9, entirely yellow, 3.7–4.0 cm long, obovate, staminal filaments yellow or yellow-green, stigma white, 6–7 lobed. Berries green, red, or orange-red at maturity, 4.2–4.8 cm long. Seeds 3.0–3.5 mm long, funicular girdle 0.4–0.7 mm wide, often bumpy or irregular, funicular envelope raised along the margin from the increase in size of the cotyledons and hypocotyl, bumpy, portion of the funicular envelope surrounding the radical not evidently raised.

Phylogenetic placement:—*Opuntia humifusa* is an allotetraploid derivative of the southeastern and southwestern diploid subclades of the *Humifusa* clade (Majure *et al.* unpubl. data).

Phenology:—**Flowering** May–June (to July in more northerly locations), fruiting August–March (or rarely to May).

Distribution and habitat:—*Opuntia humifusa* is most common along the eastern edge of the Appalachian Mountains to the Atlantic seaboard. It also occurs sporadically in the southeastern US (see Additional specimens examined and Fig. 11). Although, not recorded from Alabama here, the species certainly could occur there, as well as northwestern GA in close proximity to populations of both *O. mesacantha* and *O. cespitosa*. *Opuntia humifusa* is most commonly found on rock outcrops (commonly slate or sometimes limestone) on the eastern slopes of the Appalachian Mountains or sandy soils of the Atlantic Coast. In other parts of its range, it is often found in sandy or clayey soils on xeric hilltops (e.g., Mississippi). This species appears to be more tolerant of mesic conditions than *O. mesacantha*. It can be found with *Danthonia spicata* (Linnaeus 1753: 80) Beauvois ex Roemer & Schultes (1817: 690), *Dichanthelium depauperatum* (Muhlenberg 1817: 112) Gould (1974: 59), *D. linerifolium*, *Diospyros virginiana* Linnaeus (1753: 1057), *Fraxinus americana* Linnaeus (1753: 1057), *Juniperus virginiana*, *Pinus echinata* Miller (1768:), *P. virginiana* Miller (1768), *Prunus serotina* Ehrhart (1784: 285), *Quercus alba* Linnaeus (1753: 996), *Q. marilandica* Muenchhausen (1770: 253), *Q. stellata* Wangenheim (1787: 78), *Sassafras albidum* (Nuttall 1818: 259) Nees von Esenbeck (1836: 490), as well as many other species.

Conservation status:—As circumscribed here, *O. humifusa* occupies a much-reduced distribution than that traditionally recognized. Populations of *O. humifusa* tend to be small and disjunct from other populations. Likewise, the species is highly prized and oftentimes over collected by aficionados, as it is one of the few species of cacti that grow in the eastern US at such northerly and seemingly "atypical" locations for a cactus. Overcollection is one of the primary drivers of species endangerment in the family (see Goettsch *et al.* 2015). Thus, we consider *O. humifusa* to be endangered from habitat loss, small population sizes, as well as overcollection. This is contrary to the least concern evaluation by Majure (2013c), which based the evaluation on a more widely circumscribed *O. humifusa*.

Chromosome number:— $2n=44$ (tetraploid) (Majure *et al.* 2012b).

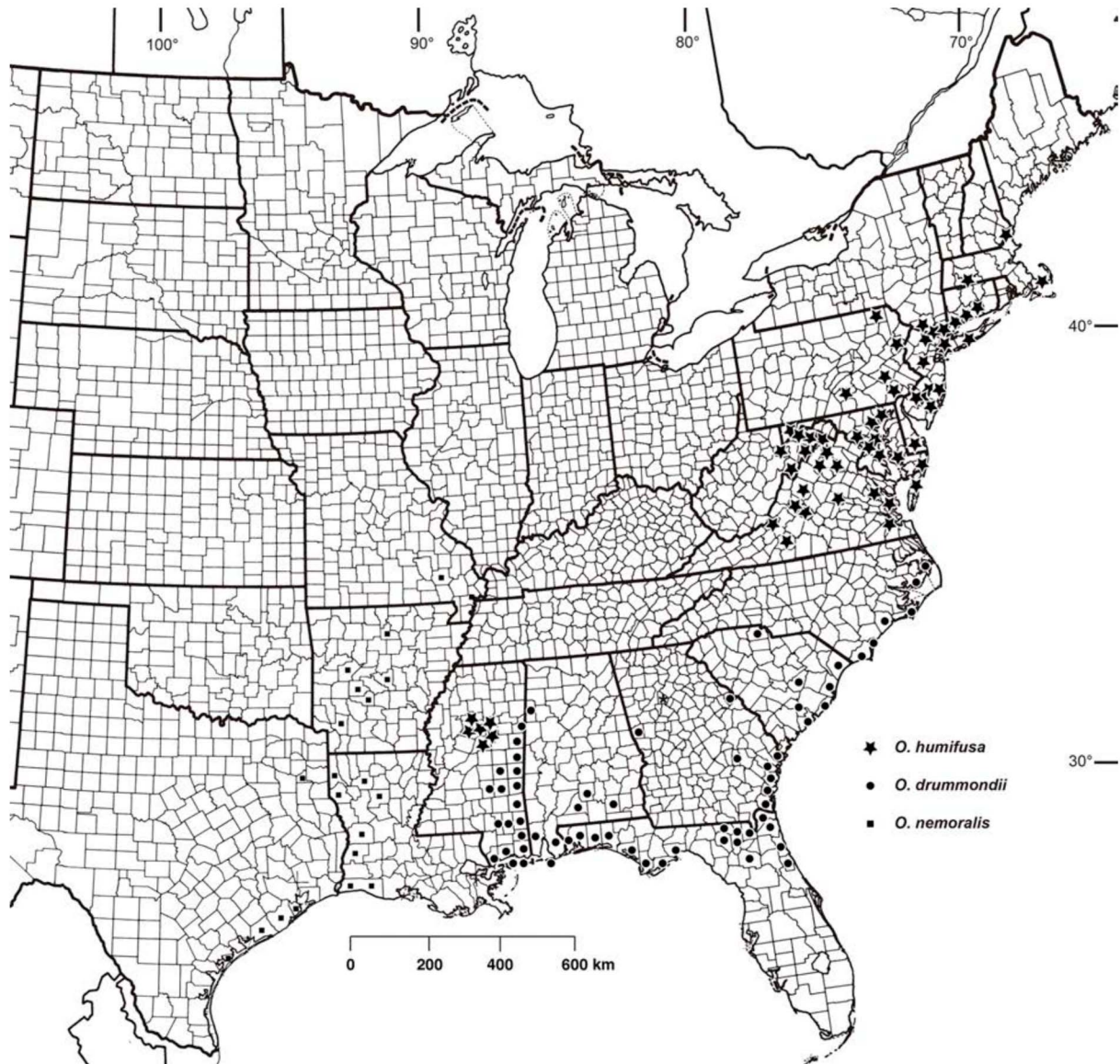


FIGURE 11. Distribution of *O. humifusa* (stars), *O. drummondii* (circles), and *O. nemoralis* (squares). Putative hybrid specimens of *O. drummondii* × *O. mesacantha* from Dekalb Co., GA, denoted with asterisk.

Notes:—*Opuntia humifusa*, geographically, is most often found between regions dominated by *O. mesacantha* subsp. *mesacantha* and *O. cespitosa*, suggesting those two taxa, or their ancestors could have been involved in the origin(s) of *O. humifusa*, which is derived from the SW (paternal lineage) and SE clade (maternal lineage), as is *O. cespitosa*. Although, *O. cespitosa* is suggested to have been derived from *O. mesacantha* subsp. *mesacantha* (maternal lineage), backcrosses of *O. cespitosa* to *O. mesacantha* subsp. *mesacantha* could have resulted in the formation of *O. humifusa*. Crossing studies need to be performed to further test this hypothesis. Kalmbacher (1975) noted that individuals in some populations of *O. humifusa* in New York may have yellow flowers or flowers with red centers. The first author has seen *O. humifusa* growing with *O. cespitosa* at one location in VA (presumably cultivated), but otherwise has not seen populations with mixed flower colors. Kalmbacher (1975) also mentioned that some plants in New York produced two types of flowers, purely yellow or yellow with reddish-blotched centers on the same plant. Although, the first author has never seen this, it does seem possible that putatively introgressed populations could yield the exhibition of such morphological characters within a population—such putatively introgressed populations occur in Massachusetts (see *O. cespitosa*). On the contrary, at the time of Kalmbacher's publications (1975–1976), all eastern *Opuntia* were recognized as *O. humifusa* s.l. It is possible that Kalmbacher actually was seeing populations of both *O. cespitosa* and *O. humifusa*, both of which occur in New York.

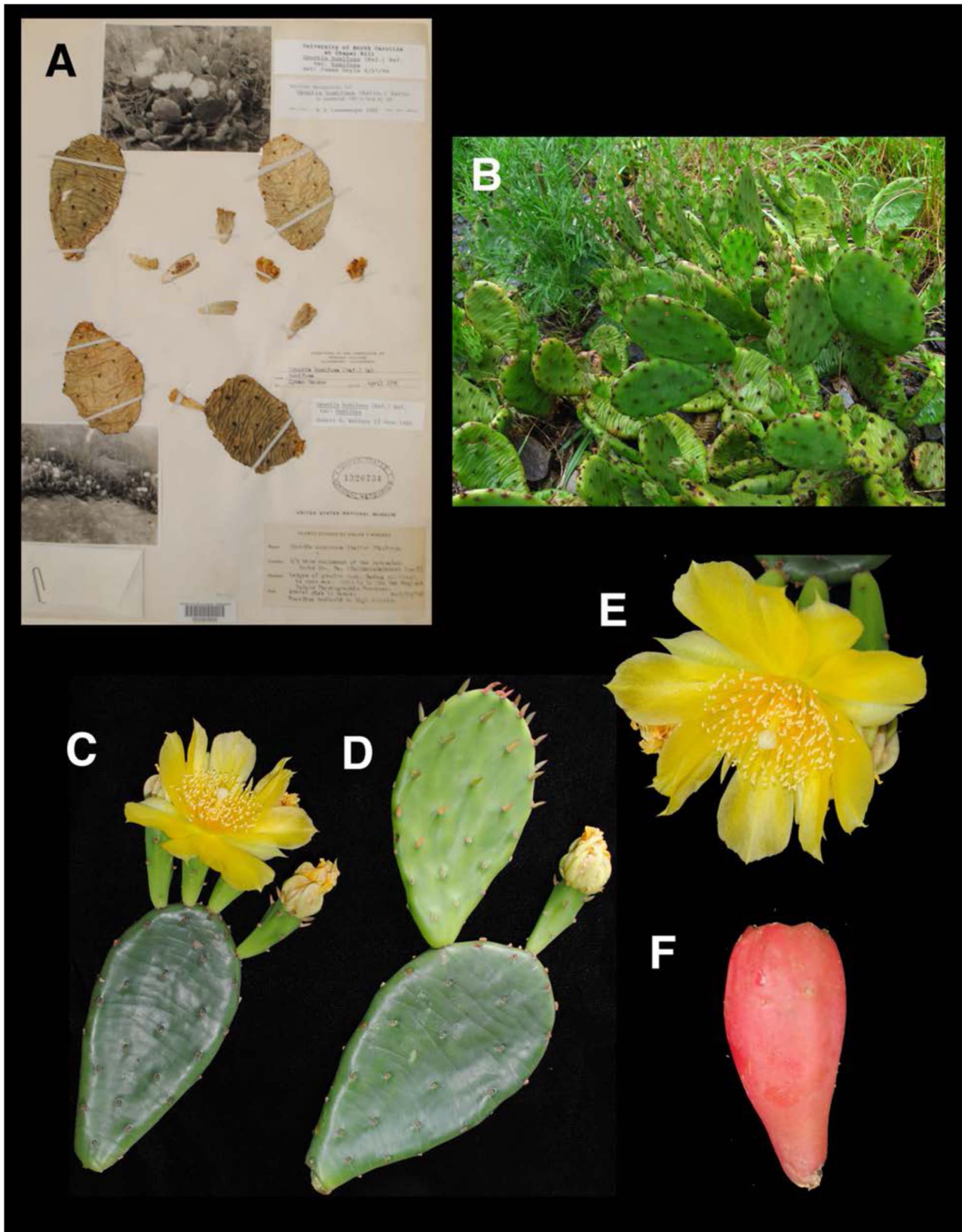


FIGURE 12. Morphological features of *O. humifusa*. A) neotype specimen of *O. humifusa*, C.T. Wherry s.n., Berks Co., PA (US), B) clumping/spreading growth form of *O. humifusa* from Page Co., VA (Majure 3798), C-E) flower, mature cladodes showing inconspicuous glochids, and immature cladode with leaves from Attala Co., Mississippi (Majure 3357), and F) mature fruit of *O. humifusa* from Webster Co., Mississippi (Philly 498). All photos taken by L.C. Majure.

Majure (2012) recognized three subspecies of *O. humifusa*, two of which in this treatment are included within *O. mesacantha*. The decision to split those taxa recognized as three subspecies in Majure (2012) into two species, *O. humifusa* and *O. mesacantha* (with two infraspecific taxa), is based on further morphological and phylogenetic work that demonstrated that *O. humifusa* is a putative allopolyploid derived from both the SE and SW subclades of the *Humifusa* clade, while *O. mesacantha* is apparently derived only from within the SE subclade. Although rather difficult to separate morphologically (see also Majure 2015), the circumscription presented here allows for the recognition of more biologically/phylogenetically realistic taxa rather than species based on phenetic differences alone. Further work will likely shed more light on the differences between these two taxa making it easier to separate them.

Benson (1982) also placed *O. allairei* Griffiths (1909: 83), *O. fuscoatra* Engelm. (1857: 297) and *O. xanthoglochis* Griffiths (1910: 166) within his circumscription of *O. humifusa* s.l. All three of those taxa clearly (i.e., morphologically and genetically) are more closely related to, and may be synonymous with, *O. macrorhiza*, and all have been collected and analyzed by L. C. Majure (see Majure *et al.* 2012b; Majure *et al.* unpubl. data).

Recently, Kim *et al.* (2014) carried out a phylogenetic analysis on accessions of *Opuntia* introduced into Korea and named the taxon, *O. humifusa* (Raf.) Raf. f. *jeollaensis* E.J.Kim & S.S.Whang (2014: 185). The photo of the material used to describe this new form conforms mostly to a form of *O. macrorhiza*, not *O. humifusa*. Likewise, their phylogenetic analysis shows no close relationship with *O. humifusa*, so it is unclear why they named this form of *O. macrorhiza* under *O. humifusa*. Likewise, the new form they proposed has yellow tepals with red bases and multiple (up to three) deflexing spines per areole, both characters of *O. macrorhiza*. They resolved this taxon within the *Macrocentra* clade, however, there were no support values on their cladogram, and the *Humifusa* clade was not resolved as monophyletic, so it appears most likely that poor resolution and lack of sufficient taxon sampling resulted in the observed topology.

Although Wherry (1926) cited his specimen *O. calcicola* as collected, 9 June 1925, only collections from the 10 June, 1925, exist at the two repositories listed in his description (i.e., US and NY) and are here designated as the holotype and isotype based on the interpretation that Wherry merely mistakenly altered the date of collection by a day in the protologue. These type specimens replace the neotype designation by Benson (1982) of a specimen collected by Wherry in 1932.

Additional specimens examined. UNITED STATES. **Connecticut:** Fairfield Co., near Stratford, 25 Aug 1894, Pollard 256 (US). New Haven Co., Leete's Island, 20 Jul 1958, Neale s.n. (FLAS); New Haven, West Rock, Oct 1873, Young s.n. (NY). Middlesex Co., Madison, 12 Sep 1970, F.C. Seymour s.n. (MO). **Delaware:** Sussex Co., Lewiston, Jul 1874, Canby s.n. (NY); at Frankford off of Hwy. 113 S at jct. with Catmans Rd., 2 Jun 2009, Majure 3824 (DES, FLAS); sand dunes, Atlantic Coast, Lewes, 12 Dec 1971, Reed 91882 (MO); Laurel, 25 Apr 1882, Smith 721 (US). **District of Columbia:** Washington Co., Bare rocks, island in Potomac, 22 Jun 1897, Steele s.n. (MU); rocks, vicinity of D.C., 22 Jun 1897, Steele s.n. (MU). **Maryland:** Alleghany Co., between Interstate 68 and Hwy. 144 E just E (ca. 1 km) of the town of Flintstone, 30 May 2009, Majure 3810 (FLAS); along US Hwy. 40 between Flintstone and Pratt, ca. 1.7 mi E of Polish Mt. summit and 0.2 mi E of Town Cr., 12 Jun 1977, Reveal 4670 (US); along US Rt. 40, just (ca. 1 mi) E of Flintstone, above Flintstone Cr., 3 Sept 1989, Vincent 3316 (MU). Anne Arundel Co., along Chesapeake Bay, Sandy Pt. St. Park, 17 Jul 1959, Reed 43690 (MO). Baltimore Co., edge of field at Loch Raven, Reed 5362, 10 Jul 1946 (MO). Calvert Co., S of Upper Marlboro, 4 Jul 1946, Reed 6075 (MO). Dorchester Co., Wet Swag, 1 mi N of Eldorado, Rt. 313, 17 Jun 1970, Reed 93538 (MO). Harford Co., Cedar Church Rd. off Rt. US #1, near Dublin, 27 Feb 1982, Reed 121327 (MO). Montgomery Co., Plummer's Island, 12 Sep 1910, MacAtee s.n. (NY). Worcester Co., along Rt. 388, 8–12 mi W of Snow Hill, 3 Nov 1990, Reed 132951 (MO). Prince George Co., Rt. US 50 and 301, Priests Bridge, 3 May 1960, Reed 46305 (MO). **Massachusetts:** Barnstable Co., off of Pilgrims Springs Rd., ca. 1.3 km S of WellFleet Harbor, 31 May 2009, Majure 3814 (FLAS). Hampden Co., Southwick, 26 Apr 1910, Gillette 15057 (US). **Mississippi:** Attala Co., off of rd. 5217, SE of Ethel from Kings Rd., 33.08230 89.42710, 15 May 2007, Majure 2364 (MISSA). Carroll Co., Holly Property adj. to Hwy 82 W, 8 Mar 2005, Majure 799 (MISSA, MMNS). Choctaw Co., 6.5 km E of Stewart, 1 Jun 2009, Philley 499 (FLAS). Grenada Co., Gore Springs, off of Betterton Dr. from Gore Springs Rd., 17 Sep 2006, Majure 1833 (MISSA, MMNS). Montgomery Co., Sam Marter property, N of CR 404, 13 Jan 2005, Majure 768 (MISSA, MMNS). Webster Co., 1.6 km SW of Tomnolen, 1 Jun 2009, Philley 498 (FLAS). **New Hampshire:** Hampshire Rockingham Co., at Seabrook, 1 Aug 2011, Nichols s.n. (FLAS). **New Jersey:** Atlantic Co., ca. 0.25 km SE of Nesco Rd. (Hwy. 542), E of Nescoghague Lake, P.E. Marucci Center for Cranberry and blueberry

Research, Hammonton, 1 Sep 2008, *Oudemans s.n.* (FLAS). Burlington Co., ca. 1.5 km SE of Pemberton, along Hwy. 530 N, 1 Jun 2009, *Majure 3821* (FLAS). Camden Co., without definitely locality, 25 Jun 1874, *Redfield 2459* (MO). Gloucester Co., Wenonah, 1 Oct 1904, *Hastings* (NY). Ocean Co., Tom's River, 14 Jul 1919, *Hunnewell 6465* (NY). Passaic Co., 5 mi W of Boardville, 14 Jul 1907, *Mackenzie 2738* (NY). Somerset Co., Rock Cliffs, near Biltmore, 1 Jun 1896, *Anonymous s.n.* (US). **New York:** New York Co., NY, NY, Van Cortlandt Park and vicinity, 1 Jan 1925, *Bicknell s.n.* (NY). Orange Co., West Point, 14 Mar 1905, *Means s.n.* (NY). Queens Co., Hunters Point, 28 Jun 1865, *Leggett s.n.* (NY). Richmond Co., Cooke's Point, Staten Island, 16 Jul 1914, *Photo* (NY). Rockland Co., Rocky Knoll, S end of Palisades Interstate Park, sec., Iona Island, 30 Jun 1953, *Lehr 283* (NY). Suffolk Co., at Ashrokan, Huntington, Long Island, 16 Oct 1926, *Banker 3844* (NY). Westchester Co., White Plains, *Willis s.n.* (NY); Pelham, 9 July 1882, *Day s.n.* (NY). **Pennsylvania:** Chester Co., Fern Hill, 0.83 km WNW of Fern Barrens, 6 Oct 2008, *Rhoads & Helm s.n.* (MOAR). Cumberland Co., E of Mechanicsburg, 13 Sept 1935, *Adams & Wherry 2461* (MOAR). Monroe Co., near top of Mosier's Knob, Shawnee on the Delaware, 29 Jun 1936, *Glowneke 1052* (MOAR). Susquehanna Co., Round Top Island, East of Harrisburg, 1 Jan 1912, *Gillett s.n.* (NY). **Virginia:** Accomac Co., just S of Wachopreague on CR 605, 5 Mar 1966, *James 3843* (UNC). Amherst Co., Rt. 130, 1.3 mi W of Rt. 635, NW of Elon, 25 Apr 1983, *Doyle 444* (UNC). Augusta Co., jct. of CR 1212 and CR 608, ca. 2 mi N of Vesuvius, 31 May 1986, *Doyle 827* (UNC). Craig Co., Rt. 311 ca. 0.1 mi W of Rt. 611 near Johns Creek, 5 Sep 1982, *Doyle 310* (UNC). Culpeper Co., near Cedar Hill, Rt. 522, 3 May 1969, *Reed 87781* (MO). Franklin Co., Bald Knob, Rocky Mount, 26 Jun 1976, *Stevens 13064* (MO). Fredrick Co., off of Hwy. 50 W at Hayfield, jct. of N Hayfield St. and Hwy. 50 W, 30 May 2009, *Majure 3807* (FLAS). Gloucester Co., G.P. Coleman Memorial Building on US 17 (S point of county), 5 Jul 1966, *James 4926* (UNC). Goochland-Fluvanna Co., cliffs, Rt. 6, at Columbia, 30 Jun 1970, *Reed 97330* (MO). Isle of Wight Co., near Franklin, 7–28 Jun 1893, *Heller 737* (US); *ibid*, *Heller 916* (MO, NY). King & Queen Co., Rt. 360, just S of Stephen's Church, 25 Nov 1974, *Reed 96621* (MO). Page Co., off of Hwy. 34 N, 5.9 km N of town of Shenandoah and 0.10 km N of Shenandoah River, 29 May 2009, *Majure 3798* (FLAS); At junction of Hwy. 340 N and 211 W, 29 May 2009, *Majure 3799* (DES, FLAS); limestone cliffs, Rt. 211, just W of Luray, 17 May 1969, *Reed 84825* (MO). Rockbridge Co., Central Blue Ridge, Taylor Hollow, 4 mi S of Vesuvius, Rt. 608, 8 Apr 1967, *Freer s.n.* (UNC). Warren Co., off of Hwy. 11 W just E of Middletown ca. 0.1 km at Cedar Creek Battleground, 29 May 2009, *Majure 3800* (FLAS). **West Virginia:** Hampshire Co., At the town of jct. just W (ca. 0.25 km) along shaly slopes of Hwy. 50 W, 30 May 2009, *Majure 3808* (FLAS); Limestone shales, Rt. 220, S of Junction, 14 Sept 1968, *Reed 78644* (MO). Hardy Co., Moorefield, 1 Jan 1913, *Gamble 245* (NY). Mineral Co., on dry bank near Burlington, 21 Aug 1930, *Berkley 1671* (MO); ca. 3 km W of the town of jct. along Hwy. 50 W, 30 May 2009, *Majure 3809* (FLAS). Pendleton Co., ca. 1.2 km S of Brandywine, 1 Jun 2011, *Ribbens s.n.* (FLAS). Tucker Co., Canaan Valley, old shale barrens near Old Boyer Place near Boyer's Spring, 29 Sept 1945, *Allard 11785* (US).

7. *Opuntia mesacantha* Rafinesque (1830: 216) (Figs. 13,15). Neotype (designated by Majure 2014: 1):—UNITED STATES. **Virginia:** Hampton, 31 May 1878, *Chickering, Jr. s.n.* (US-00292862!, image available at <http://collections.nmnh.si.edu/search/botany/>)

Description:—Sprawling shrubs, procumbent or cladodes often slightly ascending directly from the base of the plant, forming large colonies, sometimes several meters in diameter; roots typically fibrous, although generally thickening proximally. Cladodes obovate, elliptical, or rotund, margins smooth or scalloped, dark green to light yellow-green, not glaucous, cross-wrinkling during the winter, 3.1–17.7 × 2–9 cm, 3.6–19.9 mm thick, occasionally cladodes disarticulating with ease in summer months, although, generally not disarticulating without force, areoles 3–4 (generally 3) per diagonal row at midstem. Leaves light or dark green, ascending parallel to the cladode or slightly spreading, triangular or ovate, 4.8–7.8 mm long. Glochids conspicuous, exerted or inconspicuous, included within the areole, stramineous, aging light brown, or light amber. Spines 0–5 per areole, relatively long or short, conspicuous in many specimens, robust or delicate, 0.9–4.9 cm long, 0.7–1.3 mm in diameter, strongly retrorsely barbed when young to several years old, this often being lost in older spines, dark brown-white mottled, yellow-brown, or brown-yellow-white mottled during development, white when mature, aging gray. Flowers: outer tepals green, broadly triangular, erect or commonly incurved in bud, inner tepals 8, entirely yellow, 2.3–4.3 cm long, obovate to obtriangular, apex margins often moderately lacerate, mucronate, stamen filaments yellow or yellow green, stigma white, 6-lobed. Berries 2.1–4.9 cm long, clavate to barrel-shaped,

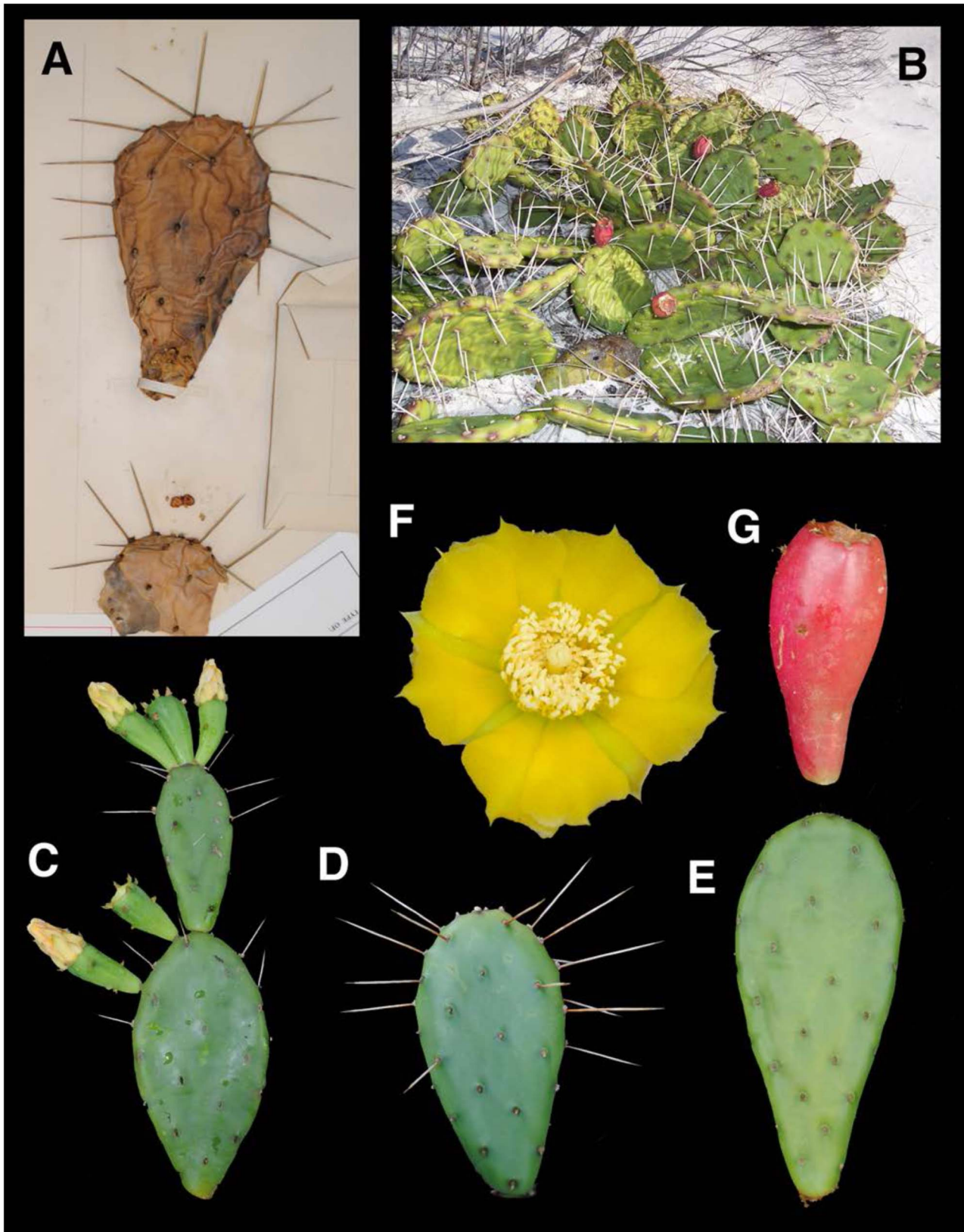


FIGURE 13. Morphological features of *O. mesacantha* subsp. *mesacantha*. A) holotype specimen of *O. pollardii*, C.L. Pollard 1138, Harrison Co., Mississippi (NY) showing typical characters of *O. mesacantha* subsp. *mesacantha*, B) growth form of *O. mesacantha* subsp. *mesacantha* from Jackson Co., Mississippi (Majure 1921), C-E) cladode and spine production variation in *O. mesacantha* subsp. *mesacantha*, F) flower and G) fruit of *O. mesacantha* subsp. *mesacantha*. C from Harrison Co., Mississippi (Majure 1603), D from Winston Co., Mississippi (Majure 769), E-G from Forrest Co., Mississippi (Majure 806). Photos C & F taken by M. Pajuelo; all other photos taken by L.C. Majure.

green, red, orange-red at maturity. Seeds 4.7–5.9 mm long, funicular girdle 0.6–1.3 mm wide, bumpy, irregular (margins undulating) or smooth, funicular envelope raised along the margin from the increase in size of the cotyledons and hypocotyl or not raised, bumpy or not, portion of the funicular envelope surrounding the radical not evidently raised.

Phylogenetic placement:—See below for phylogenetic placement of the two subspecies.

Phenology:—Flowers mid March–June (rarely in July & August), fruiting August–May.

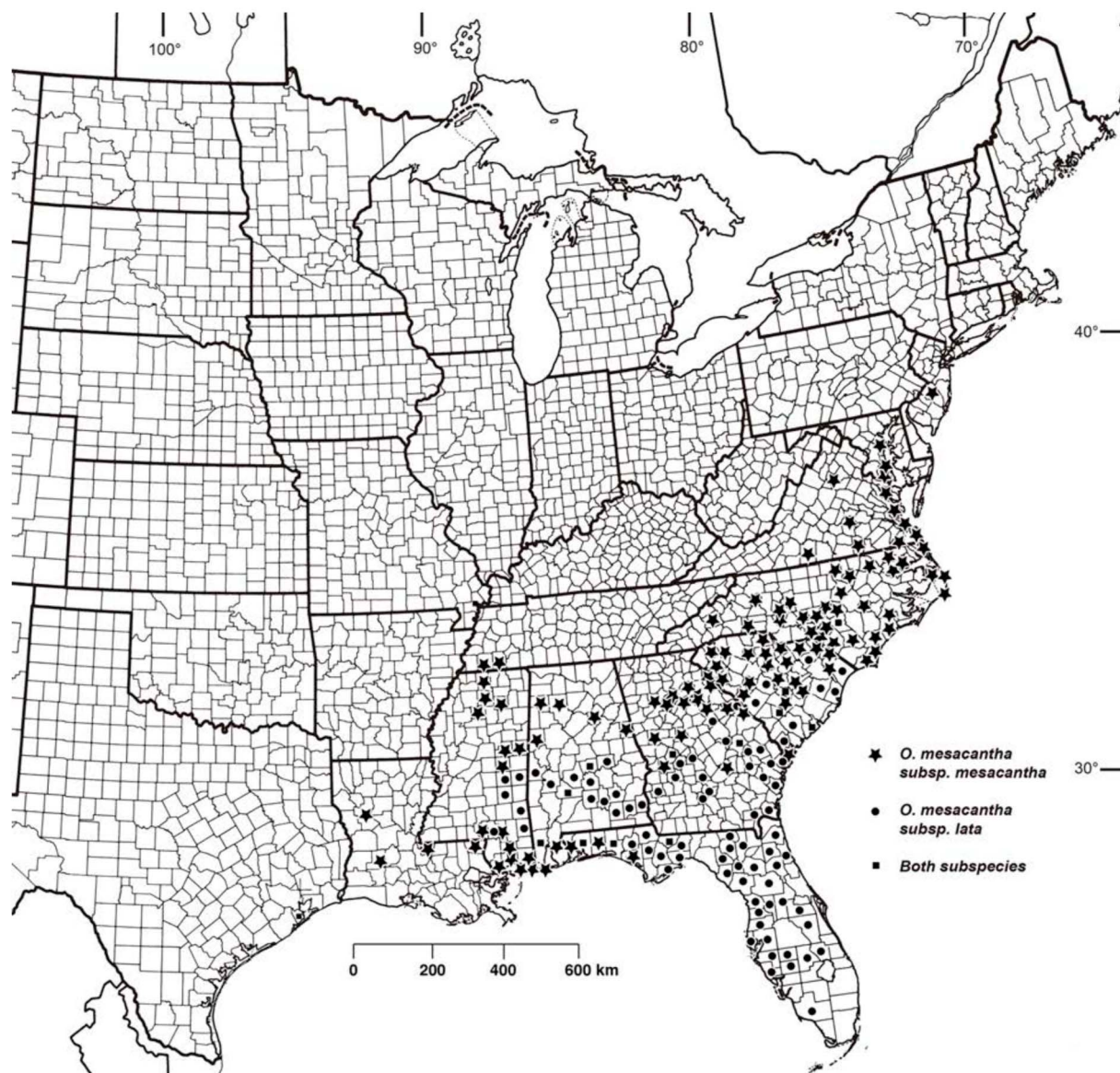


FIGURE 14. Distribution of *O. mesacantha*. *O. mesacantha* subsp. *mesacantha* (stars), *Opuntia mesacantha* subsp. *lata* (circles), both subspecies (squares).

Distribution and habitat:—*Opuntia mesacantha* is one of the most widespread species of *Opuntia* in the eastern US occurring throughout the inner and outer coastal plains from Maryland to coastal Mississippi and Louisiana (Fig. 14). *Opuntia mesacantha* typically occurs on sandy soils or thin soils over granite and is associated with a number of species that typically occur in xeric areas including *Ceratiola ericoides*, *Danthonia sericea*, *Dichanthelium aciculare* s.l., *D. oligoanthes*, *D. ovale*, *D. sphaerocarpon* (Elliott 1816: 125) Gould (1974: 60), *D. tenue* (Muhlenberg 1817: 118) Freckmann & Lelong (2002: 171), *Diospyros virginiana*, *Juniperus virginianus*, *Pityopsis graminifolia* (Michaux 1803: 122) Nuttall (1840: 317), *Quercus hemisphaerica* Bartram (1791: 320), *Q. incana* Bartram (1791: 403), *Q. laevis*, *Rhynchospora megalocarpa* Gray (1835: 208), *Rhus copallinum* Linnaeus (1753: 266), *Rubus cuneifolius* Pursh (1813: 347), *Serenoa repens*, and *Yucca filamentosa* Linnaeus (1753: 319).

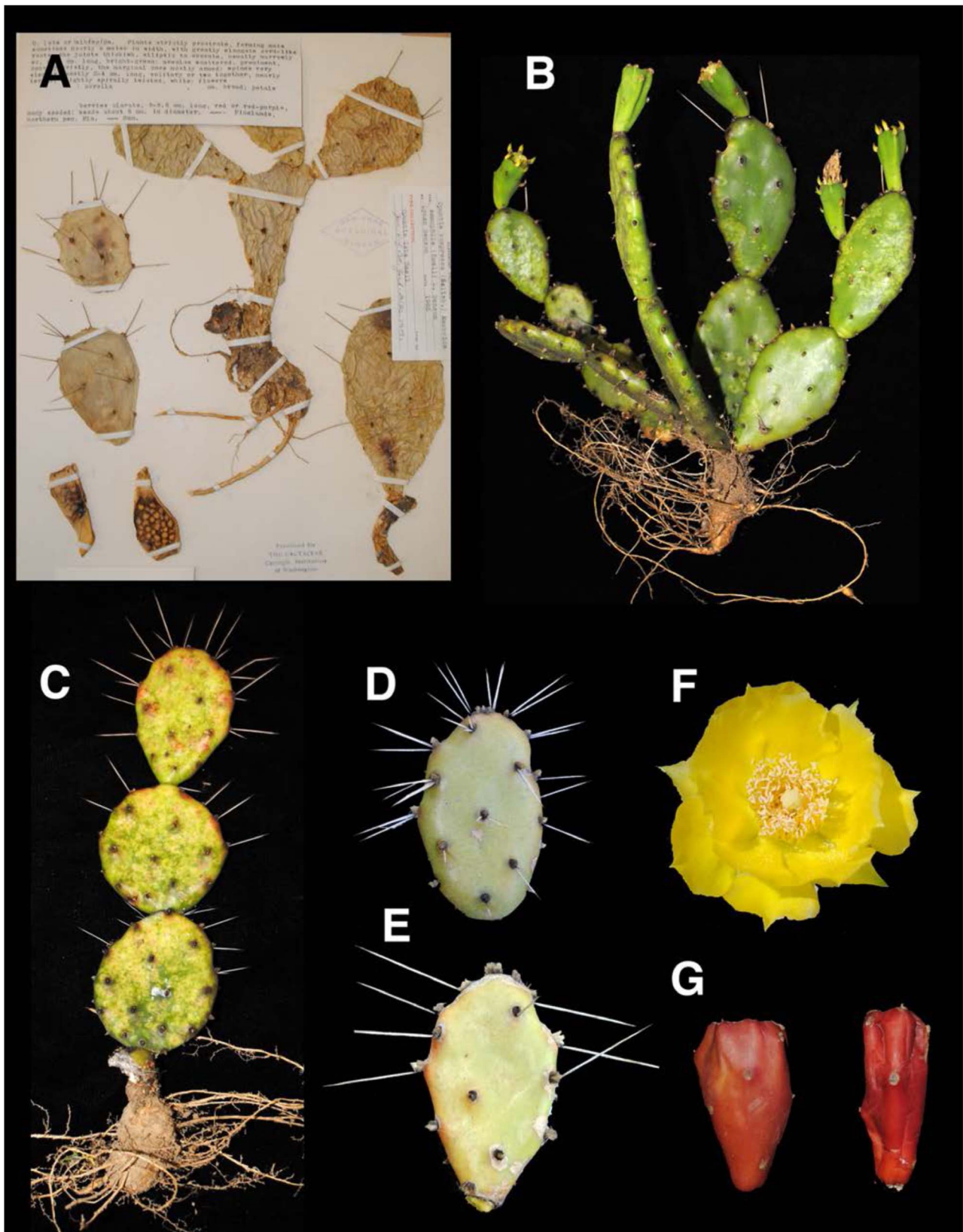


FIGURE 15. Morphological features of *O. humifusa* subsp. *lata*. A) type specimen of *O. lata*, J.K. Small s.n., Alachua Co., Florida (NY), B-E) growth form, cladode shape, and spine production variation in *O. humifusa* subsp. *lata*, F) flower and G) fruits of *O. humifusa* subsp. *lata*. B-C and F-G from Wakula Co., Florida (Majure 3378), D from Wayne Co., Mississippi (Majure 1290), E from Levy Co., Florida (Majure 3645). All photos taken by L.C. Majure.

Conservation status:—*Opuntia mesacantha* is one of the most widespread species in the eastern US, as circumscribed here. Large populations of the species exist in the outer coastal plain, however, more inland populations tend to be smaller and widely separated from one another, usually restricted to very specific soil types (e.g., granite outcrops, inland sands) creating dry edaphic conditions. Outer coastal plain populations also are often fragmented and threatened by anthropogenic disturbance and development. Thus, we consider the species as vulnerable to habit loss and fragmentation.

Chromosome number:— $2n=22$ (diploid), $2n=44$ (tetraploid) (Majure *et al.* 2012b).

Notes:—Rafinesque first mentioned this species, as *Cactus mesacantha* [sic], in his work on botanical discoveries in Kentucky and other parts of the southeastern US (Rafinesque 1821) and then later in his Medical Flora (Rafinesque 1830), but he did not provide a description of the species, and thus validate it, until later in 1830 (Rafinesque 1830). Although all other authors have included this species in synonymy with *O. humifusa*, this species can be distinguished by a number of characters including ploidy (in part), as well as vegetative and reproductive characters (see key and taxon descriptions). The name *Opuntia compressa* has been applied to this type of material (and *O. humifusa* in general), however, Leuenberger (1993) unequivocally showed this name to be superfluous and illegitimate, as the name *Cactus compressus* Salisbury (1796: 348) was coined by Salisbury to replace the tautonym *Opuntia opuntia*, and likewise *O. opuntia* is a synonym of the earlier described *Opuntia ficus-indica* (see Leuenberger 1993 for further details).

The use of the name *O. mesacantha* for this species is warranted, as it is clear from the descriptions of *O. humifusa*, *O. cespitosa* and *O. mesacantha* that Rafinesque did not fully understand the distributions of those taxa but did recognize morphological differences among them, which have been corroborated to some extent by other authors as well (Engelmann 1856, Britton & Rose 1919, Benson 1982, Doyle 1990, Majure & Ervin 2008, Majure *et al.* 2012b). Rafinesque (1830) cited Kentucky as the region in which *O. mesacantha* was native, and that is normally cited as the type location for the species (Crook & Mortram 2000). However, in his description of *O. mesacantha* Rafinesque explained that the flowers are yellow, although all material that has been seen from Kentucky has yellow flowers with red centers (Majure pers. obsv.) and is referable to our circumscription of *O. cespitosa*. He also mentioned that the species has long central spines, a character that fits with *O. mesacantha* in the way we have circumscribed it here, and not with the yellow-flowered *O. humifusa*, which is spineless. Thus, it appears that Rafinesque may have based his circumscription of *O. mesacantha* on material that was collected from around Kentucky where *O. mesacantha* is also native, but perhaps not necessarily in Kentucky.

Hanks and Fairbrothers (1969b) estimated 17+ and 19+ counts for *O. humifusa s.l.* in New Jersey and state that another researcher M. Carson obtained a somatic count of $2n=22$ from a population from Atsion, NJ. Unfortunately, no specimens appear to have been made during this study (none were cited), and thus, we have not been able to confirm whether or not *O. mesacantha* subsp. *lata* could potentially exist in New Jersey. All other chromosome counts from New Jersey have been at the tetraploid, $2n=44$, level (see Majure *et al.* 2012b). A diploid count from North Carolina was reported by Bowden (1945) from Brunswick Co. and must certainly represent *O. mesacantha* subsp. *lata*, although the specimen has not been seen by the authors. All other counts from that area are of tetraploids (Majure *et al.* 2012b).

Key to Subspecies of *O. mesacantha*:—It follows:

1. Seeds with funicular envelope smooth, only moderate, if any, protrusion of the cotyledons and hypocotyl, cladodes typically scalloped-margined, elliptical or rotund, spines delicate, 0.7–0.9 mm in diameter, outer coastal plain *O. mesacantha* subsp. *lata*
- Seeds with funicular envelope bumpy, cotyledons and hypocotyl noticeably protruding, cladodes typically smooth-margined, obovate or rotund, spines robust, 0.95–1.3 mm in diameter, outer and inner coastal plain and piedmont *O. mesacantha* subsp. *mesacantha*

7a. *Opuntia mesacantha* subsp. *mesacantha* (Fig. 12)

= *Opuntia pollardii* Britton & Rose (1980: 523) (Fig 13). Type:—UNITED STATES. **Mississippi:** Harrison Co., Biloxi, 01 August 1896, *Pollard 1138* (holotype NY-385998!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=333222; isotypes MO-178316!, image available at <http://www.tropicos.org/Image/65492>; US-00117022, 00117023!, images available at <http://collections.nmnh.si.edu/search/botany/>)

Description:—Cladodes commonly obovate, margins smooth, leaves 4.8–5 mm long, spines 0.9–3.2 cm long, 0–3

per areole (spines generally 1–2 restricted to the upper areoles when present), 0.95–1.3 mm in diameter, tepals 2.3–3.0 cm long, Seeds 5.0–5.9 mm long, funicular girdle 0.7–1.3 mm wide, often bumpy or irregular, funicular envelope raised along the margin from the increase in size of the cotyledons and hypocotyl, bumpy.

Phylogenetic placement:—*Opuntia mesacantha* subsp. *mesacantha* is a tetraploid, apparently derived solely from the SE clade, and it is very closely related to *O. cespitosa* and *O. nemoralis* according to plastid DNA sequence data, and likely was, or an ancestor thereof was, one of the progenitors (maternal) of both species.

Phenology:—Flowering April–June, fruiting June–May.

Distribution and habitat:—*Opuntia mesacantha* subsp. *mesacantha* is mostly confined to the coastal plain of the eastern US (see specimens examined), however this subspecies covers the broadest distribution of the two subspecies of *O. mesacantha*. *Opuntia mesacantha* subsp. *mesacantha* is one of the most common taxa of *Opuntia* along the Gulf Coast of Alabama, Mississippi, and along the panhandle of Florida (Fig. 14). *Opuntia mesacantha* subsp. *mesacantha* is most common in the eastern US pine belt in sandy soils in *Pinus palustris* sandhills or mixed *Pinus-Quercus* sandhills, although, it is frequently encountered on granitic outcrops in Georgia, South Carolina, and North Carolina. In Alabama, Mississippi, and the Florida panhandle it is common in non-shifting dunes behind primary dunes, similar to *O. drummondii*, with which it is commonly sympatric. It also occurs with *Carex tenax*, *Ceratiola ericoides*, *Dichantheium oligosanthes*, *Ilex vomitoria* Aiton (1789: 170), *Opuntia stricta*, *Packera anonyma* (Wood 1861: 464) Weber & Löve (1981: 45), *Piptochaetium avenaceum* (Linnaeus 1753: 78) Parodi (1944: 229), *Pinus echinata*, *P. virginiana*, *Phemeranthus teretifolius* (Pursh 1813: 365) Rafinesque (1814: 86), *Physalis angustifolia*, *Prunus serotina*, *Pteridium aquilinum* (Linnaeus 1753: 1075) Kuhn (1879: 11), *Sassafras albidum*, *Serenoa repens*, *Smilax pumila* Walter (1788: 244), *Triplasis americana*, and *Yucca filamentosa*.

Conservation status:—*Opuntia mesacantha* subsp. *mesacantha* is widespread throughout the piedmont and coastal plains of the eastern US. The taxon is vulnerable due to small population sizes, habitat fragmentation and loss, especially in the piedmont and along coastal areas that are subject to commercial development. Majure (2013d; as *O. pollardii*) considered this taxon of least concern but did not take into account man-mediated habitat destruction along coastal areas where it often occurs.

Chromosome number:— $2n=44$ (tetraploid) (Majure *et al.* 2012b).

Notes:—The polyploid *Opuntia mesacantha* subsp. *mesacantha* apparently originated solely from the SE clade, although, the nature of its formation has not been determined. Considering morphological characters as compared to its diploid relative, *O. mesacantha* subsp. *lata*, it seems likely that *Opuntia mesacantha* subsp. *mesacantha* could have arisen via autopolyploidy, although this needs further study. One specimen of *O. mesacantha* subsp. *mesacantha* collected by J.B. Nelson 23694 (USCH) from Beaufort Co., SC, had abnormally large cladodes reaching lengths of 34.5 cm. This was likely caused by atypical growth conditions.

Majure has collected one putative hybrid between *O. stricta* and *O. mesacantha* subsp. *mesacantha* from Baldwin Co., AL (Majure 1092; MISSA, in part) and seen another specimen from Ft. Gaines (Dauphin Island, Mobile Co.), AL, (Parfitt 5157; ASU), both of which demonstrated the low growth form of *O. mesacantha* and the robustness and yellowish spines of *O. stricta*. Interestingly, this putative hybrid grown side by side in central Mississippi with *O. stricta* from Mobile Co., AL (Majure 823; MISSA), suffered much less frost damage than the latter species, suggesting a degree of frost tolerance gained through the union with the frost tolerant *O. mesacantha*.

Additional specimens examined. United States. **Alabama:** Autauga Co., field E of Walker's Lake and just N of dirt rd., ca. 3 mi E of Mulberry Creek, T19N, R12E, SE1/4, Sec. 33, 15 Sept 1979, *Wiersema 1313* (UNA). Baldwin Co., 8 air miles W of Gulf Shores. Bon Secour National Wildlife Refuge; 30°14'6"N 87°49'54"W, 26 May 2002, *Haynes 10260* (UNA); Bon Secour National Wildlife Refuge, off of Hwy. 180, E of Ft. Morgan, 29 Jun 2005, *Majure 1082* (MISSA, MMNS); Bon Secour Nat'l Wildlife Refuge; off of Mobile St, 30.23235 -87.83290, 29 May 2006, *Majure 1511* (MISSA, MMNS); frequent along sand dunes in open area along AL 182, ca. 1.5 mi W of jct. with AL 161, ca. 0.25 mi from Gulf. T9S R5E N1/2 Sec. 18, 13 Mar 1979, *Wiersema 504* (UNA). Marion Co., 6 mi SW of Hackelburg, 22 Aug 2007, *Hill s.n.* (FLAS). Mobile Co., Dauphin Island, 1 Jan 1912, *Howell* (NY); Mobile, Springhill, 12 May 1888, *Mohr 587* (UNA). Pickens Co., Sipsey River at Al 14 crossing, 6.6 mi SSE of Aliceville, 2 Aug 1967, *Clark 17281* (UNC). Randolph Co., granite outcrop (Bald Rock), Almond Community, 3.5 mi W of Wadley, 2 Aug 1966, *Clark 6526* (UNC). St. Clair Co., Pottsville sandstone outcrops, E end of mt., 4 Jun 1963, *Bostick 284-1* (UNC). Wilcox Co., Hwy. 61, 2.5 mi N of Alabama Hwy. 10, 31°50'40.6"N, 86°56'52.1"W, 30 Aug 2007, *Diamond 17991* (TROY). Winston Co., 4.8 mi N of Haleyville, 10 May 1967, *Clark 13102* (UNC). **Florida:** Bay Co., W of Panama City, 7 Jun 1938, *Young s.n.* (FLAS). Escambia Co., W end of Santa Rosa Island at Gulf

Islands National Seashore, S of Ft. Pickens Rd., ca. 0.7 mi W of Battery Langdon, 5 May 1979, *Burkhalter 6397* (FLAS); Ca. 2 mi W of Gulf Beach along Rt. 292 just E of public dunes park, 18 Mar 1982, *Wilhelm 9999* (USF). Gadsden Co., Bear Creek Educational Forest (E of Rt. 267 and ca. 10 air mi SSW of Quincy); 30.47650°N 84.62331°W, 22 May 2014, *Anderson 25542* (FSU). Okaloosa Co., vicinity of Ft. Walton Beach, off of Hwy. 98 W, 25 Jun 2005, *Majure 1075* (MISSA). Santa Rosa Co., jct. of US 98 and Hwy. 399, 25 Jun 2005, *Majure 1081* (MISSA). Walton Co., off of Hwy. 30A, Grayton Beach State Park, 25 Jun 2005, *Majure 1067* (MISSA); Point Washington State Forest, off of US 98E, 25 Jun 2005, *Majure 1070* (MISSA). **Georgia:** Clarke Co., Princeton, 20 Mar 1929, *Drury s.n.* (GA); waste ground and granite outcrop, East Athens. 14 May 1929, *Reade s.n.* (UGA). Cobb Co., Marietta/Kennesaw: Kennesaw Mountain National Battlefield Park, rock outcrop along trail on Pigeon Hill, ca. 0.4 km from Burnt Hickory Rd./Old Mountain Rd., 33°57.89'N, 84°35.5'W, 24 May 2006, *Zomlefer 918* (GA). DeKalb Co., off of Hwy. 124 N from exit 75 off of Interstate 285N, 27 May 2009, *Majure 3787* (DES, FLAS). Elbert Co., S of GA Hwy. 72 on Co. Rd. 78, 6 Sept 1977, *N.C. Coile 1380* (GA). Emanuel Co., Ochopee Dunes SNA, 32° 32' 15" 82° 27' 40", 16 May 2007, *Hill s.n.* (MISSA). Greene Co., Oconee National Forest, 26 Apr 1998, *Tilgner 57* (UGA); Rd. 15, about 15 mi S of Athens, 1 mi from entrance to recreation area, on the right, Oconee National Forest, 26 Apr 1998, *Volkova 55* (GA). Gwinnett: Co., Yellow River, near McGuire's Mill, 20 July 1893, *Small s.n.* (NY). Hart Co., N side of Cedar Creek, which flows into Savannah River, 34°18'12"N, 82°47'40"W, ca. 1.75 mi S of GA 181 bridge over Savannah River, and ca. 0.5 mi W of the Savannah, 29 May 1979, *Credle 788A* (GA); open pines on hilltop ridge just back of bluffs overlooking Tugaloo River NE of Lavonia; Piedmont Province, 16 May 1949, *Duncan 9584* (UGA). Jackson Co., off of Interstate 85 S; ca. 6.7 km NW of Commerce, 0.3 km NE of Oconee River, 27 May 2009, *Majure 3789* (DES, FLAS). Marion Co., 2 mi SE of Juniper, Fall Line Sandhill, 25 Aug 2010, *Hill s.n.* (FLAS). McDuffie Co., low sandy ridge ¾ mi S of Marshall Church 5.1 mi W 17° N of Thomson, 18 May 1952, *Duncan 13577* (GA). Meriwether Co., rocky soil of Pine Mt. along GA 190 ca. 0.5 mi W RJ 85W and 190, 3.25 mi SSW of Warm Springs, 8 Jun 1972, *Jones 21986* (GA). Monroe Co., 0.5 mi off I-75 at exit 65, on High Falls Rd., High Falls State Park, 18 May 1987, *Howel 285* (GA). Oconee Co., near Carither's Mill on Apalachee River, 8 Nov 1935, *Pyron 64* (GA); Granite rock outcrop at GA Hwy. 186 and High Shoals on the Apalachee River, 17 May 1991, *Seward 345* (UGA). Richmond Co., Camp Hancock, Augusta, 1918, *Leslie s.n.* (NY). Taylor Co., along side of GA-96, 3 mi W of Butler; 7 mi W of Howard, 20 May 1972, *Register s.n.* (UNC). Walton Co., Hard Labor Creek State Park: 2 mi N of Rutledge, 23 Sep 1979, *Hill 1206* (GA, NY). Wheeler Co., 0.4 mi E off Hwy. US-441/319, on Friendship Church Rd., 1 May 1981, *Faircloth 8631* (GA). **Louisiana:** Allen Parish: infrequent in dry, sandy soil between RR and US 190 ca. 4 mi W of Kinder, 2 May 1981, *Allen 10766* (LSU); N side of rr tracks; S of LA 190; ca. 5 mi W of Kinder, 16 Apr 1983, *Doyle 358* (UNC). Natchitoches Parish: 3.25 mi W of Natchitoches on Hwy. 6, 8 Aug 1980, *Holmes 3951* (NY). Washington Parish: N of LA 437 via logging roads, ca. 1.5 mi W of Bogue Chitto River; ca. 1.5 air mi WSW of Enon, 1 Sep 2008, *Reid s.n.* (FLAS). West Feliciana Parish: along Thompson Creek near Hwy. 61N of Baton Rouge, 11 May 1982, *Givens 2630* (LSU). **Maryland:** Anne Arundel Co., Rt. 4 near Waysons Corner, 4 Jun 1969, *Reed 112805* (MO). Calvert Co., Broome Island, District 1, 25 Jul 1956, *Seymour 16727* (MO). St. Marys Co., Piney Point, 26 Apr 1958, *Reed 40649* (MO). **Mississippi:** Forrest Co., Vic of Maxie off of Hwy 49; UTM 16 0291162 3425838, 17 Jan 2005, *Majure 770* (MISSA, MMNS); jct. of Hwy 49 S with Hwy 13 E; Vic of Maxie, 17 Mar 2005, *Majure 806* (MISSA, MMNS). Hancock Co., St. Joseph's Cemetery, vicinity of Diamondhead, 9 Dec 2006, *Majure 1924* (MISSA). Harrison Co., DeSoto National Forest, Little Florida, off of Redmond Rd. from Hwy. 67, 30.66730 -89.10650, 9 Jul 2006, *Majure 1603* (MISSA, MMNS); Biloxi, no date, *Tracy s.n.* (NY). Jackson Co., Petit Bois Island, 12 Feb 1912, *Howell s.n.* (NY); Greenwood Island at Bayou Casotte, 14 Jan 2006, *Majure 1297* (MISSA, MMNS); E end of Horn Island, 30.22200°N 88.57950°W, 26 Nov 2006, *Majure 1921* (MISSA, MMNS). Lafayette Co., off of Hwy. 7, S of Oxford, 34.35054°N 89.51003°W, 27 May 2007, *Majure 2448* (MISSA). Marion Co., E Marion County, just N of Hwy. 13 E of Lamar Co., Lower Little River, 18 Jun 2009, *Mann s.n.* (FLAS). Marshall Co., Wall Doxey State Park, 19 May 1967, *Lassetter 234* (MISS); off of Hwy. 78 E, ca. 1 mi NE of Wall Doxey State Park, 30 Dec 2005, *Majure 1293* (MISSA, MMNS); W of Wall Doxey Lake, Wall Doxey St Park, 12 Jun 1966, *Temple 2912* (MISS). Neshoba Co., off of Hwy. 15 N, adjacent to Pearl River, ca. 0.25 mi S of bridge, 18 Sep 2005, *Majure 1201* (MISSA, MMNS). Noxubee Co., Gholson, off of Hwy. 21, 20 Aug 2005, *Majure 1156* (MISSA, MMNS). Pontotoc Co., 10 mi W of Pontotoc-Lafayette Co. line, 29 Aug 1967, *Musselman 1210* (UNC). Stone Co., sand hill across from Maxie Fire tower on Hwy. 49 S, 1 Nov 1975, *Snow s.n.* (USMS), 3 mi S of Maxie on Hwy. 49 S, 18 May 1976, *Snow s.n.* (USMS). Winston Co., Tombigbee National Forest, off of Sturgis Rd., 16 Jan 2005, *Majure 769*

(MISSA, MMNS); Yalobusha Co., trailside off of Co. rd 221, 13 Jan 2005, *Majure 767* (MISSA, MMNS); off of Gore Springs Rd, just S of Gums Crossing, 33.90090 -89.62770, 17 Sept 2006, *Majure 1837* (MISSA, MMNS). **New Jersey:** No County. Pine Barrens, Sept 1863, *Canby s.n.* (NY); Burlington Co., Atsion along NJCRR, 29 Aug 1951, *Stern s.n.* (ILL). **North Carolina:** Alexander Co., SW base of Rocky Face Mt. along CR 1426, 4 Jun 1973, *Downs 13671* (UNC). Bertie Co., 8.2 mi SW of Woodard on rd. paralleling Roanoke River, 9 Jul 1958, *Ahles 46275* (UNC). Bladen Co., Rt. 701, 4 mi N of White Lake, 25 Dec 1978, *Reed 103135* (MO). Brunswick Co., dock area along Cape Fear River, Southport, 11 Jun 1958, *Bell 13248* (UNC); C.C.C. Camp, Southport, 10 May 1935, *Matthews s.n.* (UNC). Buncombe Co., outcrop above Parkway near Bull Gap, 2 mi N of Riceville, 3 May 1953, *Radford 6968* (UNC). Cabarrus Co., N side of NC 49, 4.5 mi E of Harrisburg, 7 Oct 1970, *Musselmann 3963* (UNC). Chowan Co., 4 mi W of Small's Crossroads, 24 Jun 1958, *Ahles 44231* (UNC). Cleveland Co., along the Broad River, ca. 4.5 mi S of Boiling Springs on NC Rt. 150, 22 Jun 1956, *Ahles 15375* (UNC). Cumberland Co., near Cedar Creek, 28 Sep 1963, *Clark E216* (EKY); NC 87, 12 mi S of Fayetteville, 21 Jun 1958, *Dukes 1204* (UNC). Currituck Co., Church's Island, 6 Sept 1909, *MacAtee 318* (US); off of Hwy. 158 E just N of Kitty Hawk, 2 Jun 2009, *Majure 3825* (DES, FLAS); sands of outer banks near Virginia line, 22 May 1954, *Radford 8096* (UNC); Church's Island, 2 Feb 1919, *Small s.n.* (NY). Dare Co., along Hwy. 12 S, S of the town of Kitty Hawk at jct. with Palmetto St., 2 Jun 2009, *Majure 3827* (DES, FLAS); Nag's Head; Vacant lot beside Blackman St. beach access parking area, off of S Virginia Dare Tr. (Rt. 12), 13 Jun 2001, *Vincent 9386* (MU). Davidson Co., 1 mi E of Linwood-Southmont Rd., 0.25 mi N of Rockcrusher Rd., 19 Jun 1966, *Leonard 192* (UNC). Franklin Co., Rt. 98; 0.2 mi E of Jct. 1001; 1.8 mi W of Bunn, S side, 7 Jun 1983, *Doyle 472* (UNC); 0.8 mi S of Stallings Crossroads (NC56) on 1002, 7 Jun 1983, *Doyle 476* (UNC). Granville Co., 0.7 mi W of Franklin Co. line on NC 56 and 1.5 mi NW of dirt rd., 28 Sep 1956, *Ahles 20204* (UNC); NC 2.7 mi E of Wilton on NC 56; 0.4 mi N of CR 1707; 1 mi W on CR 1629, 20 Aug 1982, *Doyle 233* (UNC). Halifax Co., 3.3 mi S and E of Halifax on NC 561, 19 Jul 1956, *Ahles 17155* (UNC). Harnett Co., 2.0 mi SE of Spout Springs on NC 87, 8 May 1957, *Laing 1200* (UNC). Hertford Co., 0.8 mi S of Barretts Crossroads, 8 Jul 1958, *H.E. Ahles 46028* (UNC). Hoke Co., 0.1 mi S of CR 1101 on 401; ca. 8 mi S of Raeford, 28 May 1986, *Doyle 814* (UNC). Jones Co., Island Creek, E of the junction of Trent River & Island Cr., 5 mi NE of Pollocksville, 3 Oct 1965, *Sears 6841* (UNC). Lee Co., 1 mi S of Juniper Spring Church, 17 Jun 1958, *Stewart 696* (UNC). Montgomery Co., E shore of Yadkin River at Falls Dam, Uwharrie WMA, off NC 109 2 mi NW of Uwharrie, 15 Sep 1969, *Wells 2193* (UNC). Moore Co., wildlife refuge E of Rosewood, 19 Oct 1957, *Burk 37-10* (MU). New Hanover Co., S of Masonboro, cut-off on rd. to Myrtle Grove, 12 Jun 1958, *Ritchie Bell 12932* (UNC). Onslow Co., Bear Island, Hammocks Beach St. Park, 15 May 1977, *Dickerson 114* (UGA); off of Hwy. 17 N ca. 1.8 mi N of jct. with Hwy. 172 E, 2 Jun 2009, *Majure 3829* (DES, FLAS). Pender Co., sandhill, 1 mi E of jct. of US 421 and NC 53 on NC 53 (W of Burgaw), 13 Jun 1957, *Ahles 28102* (UNC). Richmond Co., Rt. 74, 0.8 mi W of Scotland Co. line, 1.3 mi W of CR 1156, 28 May 1986, *Doyle 811* (UNC). Robeson Co., 4.3 mi SE of Red Springs near ACLRR, 2 Jun 1958, *Britt 1972* (UNC). Rowan Co., town of Granite Quarry off of Dunn Mt. Rd. at Dunn Mt. (summit), 28 May 2009, *Majure 3793*, (FLAS). Scotland Co., 1.5 mi W of junction of NC 79 & US 74 on NC 79 (W of Laurinburg, 8 May 1957, *Ahles 25819* (UNC); Rt. 401, 2 mi S of Lumber River, 19 Apr 1967, *Reed 79087* (MO); sandy roadside; co. rd. 1128, 0.25 mi N of Masons Crossroads, 26 Oct 1973, *Sharp 2407* (UNC). Wake Co., Mitchell's Mill, 3.6 mi E of 401 on 96; 0.2 mi SE on 2224, N 0.2 mi on 2300, 17 May 1983, *Doyle 447* (UNC). Wayne Co., NC 55, 2.5 mi E of NC 403; ca. 10 mi E of Mt. Olive; S side of rd., 26 May 1986, *Doyle 802* (UNC). **South Carolina:** Abbeville Co., near SC 81, 3 mi S of Calhoun Falls, 13 May 1957, *Radford 22826* (UNC). Anderson Co., dry field 3 mi ESE of Fair Play, 31 May 1956, *Ahles 13415* (UNC); Silver Brook Cemetery, Anderson, 16 Oct 1920, *Davis 1737* (MO). Bamberg Co., 0.7 mi S of jct. CR 27 and 22 on CR 27 (SW of Govan), 26 May 1957, *Ahles 26037* (UNC). Beaufort Co., 1 mi E of Co. Rt. 76 on US Rt. 21, 10 May 1956, *Ahles 12357* (UNC). Calhoun Co., on E angle of jct. formed by SC 6 and Sec. Hwy. 44, about 3 mi SE of St. Matthews within Wannamaker Nature Preserve, ca. UTM 17 525553E 3722644N, 28 Nov 2001, *Nelson 22339* (USCH). Charleston Co., Isle of Palms, Charleston, 1 Feb 1916, *Small s.n.* (NY). Chester Co., Fishing Cr. pond dam, 13 May 1957, *Bell 7437* (UNC). Chesterfield Co., 0.5 mi S on CR 20 from jct. with US 1, S of Cheraw; 34°34'N 79°53'W, 16 May 1976, *Solomon 1945* (MO). Clarendon Co., SE side of Guise Bay, 16 Aug 1985, *Nelson 4186* (USCH). Dillon Co., SE side of Ashpole Swamp, about 2.5 mi NW of Lumber River, SE of Lake View near NC state line, 14 Aug 1986, *Nelson 4884* (USCH). Edgefield Co., near US 25, 9 mi SSW of Trenton, 13 May 1957, *Radford 22825* (UNC). Fairfield Co., 0.6 mi S of Sec. Hwy. 60 (Glenns Bridge Rd.) and 0.25 air mi NE of SC 215, community of Rock Hill; about 3 mi SE of Jenkinsville, UTM 17 477342E 3789416N, 24 May 2002, *Nelson 22656*

(USCH). Greenville Co., slopes of Cesar's Head, North Cove, 3 Sep 1876, *Engelmann s.n.* (MO); Cesar's Head, Blue Ridge, 3 Sept 1876, *Redfield 5577* (MO). Kershaw Co., Rt. 601 of Rt. 20, near Lugoff, 23 Mar 1986, *Reed 125526* (MO). Lancaster Co., Forty Acre Rock, 4 Apr 1977, *Jacobs 14* (MU). Marion Co., Britton's Neck, W of Britton's Neck Rd. on N side of Woodbury, about 0.7km N of major power line; 33.7594°N, 79.2651°W, 17 May 2006, *Nelson 25855* (ASU, DES, USCH). Marlboro Co., 2 mi NW of Drake, 10 Jun 1956, *Radford 12543* (UNC). Orangeburg Co., Santee Club, 1 Jun 1910, *Beekauree s.n.* (NY). Pickens Co., Glassy Mt., ca. 3 mi NE of Pickens, 28 May 2009, *Majure 3790* (FLAS). Richland Co., Ft. Jackson Army Installation, NW edge of BRM Range 12; S side of Semmes Rd., 1 Jun 1992, *Nelson 12724* (USCH). Saluda Co., SC 392, 2 mi S of Ridge Spring, 26 May 1957, *Radford 23214* (UNC). Sumter Co., S side of US 378 just W of Roxie's (Tavern), S of main runways, 16 Mar 1994, *Nelson 15100* (USCH). Union Co., near Farming Cr. of Robat, 5 Jun 1957, *Bell 8547* (UNC). York Co., ca. 3 mi NE of Clover off of Hwy. 321 N then off of Old Carriage Rd., 28 May 2009, *Majure 3791* (DES, FLAS). **Tennessee:** Fayette Co., Ames Plantation, 19 Oct 1972, *Deselm s.n.* (TENN). Hardeman Co., NE of Newcastle, 21 Aug 1947, *A.J. Sharp 6629* (TENN). **Virginia:** Amelia Co., Rock Sable, SW of Deatonville; 0.7 mi S on 1st dirt rd. to left, ca. 0.4 mi W of jct. 618 and 617; near Saylers Cr. St. Battlefield, 31 May 1986, *Doyle 815* (UNC). Brunswick Co., off Rt. 626 and Rt. 705, near Gasburg, 19 Aug 1978, *Reed 103249* (MO). Gloucester Co., sandy fields, Gloucester Point, 17 Apr 1983, *Reed 117312* (MO). Hampton Co., Ft. Monroe, Hampton, 7 May 1977, *Reed 102057* (MO). Madison Co., Rt. 29 at Robinson Run, N of Madison, 27 Apr 1981, *Reed 114429* (MO). Pittsylvania Co., jct. of CR 734 and 730 (1 mi S of Ringgold), 2 Oct 1965, *James 3227a* (UNC). Princess Ann Co., near Cape Henry, entrance to Seashore Natural Area Campground, 0.4 mi NW of turnoff to Ft. Story on Rte. 60 to Virginia Beach, 13 Nov 1971, *Walkington 806* (ASU); Cape Henry, 1 mi E of Great Neck Rd., on S side of Rte. 60, just W of turnoff to Seashore St. Park, 13 Nov 1971, *Walkington 807* (ASU). Richmond Co., Richmond, *Chalmot s.n.* (US). Suffolk Co., Nansemond, ca. 1 mi E of Blackwater River and 6 mi N of VA-NC state line, 22 Jun 1963, *Ahles 58238* (UNC). Virginia Beach, Cape Henry, Rt. 6, 3 Sep 1940, *Egler 40-370* (NY); Cape Henry, 30 May 1922, *Wherry 22-116* (US).

7b. *Opuntia mesacantha* subsp. *lata* (Small) Majure, *Phytoneuron* 106: 1. 2014 (Fig. 15). ≡ *Opuntia lata* Small (1919: 26). Type:—UNITED STATES. **Florida:** [Alachua Co.,] pine-woods, 12 mi west of Gainesville, 13 December 1917, *Small s.n.* (holotype NY-00385985!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=649536)

- = *Opuntia macrarthra* Gibbes (1859: 273). Neotype (designated by Majure 2014: 2):—UNITED STATES. **South Carolina:** within a few miles of Charleston (presumably destroyed in the US Civil War), **South Carolina:** Charleston Co., Isle of Palms, near Charleston, 14 Feb 1916, *J.K. Small s.n.* (US-00292752!, image available at <http://collections.nmnh.si.edu/search/botany/>; isoneotypes NY! US-00240569!, image of the US specimen available at <http://collections.nmnh.si.edu/search/botany/>).
- = *Opuntia youngii* Nelson (1919: 119). Type:—UNITED STATES. **Florida:** nine miles northeast of Tampa, FL, [date?], *Young* (n.v.), apparently no type selected by author and no specimen ever found. Neotype (designated here):—UNITED STATES. Florida: Hillsborough Co., Little Manatee River State Park, E side of main park drive, 250 ft, S of Ranger Station, 27 Apr 1999, *J. Myers 360* (USF-230053!, image available at <http://florida.plantatlas.usf.edu/SpecimenDetails.aspx?CollectionID=24204>).
- = *Opuntia eburnispina* Small ex Britton & Rose (1923: 24). Type:—UNITED STATES. **Florida:** [Collier Co.,] sand-dunes, Cape Romano, 10 May 1922, *Small s.n.* (holotype NY-00385979!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=530175).
- = *Opuntia impedita* Small ex Britton & Rose (1923: 257). Type:—UNITED STATES. **Florida:** Duval Co., Atlantic Beach, east of Jacksonville, 26 April 1921, *Small s.n.* (holotype NY-00385981!, image available at http://sweetgum.nybg.org/science/vh/specimen_details.php?irn=371129; isotype US-00115886!, image available at <http://collections.nmnh.si.edu/search/botany/>).

Description:—Cladodes typically elliptic, margins commonly scalloped, leaves 7.2–7.8 mm long, Spines 2.4–4.9 cm long, 0.7–0.9 mm diameter, 0–5 per areole (restricted to the upper areoles or occurring over the cladode surface when present), tepals 3.4–4.3 cm long, Seeds 4.7–5.3 mm long, funicular girdle 0.6–1.1 mm wide, regular, generally not bumpy, funicular envelope smooth, usually not raised from the expansion of the cotyledons or hypocotyl, if slightly raised then generally not bumpy.

Phylogenetic placement:—*Opuntia mesacantha* subsp. *lata* is sister to the clade containing *O. abjecta* and *O. austrina* (Fig. 1).

Phenology:—Flowering mid-March-May (rarely also in June), fruiting June-February.

Distribution and habitat:—*Opuntia mesacantha* subsp. *lata* is distributed through the outer coastal plain of the southeastern US from North Carolina south to Florida and west to Mississippi (Fig. 14). *Opuntia mesacantha* subsp. *lata* is most common in the southeastern US in *Pinus palustris* or *P. elliotii* sandhills, or mixed *Quercus geminata*, *Q. incana*, *Q. laevis*, *P. palustris* xeric sandhills. *Opuntia mesacantha* subsp. *lata* also grows with *Ceratiola ericoides*, *Chrysopsis mariana* (Linnaeus 1763: 1240) Elliott (1823: 335), *Cnidoscolus stimulosus* (Michaux 1803: 216) Engelm. & Gray (1845: 234), *Dichantheium aciculare*, *D. sphaerocarpon*, *D. tenue*, *Licania michauxii*, *Pityopsis graminifolia*, *Rubus cuneifolius*, *Sabal etonia*, *Serenoa repens*, *Smilax auriculata*, *Stillingia sylvatica* Linnaeus (1767), *Triplasis americana*, *T. purpurea*, *Vaccinium arboreum* Marshall (1785: 157), and *Yucca filamentosa*.

Conservation status:—*Opuntia mesacantha* subsp. *lata* is widespread throughout the southeastern US. Majure (2013e) considered the taxon to be of least concern. However, the periphery of the taxon's distribution is mostly occupied by small populations quite some distance from other populations. Likewise, the reduction of a consistent fire regime in the southeastern US to maintain open habitat in sandhills reduces the overall niche space available for the taxon. We consider *O. mesacantha* subsp. *lata* to be vulnerable to habitat loss and fragmentation, as well as small, local population sizes.

Chromosome number:—*Opuntia mesacantha* subsp. *lata* is diploid, $2n=22$, throughout its range (Majure *et al.* 2012b).

Notes:—Morphologically, *Opuntia mesacantha* subsp. *lata* is the diploid version of *O. mesacantha* subsp. *mesacantha*. Both taxa have the same growth form and *O. mesacantha* subsp. *lata* can be easily confused with *O. mesacantha* subsp. *mesacantha*. *Opuntia mesacantha* subsp. *lata* tends to have non-uniform cladodes that are often scallop-margined, unlike *O. mesacantha* subsp. *mesacantha* that mostly has smooth-margined cladodes. Spines are generally more delicate and diameter of spines are generally 0.7–0.9 mm in *O. mesacantha* subsp. *lata* vs. more robust and 0.95–1.3 mm in diameter in *O. mesacantha* subsp. *mesacantha*. *Opuntia mesacantha* subsp. *lata* also tends to have seeds with a smooth funicular envelope, which contrasts with the bumpy funicular envelope of *O. mesacantha* subsp. *mesacantha*.

Certain populations of *O. mesacantha* subsp. *lata* verge towards *O. drummondii* morphologically. Likewise, there are numerous populations in Mississippi that were initially considered to be putative hybrids between *O. drummondii* and *O. mesacantha* subsp. *lata* (as *O. pusilla* and *O. humifusa* in Majure & Ervin 2008). It is still undetermined whether or not those populations are morphological extremities that form part of *O. mesacantha* subsp. *lata* or whether they could indeed be of hybrid origin or introgressive forms between *O. drummondii* and *O. mesacantha* subsp. *lata*. Those populations are included tentatively within *O. mesacantha* subsp. *lata* here (see Majure 764, 795, 828, 1199, 1548, 1617), with the caveat that more work needs to be carried out to more fully understand those populations, which are all diploid based on those that have been analyzed (Majure *et al.* 2012b). Benson (1982) considered *O. eburnispina* to be an interspecific hybrid between *O. humifusa* and *O. stricta*, based on the numerous spines produced from the areole. Here *O. eburnispina* is considered synonymous with *Opuntia mesacantha* subsp. *lata*. The numerous spines per areole produced by *O. eburnispina* material are seen in all members of the SE diploid clade (i.e., *O. abjecta*, *O. austrina*, *O. drummondii*, *Opuntia mesacantha* subsp. *lata*), and therefore do not signify hybridization with *O. stricta*. Also, the spines are not produced in a stellate pattern as in *O. stricta* and related taxa or hybrids (see *O. ochrocentra* above).

The combination *Opuntia mesacantha* subsp. *lata* is validated here by citing the volume and page number of the description of the basionym, *Opuntia lata*, which was not properly cited in Majure (2014). The flowers collected on May 6, 1918, were also cited as type material by Benson (1982), however, those being collected on a different date (compared to Dec. 13, 1917 for the type) cannot represent type material and are here excluded from the type of *O. mesacantha* subsp. *lata*. A neotype for *O. youngii* is selected here, as the author did not select a type (Nelson 1919). *Opuntia youngii* was included in *O. austrina* by Britton and Rose (1919), however, based on the description of the species, it is more morphologically similar to *O. mesacantha* subsp. *lata*. The synonym *O. impedita* was originally described in Britton and Rose (1923) as *O. impedata*. Small (1933) later corrected the spelling of the name to *O. impedita*, which the spelling originally intended for the taxon.

Additional specimens examined. United States. **Alabama:** Autauga Co., off of Hwy. 82E just N of Vida jct., 16 0529179N 3604707E, 7 Mar 2007, Majure 2043 (MISSA); off of Hwy. 82 W S of Joffre; 16 0532421N 3601641E, 10 Mar 2007, Majure 2054 (MISSA). Butler Co., Hwy. 77, 0.93 mi N of Butler Co. Hwy. 62, 31°53'40.5"N 86°32'30.8"W, Diamond 19258, 17 May 2008 (TROY, UNA). Coffee Co., CR 43, mi marker 3,

Childree 7 (TROY); Co. Rd. 207 & Co. Rd. 213, 0.3 mi N on Co. Rd. 207; dry clay soil, 3 May 2000, *Martin* 683 (TROY). Crenshaw Co., off of Hwy. 331S, ca. 9 mi S of Brantly, 16 0572674N 3489826E, 7 Mar 2007, *Majure* 2044 (MISSA). Dale Co., 1.3 mi S of intersection of CR 51 and 5 on right, T6N R23E Sec. 5, 7 May 2000, *Pennington* 640 (TROY); Ech Lake, 10 May 1997, *Rundell* 130 (TROY); Dale County Lake, 6 Jun 2000, *Woods* 8106 (TROY). Dallas Co., bluff on Mulberry Cr., vicinity of USGS stream gauge station, 2.9 mi ENE of Valley Creek jct., 12 Aug 1967, *Clark* 18088, (UNC). Elmore Co., near Good Hope Church, 5 mi SE of Wetumpka, 27 Jul 1967, *Clark* 17129 (UNC). Henry Co., 7.5 air mi SE of Abbeville, Co. Rt. 65 off of State Rt. 95, 0.25 WSW of Hardwicksburg, 31°29'56"N 85°9'17"W, 23 Jul 2003, *Hayes* 10413 (ILL, TROY, UGA, UNA). Lowndes Co. Palmyra, off of Hwy. 263, ca. 18 km W of Ft. Deposit, 31° 57.737'N, 86° 46.070'W, 9 May 2013, *Phillips* s.n. (FLAS). Marengo Co., Myrtlewood, 1 Jan 1912, *Holt* s.n. (NY). Mobile Co., Mile marker 27, off of Hwy. 45N, 6 Mar 2011, *Majure* 4194 (FLAS). Pike Co., Pike County Lake, region 2, upland wooded area, 30 May 1996, *Holmes* 190 (TROY); N of Ozark off of Hwy. 231N; near Bama Nut Shop, ca. 3 mi S of Brundidge, 6 Jul 2007, *Majure* 2569 (MISSA). Sumter Co., ca. 1 mi NE of Woodford on CR 23, 5 Aug 1966, *Clark* 6743 (UNC); 200 yds. W of Livingston City Limits, just E of Sucarnochee River on N side of Rte. 11, 21 Nov 1971, *Walkington* 813 (ASU). Wilcox Co., along AL 41, ca. 5 mi SW of Camden, just N of Pebble Hill Community, 6 Jun 1967, *Clark* 13941 (UNC). **Florida:** Alachua Co., Micanopy, off of Hwy. 234, just E of 441N, 11 Apr 2010, *Majure* 3991 (FLAS); 8.9 km NE of Archer along roadside of Hwy. 20, 20 Jun 2011, *Majure* 4215 (DES, FLAS); old field on Archer Rd., W of Gainesville, 18 Apr 1939, *Young* 28c (FLAS). Calhoun Co., open oak woods, cultivated at Missouri Botanical Garden, 31 May 1978, *Solomon* 3836 (MO). Citrus Co., along S41 and the railroad, 9 mi N of Inverness, 15 Apr 1976, *Baltzell* 8272 (FLAS); Rose Hill, 0.5 mi over county line on Hwy. 581, 21 Apr 1959, *Cooley* 6457 (USF). Clay Co., sandy open upland area ENE of Starke, and just W of Kingsley Lake, 11 Mar 1966, *Duncan* 22616 (ILL, UGA); off of Hwy. 301 E (heading N), ca. 1.6 km S of CR 218, 28 Mar 2009, *Majure* 3699 (FLAS). Collier Co., TP Scrubs (Coll28), Secs. 2, 3 and 10, T48S, R25E (Bonita Springs quad.), 30 Mar 1986, *Huck* 3954 (FLAS). Columbia Co., off of US Hwy. 27 W, ca. 2 mi NW of Ft. White; 2.2 mi E of Itchatucknee State Park entrance, 24 Apr 2008, *Majure* 3089 (FLAS). DeSoto Co., Deep Creek, 800 ha on W side of Peace River, ca. 4.5km NE of jct. I-75 & Kings Hwy. (CR-769), 31 Jul 2008, *Franck* 751 (USF). Dixie Co., W of Suwanee River and Manatee Springs off of Hwy. 349S, 17 0306724E 3264465N, 8 Mar 2007, *Majure* 2050 (MISSA). Duval Co., St. John's Bluff, 1 Jan 1942, *H. Kurz* 274 (MICH). Franklin Co., St. Teresa, 28 Jul 1942, *Kurz* 288 (MICH). Gadsden Co., Bear Tract of Talquin State Forest (E of Rte. 267 and ca. 10 air mi SSW of Quincy), near McCall bridge, 22 May 2014, *Anderson* 28083 (FSU). Gilchrist Co., 5 mi W of Ft. White, 28 Apr 1961, *Cooley* 8190 (UNC, USF); Wilcox, 19 May 1940, *Devall* s.n. (FLAS). Hamilton Co., just S of Crossroads, off of Hwy. 141S, 24 Sep 2011, *Majure* 4217 (FLAS). Hardee Co., ca. 1 mi (by air) S of Ft. Green Springs, 9 Nov 1993, *Hansen* 12444 (USF). Hernando Co., off of Hwy. 301S at Ridge Manor, 18 May 2008, *Majure* 3235 (FLAS); off of Hwy. 93S, ca. 0.5 mi S of Withlacoochee River, 14 Feb 2010, *Majure* 3948 (DES, FLAS); Croom, 1913, *Piper* 13-434 (US). Highlands Co., Off of Hwy. 64W, just E of Avalon Park, corner of Dodd's Rd., empty lot, 11 Mar 2010, *Majure* 3977 (DES, FLAS). Hillsborough Co., Southeast of Tampa near gaging station on Little Manatee river, 24 Aug 1960, *Ray, Jr.* 10143 (USF). Jackson Co., NW of Porter Lake, ca. 12 air mi SSW of Marianna, 30.59049N, 85.27801W, 12 May 2012, *Anderson* 26318 (FSU). Lafayette Co., off of Hwy. 27 W; ca. 4 km NW of jct. with Hwy. 349, 28 Oct 2007, *Majure* 2795 (FLAS). Lake Co., Palatakaha Park, off of Hull Rd., just S of Clermont, 11 Jun 2010, *Majure* 4092 (FLAS); Along Hwy. 438, ca. 1 km W of Orange County line, ca. 1 km W of Oakland, 14 Nov 2010, *Majure* 4171 (DES, FLAS). Leon Co., along Tram Rd., 20 mi east of Tallahassee, 12 May 1976, *Blaker* 40 (FSU); Tallahassee, 1942, *Kurz* 1 (MICH); 4 mi W of Tallahassee, *Kurz* 283 (MICH). Levy Co., off of Hwy. 24W, ca. 1 mi W of Alachua Co. line, 6 Dec 2008, *Majure* 3645 (FLAS); Gulf side of Seahorse Key, 3 mi SW of Cedar Key, 12 Mar 1965, *Ward* 4435 (FLAS). Liberty Co., along SR 12, NE of Bristol, 9 May 1977, *Rosen* 10 (FSU). Manatee Co., off of Cortez Blvd. at junction with Lockhard Rd. and Ridge Manor North, 28.52232 82.25236, 23 May 2010, *Majure* 4064 (DES, FLAS); Jct. of CR 675 and Jennings Rd., 0.6 km S of the east arm of Lake Manatee, 23 May 2010, *Majure* 4065 (FLAS). Marion Co., off of Interstate 75N, ca. 0.5 mi S of reststop, ca. 6.4 km S of Ocala Exit, 28 Mar 2009, *Majure* 3709 (FLAS). Marion Co., off of Interstate 75N, ca. 0.5 mi S of reststop, ca. 6.4 km S of Ocala Exit, 28 Mar 2009, *Majure* 3709 (FLAS). Okeechobee Co., Just E of Basinger, at corner of Hwy. 68W (NW 160 St.) and NW 32 Ave., 27.390299, 80.839685; 12 Feb 2011, *Majure* 4187 (DES, FLAS); off of Hwy. 441N, 0.5km N of Ft. Dunn, 11 Feb 2011, *Majure* 4188 (FLAS). Orange Co., bundant in deep sand along RR tracks to the W, in Oakland, 10 Apr 1977, *Harriman* 13342 (NY); ca. 2.5 km W of Oakland along Hwy. 438, 14 Nov 2010, *Majure* 4174 (DES, FLAS).

Osceola Co., off of Hwy. 441S, ca. 5 mi S of jct. with Hwy. 192, 28 Mar 2009, *Majure 3703* (FLAS); Kissimmee, off of Hwy. 192 W behind Holiday Inn, ca. 1.5 mi NE of Celebration, 8 Jan 2012, *Majure 4229* (DES, FLAS). Pasco Co., along C-587, 6.2 mi SW of jct. with Florida 52; ca. 4.5 mi ENE of New Port Richey, 31 May 1984, *Hansen 9907* (USF); Starkey Wilderness Park, 2.5 mi NNW of Odessa, 7 Mar 2003, *Ferguson 217* (USF). Pinellas Co., Brooker Creek Preserve, ca. 5.5 mi N of Oldsmar, ca. 1.5 mi S of Tarpon Springs Rd., W of powerline ROW, vicinity of Brooker Creek, 4 May 1994, *Wunderlin 10421* (USF). Putnam Co., Hwy. 17 S of Crescent City, Inters. of 17 and Clifton Rd. SSE of intersection; 29°22'45.15"N, 81°30'30.77"W, 27 Dec 2006, *Beck 9171* (TENN); off of Hwy. 310 just W of Hwy. 19, just N of Rodman Reservoir, 24 May 2008, *Majure 3249* (FLAS); town of Hollister, off of Hwy. 20 W, ca. 10 km E of Interlachen, 10 May 2011, *Majure 4213* (DES, FLAS); off of Hwy. 20E, ca. 3.85 km W of Interlachen, 10 May 2011, *Majure 4214* (DES, FLAS). Santa Rosa Co., along Choctaw OLF (Dillon Field) Rd., ca. 0.5 mi W of Florida 87 and ca. 5 mi N of Holley, 4 May 1977, *Perkins 223* (FLAS). Sarasota Co., Longboat Key, along Gulf of Mexico Dr. ca. 0.1 mi NW of golf course entrance, 2 Apr 1981, *Wunderlin 8915* (USF). St. Johns Co., Rt. 204, just W of US Rt. 1, 15 Apr 1982, *Correll 53660* (NY); Atlantic Beach, E of Jacksonville, 22 Aug 1922, *Small s.n.* (NY). Sumter Co., off of Hwy. 301N along railroad tracks ca. 2.5km S of Bushnell, 18 May 2008, *Majure 3238* (FLAS). Suwanee Co., ca. 3 mi N of Beachville off of Hwy. 247 W, 17 0323021E 3322521N, 8 Mar 2007, *Majure 2049* (MISSA). Wakula Co., St. Marks National Wildlife Refuge (Wakula Unit), frequent in dry sand along W edge of Wakulla Field, 0.2 mi S of Rd. 200 along side of Rd. 211; 30.13012°N 84.30007°W, 21 Dec 2006, *Anderson 22700* (FSU); from the Niceville exit, 0.4 mi N of I-10, along Hwy. 90, 2 mi W of Mossy Head, 30.737707 86.347365, 18 May 2012, *Majure 3378* (DES, FLAS); at the jct. of Hwy. 98W and Hwy. 365, 6 Nov 2011, *Majure 4221* (DES, FLAS). Walton Co., Nekuse Preserve off of Hwy. 81, 30.53163N 85.94189W, 14 Jul 2007, *Majure 2589* (MISSA); Nekuse Preserve off of Hwy. 81S; 30.49969N 85.91898W, 14 Jul 2007, *Majure 2590* (MISSA); Eglin Air Force base ca. 1 mi S of local rte. 370 on local rte. 212; 30°35'05" 86°16'24", 25 Aug 1997, *Miller 9169A* (MO). Washington Co., T01N, R16W, Sec. 26, southern Washington Co., 3 Jun 2008, *Keppner s.n.* (FSU). **Georgia:** Bryan Co., Fort Stewart Military Reservation, training area B12, Red Cloud Hotel firing range, 9 May 1992, *Zebryk 243* (GA). Bullock Co., ca. 8.5 mi S of G.S.C. off of US 301 at Lower Lotts Creek Church, 16 Jun 1965, *Oneal 10* (UNC). Camden Co., Cumberland Island National Seashore, Stafford Field, central Cumberland Island, 30°48.43'N, 81°27.67'W, 27 Apr 2004, *Giannasi 837* (GA). Candler Co., SE of Stillmore, 3.7 km SE of Emanuel Co. line on Stillmore Rd., 30 May 1988, *Boufford 23886* (MO, NY). Charlton Co., off of Hwy. 121N, just S of St. George, 15 Feb 2011, *L.C. Majure 4190* (FLAS). Chatham Co., Savannah, 1 Apr 1927, *Heyward s.n.* (MICH). Columbia Co., off of I-20 beside Cracker Barrell; vic. of Augusta; 33.48119N 82.13245W, 10 Jun 2005, *Ervin s.n.* (MISSA). Crawford Co., 2.6 mi SE of Knoxville, 10 Aug 2009, *Hill s.n.* (FLAS). Emanuel Co., *Majure 2459* (MISSA); 5 mi S of Swainsboro on Hwy. 1, 4 May 1974, *Rodgers 74081* (FLAS). Hancock Co., slope overlooking Spring Creek, just above old mille site 9 mi E of Milledgeville, 2 Jun 1950, *Duncan 11020* (GA). Houston Co., off of Interstate 75, ca. 1 mi SW of Perry at jct. with I-75 N, 27 May 2009, *Majure 3786* (FLAS). Irwin Co., off of Hwy. 32/125, ca. 0.15 km W of Alapaha River and Big Creek, ca. 2 km W of Irwinville, 27 May 2009, *Majure 3785* (DES, FLAS). Johnson Co., E of Kite on Georgia Rte 57, just W of the Emanuel Co. line, elev. 80 m, 30 May 1988, *Boufford 23890* (MO). Long Co., Griffin Ridge WMA, at campground "Hilton," 31.69101°N, 81.83520°W, 3 May 2000, *Holland 518* (GA). Macon Co., 6.4 mi E of Montezuma on Hwy. GA-224, 8 May 1976, *Taylor s.n.* (UNC). McIntosh Co., West-central part of Sapelo Island, 16 Sept 1956, *Duncan 20519* (GA). Randolph Co., off of Hwy. 82W, ca. 3 mi W of Cuthbert, E of Springvale; 16 0706273N 3516574E, 10 Mar 2007, *Majure 2052* (MISSA); off of Hwy. 82W, just W of Springvale, 16 0698524N 3522499E, 10 Mar 2007, *Majure 2053* (MISSA). Sumter Co., 9 mi WSW of Americus, 21 Mar 1966, *Parker 140* (LSU). Tatnall Co., Big Hammock, 2.7 km SE of Birdsville, 19 Jul 2007, *Majure 2666* (MISSA). Taylor Co., Fall Line Sandhills N.A.; 32deg. 34' 37" 84deg. 16' 24", 16 May 2007, *Majure 2458* (MISSA). Tift Co., NE side of Little River at Oak Grove Church, 6.3 mi S of Tifton, 18 Jul 1968, *Fairecloth 5342* (GA). Wilcox Co., Lake Wilco in SE corner of county, 17 May 1953, *Hardin 16146* (GA). **Mississippi:** Greene Co., Palestinian Gardens off of US Hwy 98, property of James Kirkpatrick, 22 Jan 2005, *Majure 773* (MISSA, MMNS). Jasper Co., Hwy 503 S; adj. to entrance of Lake Claude Bennett; UTM 16 0306578E 3552874N, 32.10250 89.03278, 9 Jan 2005, *Majure 764* (MISSA, MMNS); Off of Hwy 503 N, N of Paulding; 16 0306154E 3555251N (NAD83), 32.03056 89.03750, 5 Mar 2005, *Majure 795* (MISSA, MMNS); Randall Hall Cemetary, within Tallahala Wildlife Mgmt. Area, 32.19445 89.21916, 18 Jul 2006, *Majure 1617* (MISSA). Lamar Co., off of Courtney Rd., S of Little Black Cr. WP; 31.08338 89.50784; 25 Jun 2006, *Majure 1548* (MISSA, MMNS). Lauderdale Co., Bonita Lakes

Recreation Trail off of Hwy. 19 E of I-20, 32.35930 -88.65360, 17 Sept 2005, *Majure 1199* (MISSA, MMNS); E of Lost Gap, N of Hwy. 80 along powerline, opposite side of rd. from "rodeo"; 32.3465°N, 88.7887°W, 3 Mar 2007, *Majure 2035* (MISSA); off of Hwy. 19 S of Meridian and I-20; 32.3629°N, 88.6205°W, 23 Mar 2007, *Majure 2094* (MISSA). Newton Co., Off of Goodhope-Decatur Rd, ca 3.5 mi NE of Decatur, 32.75683 -89.12200, 26 March 2005, *Majure 828* (MISSA, MMNS). Wayne Co., Gopher Farm, off of Brewerton Rd., off of Hwy. 63, 25 Nov 2005, *Majure 1290* (MISSA); Gopher Farm Sandhill, DeSoto National Forest, 31.46088 -88.76652, 12 May 2011, *Nicholson 59* (USMS). **North Carolina:** Cumberland Co., NC 87, 12 mi S of Fayetteville, 21 Jun 1958, *Duke 1204* (UNC). **South Carolina:** Aiken Co., along Interstate 10 W, 10 mi NW of Aiken, 23 Jul 2008, *Hill s.n.* (FLAS). Bamberg Co., ca. 3 mi S of Branchville on Hwy 21, 29 Oct 1997, *Summers 8475* (MO). Calhoun Co., ca. 2 mi NNW of Lone Star on SC 267 and 0.9 mi ENE on paved rd., 19 May 1957, *Ahles 25588* (UNC). Charleston Co., Bull Island, dunes, 19 May 1972, *403 Class 46770* (TENN). Colleton Co., Waterboro on US 15, ca. 5.5 mi W of 15-34, 14 May 1982, *Doyle 148* (UNC). Darlington Co., Lake at Hartsville, 20 May 1932, *Smith s.n.* (UNC). Georgetown Co., 9 mi N of Georgetown, 7 Jul 1939, *Godfrey 305* (MO). Horry Co., Myrtle Beach off of Hwy. 17 S (Business) at jct. with 82 Ave., 3 Jun 2009, *Majure 3832* (FLAS). Jasper Co., edge of Ridgeland on US Hwy. 17, 12 May 1956, *Bell 2579*, (UNC). Lexington Co., just S of I-20 at exit 44, side of SC 34 to Gilbert (ca. 30 mi W of Columbia), 3 May 1996, *Christy 2745* (ASU, US); Lexington, vic. of Lexington near weigh station N side ROW of I-20; 33.93766N 81.27125W, 10 Jun 2005, *Ervin s.n.* (MISSA). Williamsburg Co., 5 mi S of Kingstree, 10 Jul 1939, *Godfrey 375* (NY).

7. *Opuntia nemoralis* Griffiths (1913: 133) (Fig. 16). Type—UNITED STATES. **Texas:** Gregg County, Longview, October 1911, *Griffiths 10480* (holotype US-00117012!, image available at <http://collections.nmnh.si.edu/search/botany/>).

= *Opuntia macateei* Britton & Rose (1923: 113). Type—UNITED STATES. **Texas:** Aransas Co., Rockport, 28 Dec 1910, *McAtee 1992* (holotype US-00115910!, image available at <http://collections.nmnh.si.edu/search/botany/>; isotype NY!).

Description:—Plants forming small, spreading shrubs (Fig. 15B), oftentimes these forming masses (piles) of cladodes resulting in large patches, mounds, or clones with cladodes ascending to 30 cm tall in the summer; roots typically forming tubers (Fig. 15E), but this depends on substrate, and sometimes roots fibrous. Cladodes small, gray-green, glaucous, 4.5–8.4 cm × 2.8–5.8 cm, 8.1–14.2 mm thick, oblong, elliptical, or obovate, the terminal cladodes easily detaching, becoming strongly cross-wrinkled during the winter. Leaves glaucous, gray-green, ascending parallel to the cladode or slightly spreading, 3.7–7.7 mm, ovate. Spines 1–6 produced per areole (typically 2), white or yellowish during development, aging bright white when mature and then gray in age, strongly retrorsely barbed when developing and into maturity, 1.4–3.0 cm long, 0.5–0.8 mm in diameter. Glochids bright yellow when young turning a dull brown in age. Flowers: outer tepals triangular to ovate, glaucous, gray-green, incurved in bud, inner tepals 7–8, yellow (or rarely tinged pink basally), obovate with a mucronate tip, 2.7–3.5 cm long, staminal filaments yellow or greenish-yellow, stigmas creamy-white or more commonly light green, lobes 4–9. Berries clavate, 2.3–4.2 cm long, dark red to pink, or occasionally light green at maturity. Seeds 4.2–5.1 mm long, funicular girdle 0.9–1.4 mm wide, funicular envelope only moderately raised by the hypocotyl and cotyledons, not smooth, bumpy (or rough), funicular girdle irregular, bumpy.

Phylogenetic placement:—*Opuntia nemoralis* is an allopolyploid derivative of the southeastern and southwestern subclades of the *Humifusa* clade (Fig. 1). *Opuntia nemoralis* appears to be derived partially from an ancestor of *O. mesacantha* subsp. *mesacantha* (Majure unpubl. data).

Phenology:—Flowering April–May (–June), fruiting July–March.

Distribution and habitat:—*Opuntia nemoralis* is found from the Oachita Mountains of Arkansas south to southwestern Louisiana in Cameron Parish and through parts of eastern Texas. In Louisiana and Texas *O. nemoralis* is found in saline barrens, and in the Oachitas, the species is found mostly in shale barrens. One specimen from Missouri has been tentatively identified as *O. nemoralis*. More fieldwork is needed and likely the distribution of the species is much greater than that shown here (Fig. 14). *Opuntia nemoralis* commonly occurs on saline or sodic prairies in Louisiana and on rock outcrops in the Ouachita Mountains of Arkansas. In the Ouachitas, it is commonly associated with *O. cespitosa*. In southern Louisiana populations are in sandy prairies or sandhill communities along the coast. *Opuntia nemoralis* also grows with *Aristida oligantha* Michxaux (1803: 41), *Mononeuria minima* (Mackenzie 1914: 67) Dillenberger & Kadereit (2014: 84), *Ilex vomitoria*, *Juniperus*

virginiana, *Phemeranthus parviflorus* (Nuttall in Torrey & Gray 1838: 197) Kiger (2001: 320), *Pinus echinata*, *P. taeda*, *Quercus margarretae* (Ashe 1894: 94) Small (1903: 355), *Triplasis americana*, and *Vaccinium arboreum*, as well as many other species.

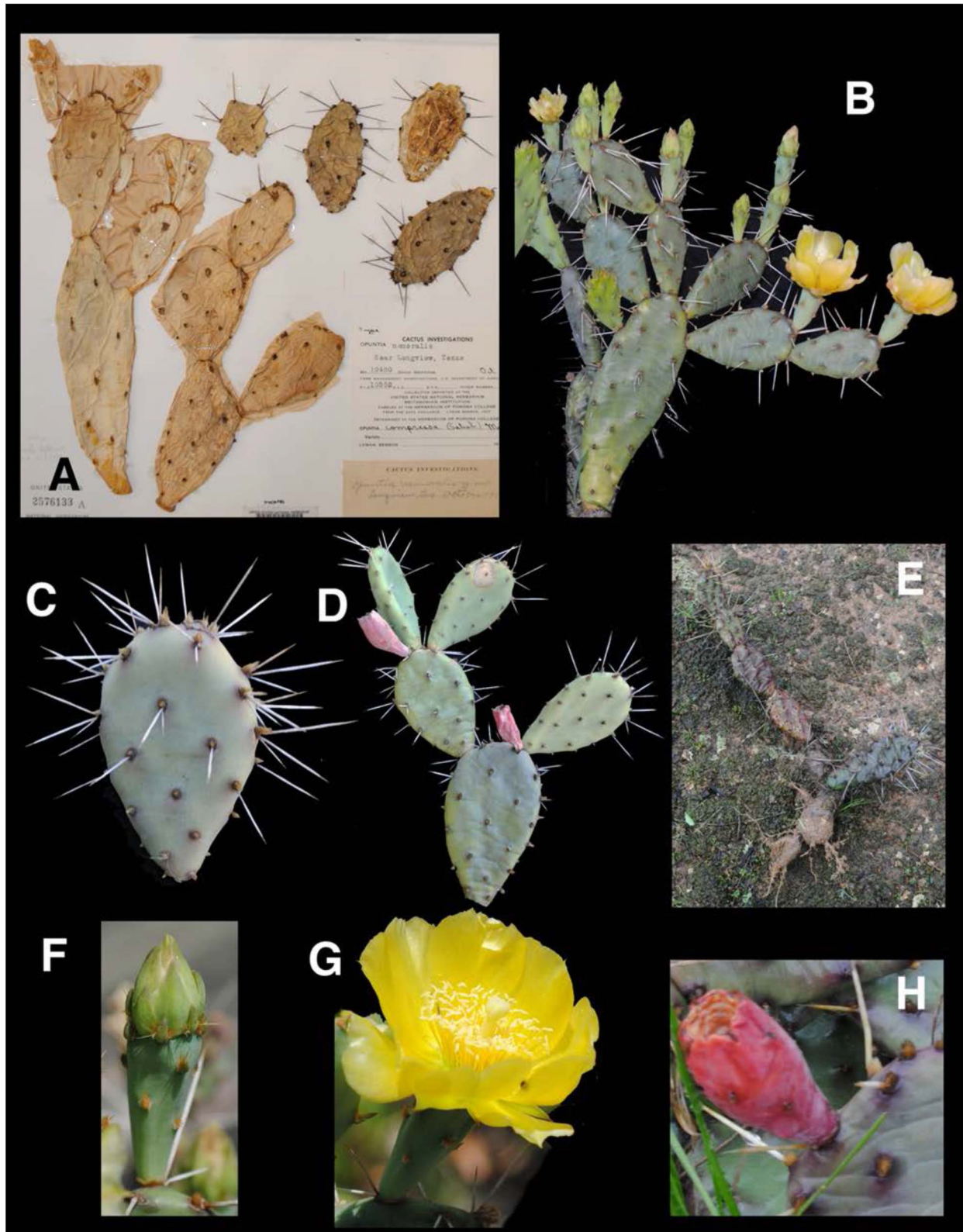


FIGURE 16. Morphological features of *O. nemoralis*. A) type specimen of *O. nemoralis*, D. Griffiths 10480, Gregg Co., TX (NY), B) growth form of *O. nemoralis*, C-D) cladode shape variation, glaucous, gray-green color, and spine variation in *O. nemoralis*, E) tuberous roots of *O. nemoralis*, F) flower bud, G) flower, and H) red fruit of *O. nemoralis*. B, E-H from DeSoto Parish, LA (Majure 4198), C-D from Garland Co., AR (Majure 4204). Photos A, C-H taken by L.C. Majure, B taken by M. Pajuelo.

Conservation status:—*Opuntia nemoralis* occurs in relatively large populations in the Ouachita Mts., as well as in saline/sodic barrens in LA. However, these populations are quite distant from one another, as well as to the populations in eastern TX, and populations along coastal LA are threatened from anthropogenic disturbance (cattle grazing, agriculture, etc.). Thus, we consider *O. nemoralis* vulnerable to habitat loss and fragmentation.

Chromosome number:—This species is tetraploid, $2n=44$, throughout its range in Arkansas and Louisiana (Majure *et al.* 2012b), although material from Texas and Missouri has not been counted.

Notes:—This species has long been placed in synonymy with either *O. macrorhiza* or *O. humifusa* (Benson 1982), but the small size of the cladodes, retrorsely barbed spines, easily disarticulating cladodes, and green stigmas set this species apart from the two aforementioned species. As a result of the disarticulating cladodes, Britton and Rose (1920) placed this species in *Opuntia* series *Curassavicae* along with *O. pes-corvi* and *O. drummondii*, a mostly synthetic series whose members are from various evolutionarily divergent clades (Majure *et al.* 2012a, Majure *et al.* 2013). Weniger (1967) described plants of *O. drummondii* from Galveston, Texas, but that material is referable to *O. nemoralis* with its sometimes faintly orange-centered flowers, and greenish stigma lobes, as well as glaucous-gray cladodes. Thus, the disjunct populations of *O. pusilla* in Texas, as indicated by Weniger (1977, 1984), Pinkava (2003), and Powell *et al.* (2008), are more appropriately recognized under *O. nemoralis*.

Additional specimens examined. UNITED STATES. **Arkansas:** Garland Co., Ouachita Nat'l. Forest, off of FS Rd. 11 in btwn. Junc. Of FS 22 and 225 w/ FS 11; 34.7454°N, 93.2842°W, 6 Apr 2007, *Majure 2196* (MISSA); Ouachita Nat'l. Forest, off of FS Rd. 11 in btwn. Junc. Of FS 22 and 225 w/ FS 11; 34.7454°N, 93.2842°W, 6 Apr 2007, *Majure 2197* (MISSA); Ouachita Nat'l Forest, N of FS Rd. 130 and Cedar Fourche Landing of Lake Ouachita; 34.6660°N, 93.2834°W, 6 Apr 2007, *Majure 2199* (MISSA); Ouachita National Forest, Ouachita Mountains, off of FR 119, just N of Hwy. 298, 34.73307, 93.31529; 9 Mar 2011, *Majure 4203* (DES, FLAS); Ouachita National Forest, shale barrens off of FR 11, 9.3 km N of Possum Kingdom and Ouachita Lake, 9 March 2011, *Majure 4204* (DES, FLAS). Hempstead Co., Fulton, sandy soil, 23 May 1909, *Bush 5718* (MO); Fulton, 6 Oct 1909, *Bush s.n.* (US). Hot Springs Co., Magnet Cove, 10 Oct 1937, *Demaree 16493* (MO). Pulaski Co., Hwy 65/I-540 about 0.9 miles north of Dixon Road exit, 34° 40' 57.96", 92° 16' 09.09", 5 Sep 2010, *B.L. Snow 2130* (FLAS). Stone Co., Mountain View, *Demaree 57932* (ASU; note mixed collection with *O. cespitosa*). Yell Co., S side of the Arkansas River, 0.75 mi S of the Hwy. 7 bridge at Dardanelle; 35.21494°N 93.14752°W, 4 Sept 2007, *Witsell s.n.* (FLAS). **Louisiana:** Beauregard Parish: off of Mouth of the Creek Rd., 24.5 km W of Deridder, 8 March 2011, *Majure 4197* (DES, FLAS); 25 km W of Deridder, 7 Aug 2008, *Reid s.n.* (FLAS). Bienville Parish: Campground Cemetery, 2 mi W of Bienville, off LA 507, 32°22'N, 93°02'W, 23 Oct 1973, *Lalanne 160* (MO); 0.6 mi N of Hwy. I-20 on state Hwy. 154, then 0.4 mi W on parish rd. 395, 21 Apr 1993, *Parfitt 5153* (ASU). Caddo Parish: Barron Road/Boggy Bayou Saline Prairie, T16N R14W, S27; N of Barron Rd. south of Boggy Bayou, 20 April 2006, *MacRoberts 7396* (LSU). Cameron Parish, Cameron, 1 Dec 1910, *MacAtee s.n.* (NY); *ibid*, 3 Dec 1910, *MacAtee 1955* (NY); off of Hwy. 27N, at Johnson Bayou, 25 km E of Sabine Pass, 7 March 2011, *Majure 4196* (FLAS); DeSoto Parish, Dalton Saline Prairie/Barren, T15N R14W, S4, 9 May 2007, *MacRoberts 7768* (LSU); off of Hwy. 152S, ca. 4 km NNW of Kingston, 8 March 2011, *Majure 4198* (FLAS); ca. 2.1 mi NE of Stonewall, and 1.4 mi E of Hwy. 171, 32.30761, 93.80470; 8 Mar 2011, *Majure 4199* (DES, FLAS); Dickinson Prairie, ca. 2 air mi NW of Stonewall, NW1/4 S9, T15N R14W; 32.1827N 93.4824, 24 May 2007, *Reid s.n.* (LSU). Vernon Parish, Rt. 111, 9 mi N of Merriville, just past Bayou River on right, 16 April 1983, *Doyle 358* (UNC). Winn Parish, railroad and pipeline along N side of state Hwy. 156, E of Goldonna and just E of Saline Bayou, 21 Apr 1993, *Parfitt 5154* (ASU); between Coldwater and Goldonna, near jct. of Hwy. 156 and Parish Rd. 882, 0.6 mi W of jct. of Hwy. 1233 and Hwy. 153, 27 Apr 2008, *Snow 2053* (FLAS). **Missouri:** Wayne Co., Greenville quad, 37.20678°N 90.49950°W, Corps access rd., 23 Sep 2003, *Pocklington 445* (MO). **Texas:** Brazoria Co., West Columbia, 8 May 1934, *Fisher 34133* (US). Galveston Co., Galveston Bay, *Weniger 687–688* (UNM) (Weniger 1967); Gregg Co., Joy Global Saline Prairie, Longview, May 2013, *Hill s.n.* (FLAS); Matagorda Co., Matagorda, 28 Dec 1910, *MacAtee 1981* (US).

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