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TAXONOMY OF THE *OPUNTIA SCHOTTII* COMPLEX (CACTACEAE) IN TEXAS

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ABSTRACT

Morphologic, field, and chromosomal studies of *Opuntia* series *Clavatae* including the three major taxa, *O. schottii, O. grahamii,* and a series of populations from Texas originally described as a putative hybrid by Anthony, suggest that *O. schottii* and *O. grahamii* are distinct and do not hybridize. The plants once considered to be hybrids are herein described as a new species, **O. aggeria**, most closely related to *O. grahamii* and *O. moelleri,* a species from northern Coahuila, Mexico.

RESUMEN

Estudios de campo, morfológicos y de cromosomas de *Opuntia* series *Clavatae* incluyendo las tres taxa mayor, *O. schottii, O. grahamii,* y una serie de poblaciónes de Texas describidos originalmente como híbridos putativos por Anthony, sugieren que *O. schottii* y *O. grahamii* son distinctos ye que no se cruzan. Las plantas las cuales se consideran originalmente como híbridos se describen aqui como una nueva especie, **O. aggeria**, más relacionado a *O. grahamii* y a *O. moelleri,* una especie del norte de Coahuila, México.

In *Opuntia* the series *Clavatae* (sensu Benson 1982), subgenus *Cylindropuntia,* is composed of 17 taxa in North America, the plants forming low mats or clumps. Two species, *Opuntia schottii* Engelm. and *O. grahamii* Engelm., colloquially known as club chollas, are common in southwestern Texas from the Rio Grande Plain into the Chihuahuan Desert. They have been reported to hybridize in the Big Bend Region of Texas in southern Brewster County (Anthony 1956; Benson 1982). These two species, their putative hybrid, and a single disjunct population of *O. emoryi* Engelm., constitute the *O. schottii* complex in Texas as circumscribed by Benson (1982) and Ralston (1987). Previous studies have differed in their treatments of *O. schottii* and *O. grahamii* (Britton and Rose 1919; Anthony 1956; Benson 1982; Weniger 1984). Previously, chromosome numbers for these two species were reported as $n=11$ and $n=22$, respectively (Weedin and Powell 1978; Pinkava et al. 1985), indicating that speciation in the group may involve polyploidy ($x=11$, Benson 1982; Grant 1981). This study uses morphologic, chromosomal, and breeding system data to clarify the taxonomic and phylogenetic re-

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lationships of the three major club chollas in Texas, and provides keys and descriptions for all four species (includes *O. emoryi*) of series *Clavatae* in Texas. The results of this study provide a clearer taxonomic arrangement concerning the *O. schottii* complex. The taxonomic and cytogenetic portions of the study are here presented.

Taxonomic History

Opuntia schottii and *O. grahamii* were described from collections made during the U.S. and Mexican Boundary Survey of 1851–1853 (Englemann 1856). The type localities for *O. schottii* and *O. grahamii* were given as "near the mouth of the San Pedro and Pecos", and "near El Paso", respectively. Britton and Rose (1919) maintained these species.

Since that time, however, several authors have altered the taxonomy at both the specific and generic level. Anthony (1956) described the putative hybrid, *O. schottii* × *O. grahamii* from populations in southern Brewster County, Texas. Benson (1969) reduced *O. grahamii* to a variety of *O. schottii,* apparently based on the overlapping ranges and intergrading morphology as reported by Anthony (1956). In his treatment of the complex, Weniger (1984) retained Engelmann's taxonomy and disputed Benson's claim of range overlap and intergradation between *O. grahamii* and *O. schottii.* Segregate genera that include these taxa have also been proposed (see synonymy), but we find no grounds, morphologic, chromosomal, or chemical, to support these alternative generic dispositions.

Habitat and Distribution

Taxa of the *O. schottii* complex grow in loosely consolidated igneous or calcareous desert alluvium, as well as on limestone outcrops. The plants grow on flats or gentle slopes and may be found both in the open or in the shade of desert shrubs, predominantly *Larrea tridentata, Prosopis glandulosa,* and *Acacia* spp.

In Texas, the *O. schottii* complex extends from extreme south-central New Mexico, southeastward along the Rio Grande to the Gulf of Mexico (Fig. 1). *Opuntia schottii* occupies the southern and eastern reaches of this range, from southern Brewster County to Cameron County, whereas *O. grahamii* occupies the more western and northern regions of the range (i.e., southern Brewster County to El Paso County, and the southeastern edge of New Mexico). The ranges do overlap in southern Brewster County with morphologic intergradation between the species reported there (Anthony 1956; Benson 1982). The two species also occur along the Rio Grande River in adjacent Mexico (Benson 1982). Our study, however, examined the members of the complex as they exist in Texas. The widely disjunct *O. emoryi* occurs as a single population in extreme

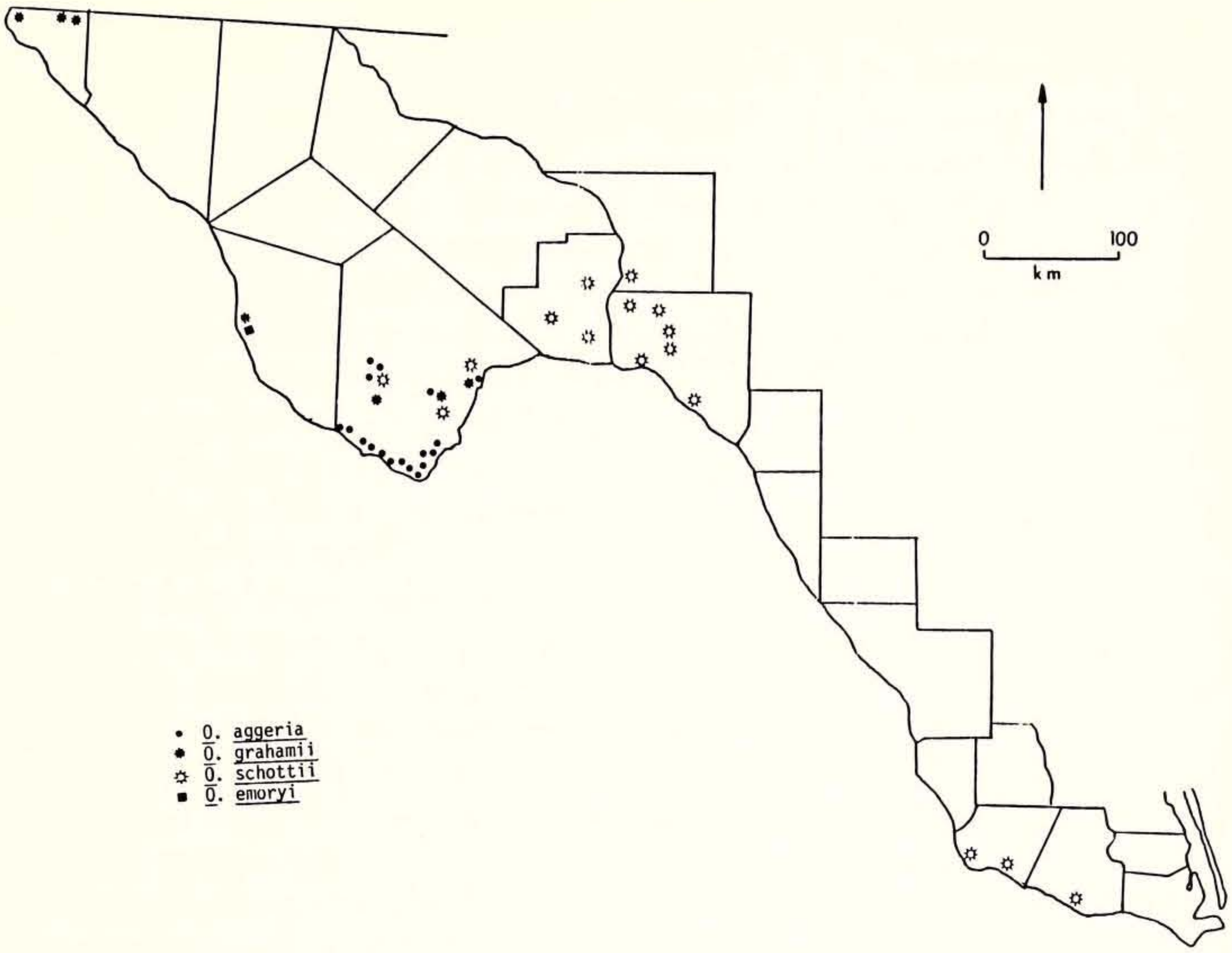

FIG. 1. Distribution of taxa in the *Opuntia schottii* complex in Texas; *Opuntia schottii* (open stars), *O. grahamii* (closed stars), *O. aggeria* (closed circles), and *O. emoryi* (closed square).

southern Presidio County and is not involved in the major taxonomic problem surrounding the complex in Texas.

METHODS AND MATERIALS

Population samples were collected throughout the geographic range of the complex in Texas, with particular emphasis on the area of reported intergradation in Big Bend National Park (BBNP). Vouchers are deposited in SRSC. Loans of herbarium specimens, including types, were obtained from ASU, LL, MICH, MO, POM, RSA, and TEX. Vegetative and floral characters were measured from dried and living material. Bud material for meiotic counts was collected in the field. The buds were fixed in modified Carnoy's solution (chloroform, absolute ethanol, and glacial acetic acid, 4:3:1, v:v:v).

RESULTS

The data in Table 1 disclose that *Opuntia schottii* is easily distinguished from *O. grahamii* by spine length and width, branching architecture, root-type, areole diameter, and relative prominence of tubercles. In Texas, *O. schottii* grows primarily east of the Pecos

TABLE 1. MORPHOLOGICAL COMPARISON OF TAXA IN THE *OPUNTIA SCHOTTII* COMPLEX IN TEXAS AND *O. MOELLERI*.

	O. aggeria	*O. emoryi*	*O. grahamii*	*O. moelleri*	*O. schottii*
Root type	Tuberous	Fibrous	Tuberous	Tuberous	Fibrous
Joint length (mm)	45–65	70–150	35–45	40–70	45–65
Tubercle size:					
Length (mm)	10–20	35–50	8–12	25	15–20
Width (mm)	8–10	10–15	4–6	15	6–8
Height (mm)	5–7	10–12	4–6	10	6–8
Areole diameter (mm)	3–4	5–7	3–4	4	5–7
Spines/areole	7–9	11–16	7–14	6–10	8–14
Spine shape	Flattened to terete	Flattened	Terete	Flattened to terete	Flattened
Spine length (mm)	55–90	35–70	30–35	12–16	40–60

River and flowers much later than *O. grahamii,* which is found west of the Pecos in the United States. Populations in southern Brewster County, mostly within BBNP, designated by Anthony (1956) as putative hybrids, only occasionally exhibit intermediate characteristics or measurements between *O. schottii* and *O. grahamii* (Table 1). Measurements of *O. emoryi* and *O. moelleri* A. Berg. are also provided; the relationship of this latter species to the taxa in the complex is addressed below.

Field work in southwestern Texas indicates that the ranges of the principal taxa within the complex overlap only in southern Brewster County (Fig. 1). Two herbarium specimens identified as *O. schottii* (*Weedin* and *Weedin 237,* and *Worthington 6910.5,* both SRSC) suggested that this species was found in BBNP and as far west as El Paso. These specimens are now properly identified as *O. grahamii,* based on spine, joint, and root morphology.

Chromosome numbers, including previously published counts, are listed in Table 2. Chromosome numbers for *O. grahamii* and *O. schottii,* are $n=22$ (Weedin et al. 1989; Pinkava et al. 1985). The $n=11$ number previously reported for *O. schottii* is now correctly attributed to the putative hybrid populations from BBNP. Chromosome counts made by us for Anthony's putative hybrid populations in and around BBNP (Table 2) reveal that all populations are $n=11$. This number is known within the series *Clavatae* only for these populations, and for the Mexican species *O. moelleri* (Pinkava and Parfitt 1982).

The geographic and morphologic data show that although *O. grahamii* and *O. schottii* are marginally sympatric in BBNP, they do not intergrade. Additionally, the chromosomal data disclose that the putative hybrid exists at the diploid level, whereas the former two species are tetraploids. These data suggest, therefore, that the *O. schottii* complex is best treated as three species: *O. schottii* and *O. grahamii,* which show no evidence of hybridization, and Anthony's putative hybrid that is herein described as new.

Taxonomy

Key to *Opuntia schottii* Complex North of the Mexican Border

a Joints ovoid to obovoid; new growth emerging near apex of previous year's growth; spines mostly terete. . . . . 2. *Opuntia grahamii*

a′ Joints more or less clavate; new growth emerging from sides or bases of previous year's growth; spines mostly flattened.

b Spines 7–9 per areole, pink to white/gray; areoles 3–4 mm wide; roots tuberous. . . . . 1. *Opuntia aggeria*

b′ Spines 8–16 per areole, yellow to red/brown; areoles 5–7 mm wide; roots fibrous.

c Plants to 8 cm high; joints 4.5–6.5 cm long; tubercles 15–20 mm long, 6–8 mm wide. . . . . 3. *Opuntia schottii*

c′ Plants to 15 cm high; joints 7–15 cm long; tubercules 35–50 mm long, 10–15 mm wide. . . . . 4. *Opuntia emoryi*

TABLE 2. CHROMOSOME NUMBERS FOR TAXA IN THE *OPUNTIA SCHOTTII* COMPLEX AND *O. MOELLERI*. Vouchers are deposited in SRSC unless otherwise indicated. R = Ralston.

Species	Haploid number (*n*)	Locality and Voucher
O. aggeria	11	TX, Brewster Co., BBNP, 19.0 km E of Castolon on River Rd, *R 128*; BBNP, 43.4 km E of Castolon on River Rd, *R 135*; BBNP, 33.0 km E of Castolon on River Rd, *R 152*; BBNP, 8.4 km N of St. Elena Canyon on Maverick Rd, *R 114*; BBNP, 5.2 km N of St. Elena Canyon on Maverick Rd, *R 120*; BBNP, 22.0 km SE of Panther Junction, *R 118*; BBNP, Boquillas Crossing parking area, *R 136*; BBNP, 15.3 km W of Mariscal Mt., *Powell 5216*; slopes of igneous hill, 0.8 km N of Lajitas, *Powell 5383*; 15 km N of Study Butte, *Powell 3074a, b* (Weedin and Powell 1978); Lajitas arroyo bottoms, *Worthington 9714* (Pinkava et al. 1985).
O. emoryi	22	TX, Presidio Co., 8.3 km NW of Candelaria near Capote Creek, *Kolle 9,* (Weedin and Powell 1978); 1 km N Capote Creek, *R 113.*
O. grahamii	22	TX, Brewster Co., BBNP, Old Ore Rd near La Noria. *Weedin* and *Weedin 237* (Weedin and Powell 1978); El Paso Co., andesite hills, NW El Paso, *Worthington 6910.5* (Pinkava et al. 1985).
O. moelleri	11	Mexico: Coahuila, Rte. 30, ca. 30 km S of Cuatro Cienagas Basin, at El Hundido, *Pinkava 13662* (Pinkava and Parfitt 1982).
O. schottii	22	TX, Brewster Co., BBNP, junction of Old Ore Rd and Ernst Tinaja Rd, *Kolle* and *Weedin 53* (Weedin et al. 1989).

1. **Opuntia aggeria** Ralston & Hilsenbeck, nom. et stat. nov., based on *Opuntia grahamii* × *schottii* Anthony, Amer. Midl. Nat. 55: 239. 1956 (Fig. 2).—TYPE: USA, Texas, Brewster County, Big Bend National Park, on Tornillo Flats, 2800 ft, 30 Jul 1948, *M. Anthony 856* (holotype, MICH!).

Plants forming low mound to 10 cm high, 1 m wide. Roots thickened, tuberous. Branches creeping; new growth emerging from lateral areoles of previous year's growth. Joints 4–7 cm long, 2.5–3 cm in diamater. Tubercles 10–20 mm long, 8–10 mm wide, 5–7 mm high, green; areoles circular, 3–4 mm wide. Spines 7–9, mostly flattened, pink to white/gray; 3–4 spines per areole 5.5–9 cm long; 4–5 spines per areole spreading, 5–25 mm long; 2–4 radial spines deflexed; glochids numerous to 5–10 mm long. Flowers 5–7 cm long and 4–5 cm wide. Petaloids in 3–4 whorls, grading from yellow-green with

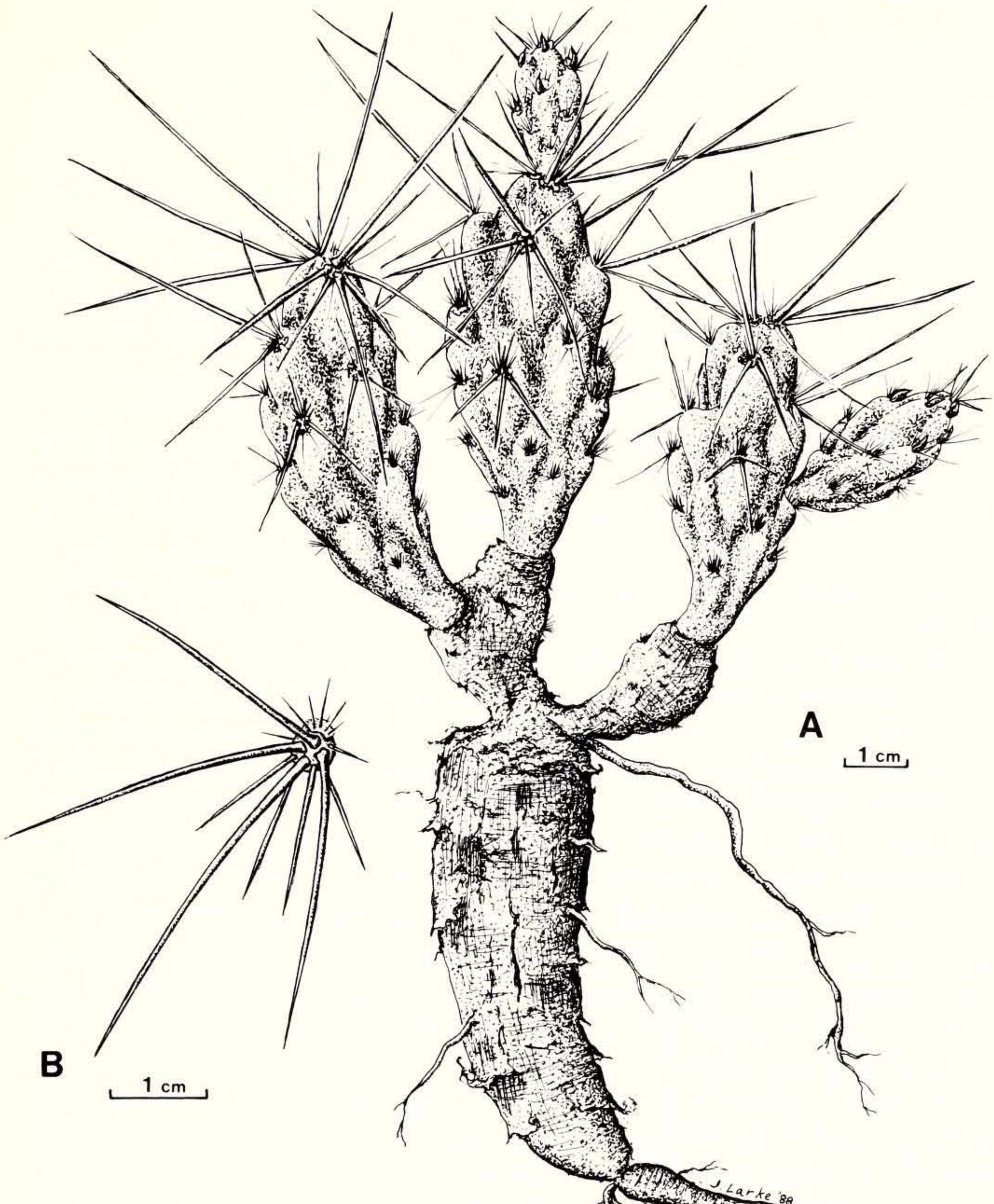

FIG. 2. *Opuntia aggeria* Ralston & Hilsenbeck. A. Habit showing tuberous root, characteristic branching pattern, and distribution of spine clusters. B. Detail of spine cluster. Illustrated from live specimen *Ralston 114*.

central pink tinge on the outer whorls to bright yellow in innermost series, to 25 mm long, 20 mm wide, spatulate, apiculate. Filaments green, to 8 mm long. Style cream, to 3 cm long. Pericarpel narrowly obconic, to 55 mm long, 20 mm wide with areoles bearing glochids. Fruits gray, dry at maturity, to 5 cm long. Seeds brown to cream, to 5 mm in diameter. $n=11$. Flowering late March to April.

Paratypes. USA, Texas, Brewster County, E of Nine-Point Mesa, 3 Aug 1948, *M. Anthony 909* (MICH); 15 mi N of Terlingua, along road to Alpine, 14 Sep 1948, *M. Anthony 1181* (MICH); flats just N of Santa Elena Canyon, BBNP, 15 Sep 1948, *M. Anthony 1246* (MICH).

The specific epithet is chosen to describe the clumped or aggregated growth habit of this mound-forming species. Phenetically, *O. aggeria* appears most closely related to *O. grahamii* by its spine morphology, tuberous root system, and areole diameter, as well as to a species located in northern Mexico, *O. moelleri.* Comparison of *O. aggeria* to both *O. grahamii* and *O. moelleri* is given in Table 1. *Opuntia moelleri* is distributed in Coahuila, Mexico (Britton and Rose 1919; Bravo-Hollis 1978). Morphology (particularly the tuberous roots), geographic distribution, and the fact that *O. aggeria* and *O. moelleri* are the only known diploids in series *Clavatae,* suggest that these two species, through past hybridization, may be the progenitors of the more northerly distributed, tetraploid *O. grahamii.*

Chromosome counts from 12 populations of *O. aggeria* are all $n=11$ (Table 2). If *O. aggeria* was the product of hybridization between *O. schottii* and *O. grahamii* as Anthony suggested, it would likely be a tetraploid, or if diploid, accompanied by possible hybrid sterility (cf. Ralston 1987). *Opuntia aggeria* is, however, highly fertile as determined by pollen stainability (Ralston and Hilsenbeck unpubl.) and, being a diploid, would be more or less reproductively isolated from the other two species of club cholla with which it cooccurs. Moreover, *O. aggeria* only occasionally exhibits characters intermediate between *O. grahamii* and *O. schottii,* whereas a true hybrid might be expected to show definite intermediacy, particularly a vegetatively propagated clonal entity as are many of the chollas, including *O. aggeria* (Grant 1981). The data thus show that the predominant club cholla occurring in BBNP (i.e., Anthony's putative hybrid) does not represent the product of hybridization between *O. schottii* and *O. grahamii* and should be formally recognized at the specific level.

2. OPUNTIA GRAHAMII Engelm., Proc. Amer. Acad. 3:304.—*Corynopuntia grahamii* (Engelm.) F. Knuth, Kactus ABC, 116 1935.—*Opuntia schottii* Engelm. var. *grahamii* (Engelm.) L. Benson, Cactus & Succ. J. (Los Angeles) 41:124. 1969.—*Grusonia grahamii* (Engelm.) H. Robinson, Phytologia 26:176. 1973.—TYPE: USA, Texas, sandy soil in the bottom of the Rio Grande, near El Paso. 1851, *Wright Opuntia no. 10* (lectotype, MO!).

Plants forming low sprawling mounds, 8 cm high, to 3 dm wide. Roots thickened, fleshy, tuberous. Branches creeping, with new

growth added apically, ascending; joints obovate, 3.5–5 cm long, 1.5–3 cm diameter; tubercles broad, not prominent, to 6 mm wide, 8–12 mm long, 4–6 mm high, green; areoles circular, 3–4 mm wide. Spines 7–14 per areole in upper half of joint. Spines mostly terete, straw-colored, with pink tinge; spine sheaths caducous, to 3 mm long; glochids numerous, increasing in number toward base of joint, to 5 mm long on old joints; 3–4 larger spines per areole, 1.5–5 cm long, spreading; 1–9 shorter spines, 5–25 mm long, spreading; 2–4 of these shorter spines deflexed. Flowers to 5 cm long, 4 cm wide; petaloids in 3–4 whorls grading from yellow with central pink tinge in outer ones to bright yellow in innermost series, to 20 mm long, 15–20 mm wide, spatulate, apiculate; filaments yellow green to 10 mm long; style cream, to 25 mm long; pericarpel obconic, 25–30 mm long and to 20 mm in diameter, with numerous glochids in areoles. Fruits and seeds unknown except in type illustration. $n=22$. Flowering early May through early June.

Many features distinguish *O. schottii* and *O. grahamii* (Table 1). Any intergradation through hybridization is now unlikely, as the ranges of the two species are marginally sympatric because of differing ecological preferences, and they differ in phenology as well.

3. OPUNTIA SCHOTTII Engelm., Proc. Amer. Acad. 3:304. 1856.—*Corynopuntia schottii* (Engelm.) F. Knuth. Kactus-ABC. 114. 1935.—*Grusonia schottii* (Engelm.) H. Robinson. Phytologia 26:176. 1973.—TYPE: USA, Texas, Rio Grande, near mouth of Pecos and San Pedro, Sep 1853, *A. Schott s.n.* (lectotype, MO!).

Plants forming extensive mats to 8 cm high, 5 m wide. Roots fibrous. Branches sprawling, forming long chains, new growth emerging from lateral areoles of previous year's growth; joints to 6.5 cm long, 3 cm diameter; tubercles prominent, 15–20 mm long, 6–8 mm wide, and 6–8 mm high, green; areoles circular, to 7 mm wide. Spines 8–14, flattened, reddish brown; spine sheaths to 5 mm long; 3–4 spines per areole 4–6 cm long, with 1 prominent central spine; 2–8 spines per areole shorter, to 30 mm long, spreading, 2–4 spines per areole deflexed; glochids not abundant, to 5 mm long. Flowers 5.5–6.5 cm long, to 3 cm wide; petaloids in 3–4 whorls grading from yellow green with central pink tinge in outer ones to bright yellow in innermost series, to 22 mm long, 10 mm wide, spatulate, apiculate; filaments yellow, to 10 mm long; style cream, to 25 mm long; stigma lobes 5–7, pink tinged; pericarpel narrowly obconic, to 30–45 mm long, 25 mm wide, with glochids in areoles. Fruits fleshy, yellow, to 45 mm long; areoles on fruits bearing spines and glochids to 5 mm long, fruits often persisting to following year. Seeds cream to brown, to 4 mm wide, with beaked aril. $n=22$. Flowering mid-June to early July.

Opuntia schottii appears most closely related, particularly through

its fibrous root system and flattened spine morphology, to *O. emoryi,* a species predominantly distributed in Arizona (however, see below). Morphology (Table 1), differing phenology, and its occupation of more mesic habitats primarily east of the Pecos River, easily distinguish *O. schottii* from the other species of club chollas in Trans-Pecos, Texas.

4. OPUNTIA EMORYI Engelm., Proc. Amer. Acad. 3:303. 1856.—*Cactus emoryi* Lemaire. Cactees 88. 1868.—*O. stanlyi* Engelm. [in Emory, Notes Mil. Reconn., 157, fig. 9. 1848, nom. prov.] ex B. D. Jackson. Index Kewensis 2:358. 1895.—*Corynopuntia stanlyi* Knuth. Kactus-ABC. 114. 1935.—*Grunsonia stanlyi* (Engelm.) H. Robinson. Phytologia 26:176. 1973.—TYPE: Mexico, arid soil south and west of El Paso, especially between the sandhills and Lake Santa Maria, 1852, *Bigelow s.n.* (lectotype, MO!, seeds only).

Plants forming low sprawling mats to 15 cm high, 4 m wide. Roots fibrous. Branches forming chains; new growth emerging from areoles of previous year's growth. Joints 7–15 cm long, 5 cm in diameter; tubercles prominent, 35–50 mm long, 10–15 mm wide, 10–12 mm high, green; areoles circular to 7 mm wide. Spines 11–16, flattened yellow to red/brown; 6–8 spines 3.5–7 cm long, 5–8 spines 10–25 mm long. Glochids sparse to 5 mm long. Flowers 5.5–6.5 cm long, and to 3 cm wide; petaloids in 3–4 whorls grading from yellow green with central pink tinge outermost to bright yellow innermost, 25 mm long, 15 mm wide, spatulate, apiculate; filaments yellow, to 10 mm long; style cream, to 25 mm long; stigma lobes 5–7, pink tinged. Pericarpel narrowly obconic, 30–45 mm long, 20 mm wide, with areoles bearing glochids. Fruits and seeds not known for Texas population. n=22. Flowering May to early June.

In Texas, *O. emoryi* appears most closely related to *O. schottii.* Although *O. emoryi* is primarily known from Arizona, a disjunct population has been recently documented in the Big Bend region of West Texas near Candelaria in southern Presidio County (Weedin and Powell 1978; Ralston 1987; Ralston and Hilsenbeck in prep.). *Opuntia emoryi,* also a tetraploid species, is peripheral to the taxonomy of *O. aggeria* but is nonetheless an important, recent addition to the Texas flora. The larger size of the plants, including the much larger joints and tubercles, distinguishes *O. emoryi* from other species in the complex. Further study within the complex, however, and within series *Clavatae,* that takes into full account the northern Mexico and Arizona taxa is warranted.

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ANNOUNCEMENT

New Publications

Crawford, R. M. M., *Studies in plant survival: Ecological case histories of plant adaptation to adversity,* Blackwell Scientific Publications, Osney Mead, Oxford OX2 0EL, 1989, x, 296 pp., illus., ISBNs 0-632-01475-X (hardbound), 0-632-01477-6 (paperbound), prices unknown. [=*Studies in Ecology,* Vol. 11. Discusses many plant examples for Arctic, montane, desert, coastal, and other areas.]

Cullmann, W., E. Götz and G. Gröner, *The encyclopedia of cacti,* trans. by K. M. Thomas, Timber Press, 9999 SW. Wilshire, Portland, OR 97225, 1986 (publ. 1987), 340 pp., illus. (most color), endpaper maps, ISBN 0-88192-100-9 (hardbound), $49.95. [Publ. in Britain by Alphabooks, Sherborne, same title, 1986. Translation of *Kakteen,* 2. Aufl., Eugen Ulmer GmbH & Co., 1984. With excellent photos, clear descriptions, and many keys to taxa.]