CLUB CHOLLAS OF THE BIG BEND 3.0: REFINING SPECIES CONCEPTS AND DISTRIBUTIONS FOR THE *CORYNOPUNTIA* [*OPUNTIA, GRUSONIA*] *SCHOTTII* COMPLEX OF WESTERN TEXAS VIA NEW CHROMOSOME COUNTS, POLLEN STAINABILITY, AND MORPHOLOGIC DATA

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ABSTRACT

Species-level understanding of the *Corynopuntia schottii* complex (*C. aggeria*, *C. densispina*, *C. emoryi*, *C. grahamii*, and *C. schottii*) within the USA has long been confused and misunderstood. Most recent taxonomic treatments are incomplete and/or inaccurate regarding four of the species (excluding *C. emoryi*). The present study helps clarify all species concepts in the Big Bend region of Texas through 97 chromosome counts, 186 pollen stainability measurements, 272 new voucher specimens, and review of previously existing herbarium specimens. Significant findings include (1) documentation of *C. schottii* as a hexaploid species that occurs from deep South Texas to just west of the Brewster County line and outside of Big Bend National Park, (2) confirmation of the previously reported chromosome numbers for the remaining taxa, despite uncovering widespread meiotic irregularities in *C. grahamii* and extremely plastic morphology of *C. aggeria*, (3) a range of fertility between and even within populations of all species, and (4) chromosomal and morphological evidence of hybridization and introgression in most taxa. Distinguishing characters, keys to the species (for both living and dried material), distribution maps, photographs of each taxon, and corrections to erroneously labeled published photographs are provided. The Big Bend endemic **Corynopuntia densispina** (Ralston & Hilsenb.) J. Fenstermacher, **comb. nov**., is formally transferred from *Opuntia*/*Grusonia*. Evolutionary origins of the taxa and their larger geographic and evolutionary context (including Mexico and the broader southwestern USA) are discussed and avenues for future research are suggested.

For over 100 years, taxonomic delineations within the Opuntioidiae have been fraught with difficulty in large part due to a high level of interspecific hybridization, extensive vegetative dispersal and reproduction, paucity of taxonomically meaningful morphological characters, and environmentally influenced morphologic variability (Pinkava et al. 1998; Rebman & Pinkava 2001; Powell & Weedin 2004). Several of the most recent authoritative taxonomic treatments involving *Opuntia* [sensu lato] occurring in the USA (e.g., Pinkava 2003; Powell & Weedin 2004; Hunt 2006) include statements to the effect that parts, or even the entirety, of this group is in need of critical study. For example in Texas, Powell and Weedin (2004) recognized 25 "normal" *Opuntia* (s.l.) taxa as occurring in the Trans-Pecos, while suspecting that between 10 and 20 potentially recognizable species were overlooked; they further emphasized that the classification of *Opuntia* (s.l.) into species and varieties "remains little more than a goal for the future."

Several recent molecular studies have attempted to elucidate intrafamilial relationships in Cactaceae (Nyffeler 2002; Wallace & Dickie 2002; Griffith & Porter 2009; Bárcenas et al. 2011; Hernández-Hernández et al. 2011; Majure et al. 2012c); however, definitive clarity at the generic and specific levels still remains elusive. Several recent field studies based on chromosome counts and morphologic observations have revealed new taxa and broadened understanding of taxon concepts

and evolutionary history (Baker et al. 2009; Donati 2010, 2011; Majure & Ribbens 2012; Majure et al. 2012a, 2012b; Baker & Cloud-Hughes 2014; Breslin & Donati 2014; Felger et al. 2014). The resurgence of non-molecular-based research addresses recognized problems implicated in obscuring clarity of opuntioid systematics including inadequate replicative chromosomal sampling, limited in-depth, field-based observations capturing detailed morphologic traits and breeding system data, and limited distributional context of studies (Pinkava et al. 1998; Rebman & Pinkava 2001; Bárcenas 2004; Rebman 2006; Majure & Ribbens 2012; Majure et al. 2012a, 2012b, 2012c; Baker & Cloud-Hughes 2014). The present study adds new, non-molecular insight into intrageneric relationships of the Big Bend Texas area club chollas. Data for the present study were accumulated over 10 years beginning in 2004 via field observations, chromosome counts, pollen stains, review of existing herbarium specimens, and new voucher collections.

Taxonomic History

The specific taxonomic conundrum focused upon here has engaged specialists for over 60 years. Known from the 1950's as the "*Opuntia schottii* complex," (Anthony 1956) the group now comprises five taxa: *Corynopuntia aggeria*, *C. densispina*, *C. emoryi*, *C. grahamii*, and *C. schottii*, all five referred to herein as the *C. schottii* complex (CSC). These five species are part of a larger clade of small-cylindroid cacti that over time have been variously placed in different genera, most recently within *Grusonia* while also giving support for a modified *Corynopuntia* concept (Bárcenas 2015). Several recent studies, including the examination of seed morphology (Stuppy 2002) and molecular analyses (Griffith 2002; Griffith & Porter 2009; Bárcenas et al. 2011; Bárcenas 2015), while lacking repeatable phylogenies for the entire *Cylindropuntia* tribe (sensu Hunt 2006), have shown that within the concept of *Corynopuntia* one subgroup consistently segregates as monophyletic, separate from others that regularly shift affiliations. The subclades involved are most clearly resolved in Griffith (2002). Strict monophyletic interpretation in Griffith (2002) and Stuppy (2002) leads to placing all cylindroid cacti (including *Cylindropuntia*) into *Grusonia*. However, the amalgamation, as Griffith stated, obscures the natural diversity evident in the lineage, leading Griffith to resurrect older generic concepts including *Micropuntia* and *Corynopuntia*, also utilized by Stuppy (2002). Though a perfectly repeatable, monophyletic *Corynopuntia* has yet to be shown, the consistently-segregating subgroup of club chollas includes the Big Bend species and does repeatedly fall within *Corynopuntia*. Applying this generic designation, as opposed to *Grusonia*, would seem to be the most appropriate because the subclade is bound by both morphologic similarity and consistent segregation in genetic analyses (Griffith 2002; Griffith & Porter 2009; Bárcenas et al. 2011; Bárcenas 2015).

The two foundation taxa for the Big Bend club cholla complex, *Corynopuntia* [*Opuntia*] *schottii* and *C. grahamii*, were described by Engelmann (1856, 1859) based on collections made by Wright, Bigelow, and Schott during the 1851-53 U.S. and Mexico Boundary Survey. The western taxon, *C. grahamii*, was initially collected near El Paso and is known from southern New Mexico south along the Rio Grande into Texas's Big Bend (Fig. 1; A). *Corynopuntia* [*Opuntia*] *schottii* was the eastern taxon, the type having been collected near the mouth of the Pecos River in present day Val Verde County, Texas. Its documented range in the USA has been thought to extend from south Texas upriver into the Big Bend region of southern Brewster County (Fig. 1; B). Both taxa have been reported as ranging much further south of the international border than they do north of it (Hernández et al. 2004; SEINet 2014). These two taxa have been variously treated as separate species (Engelmann 1856; Britton & Rose 1919; Schulz & Runyon 1930; Anthony 1956; Weniger 1988; Ralston & Hilsenbeck 1989; Anderson 2001; Pinkava 2003; Hunt 2006), or varieties of *O. schottii* (Benson 1969, 1982; Correll & Johnston 1970; Pinkava et al. 1985; Powell & Weedin 2004; Powell et al. 2008), and not all authors have believed both taxa to occur in the Big Bend (Weniger 1988).

To keen in situ observers (Anthony 1954; Ralston 1987), field characteristics easily distinguish *Corynopuntia schottii* and *C. grahamii*: both taxa have readily disarticulating distal stem segments (joints), but differ in distribution, phenology, joint growth origin, mound habit, and
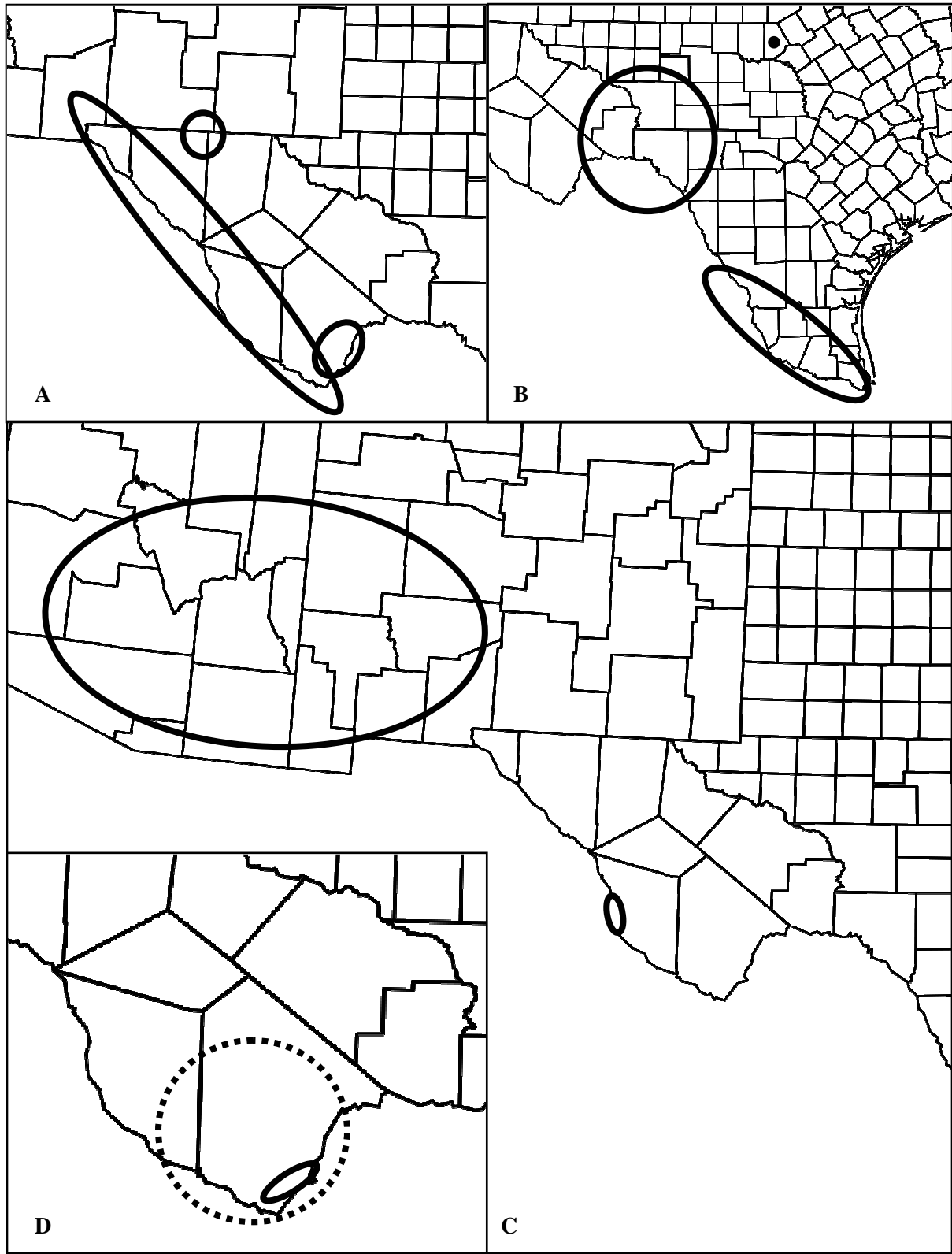
Figure 1. Previously known range extents for the *Corynopuntia schottii* complex in the USA (Texas, New Mexico, Arizona) based on Pinkava (2003) and Powell, Weedin, & Powell (2008). A. *C. grahamii.* B. *C. schottii.* C. *C. emoryi.* D. *C. aggeria*, dotted circle; *C. densispina*, solid oval.

morphology of joints, spines, and roots. Despite these multiple distinctions, the major floristic works involving Big Bend area cacti (Benson 1969; Correll & Johnston 1970; Weniger 1988; Anderson 2001; Pinkava 2003; Powell & Weedin 2004) were inconsistent in their treatments of these taxa, with only one identification guide (Powell et al. 2008) clearly identifying all previously known basic characters enabling definitive identifications of each species in the study area.

The critical key characters of the CSC species may not have been widely apparent to scientists who work, in large part, from dried herbarium specimens. Unfortunately much of the taxonomic effort over the past century likely has been based on poor or incomplete vouchers (i.e., no roots, solitary joints) and/or incomplete label data regarding important field characteristics (e.g., ease of stem disarticulation, growth habit). Additionally, a sufficient breadth of exsiccatae material may also have been lacking. As noted by other specialists (e.g., Rebman & Pinkava 2001; Powell & Weedin 2004; Majure & Ervin 2008), opuntioid species (s.l.) are regularly under-collected in light of their fiberglass-like small spines (glochids), difficulty in processing collections for mounting purposes, and in some species distal joints that easily detach and become embedded in footwear, clothing, and flesh by virtue of their retrorsely-barbed spine tips. Perhaps most confounding is the subfamily's propensity for autogamy plus high frequency of interspecific hybridization, leading to poorly segregated arrays of intermediate morphotypes.

Certainly a major confusing influence concerning CSC species identifications was the regional perception, first discussed by Anthony (1956) then enshrined in Benson (1969), that there was a large area of distributional overlap in Brewster County, Texas, where the two foundation species supposedly freely intergraded. Anthony was the first to work specifically on the Big Bend Opuntiae (Anthony 1949) and as part of her work she proposed a hybrid taxon (Anthony 1956) to account for what was perceived as an apparent abundance of intermediate individuals. This concept lasted throughout the following 20 years until, based both on robust field collections and newly advanced research techniques (i.e., chromosome counts, pollen stainability, phytochemistry), Ralston (1987) determined that the two CSC foundation species were indeed distinct with little evidence of intermediate individuals. Then Ralston and Hilsenbeck (1989) demonstrated that Anthony's "putative hybrid" was actually a distinct, fertile, diploid entity: *Corynopuntia aggeria*. It was described as the predominant club cholla occurring in Big Bend National Park (Fig. 1 C), whereas *C. grahamii* and *C. schottii* were stated to occur there sympatrically with *C. aggeria* but in a limited, undefined area without evidence of intergradation.

Ultimately, Ralston and Hilsenbeck (1992) described another club cholla species from Big Bend National Park, *Corynopuntia densispina*, based on distinct morphology and tetraploid chromosome number. Seemingly restricted to clay substrates in an isolated area just north of the Rio Grande (Fig. 1 C), *C. densispina* was not widely accepted by cactus specialists, who noted undue overlap with the concept of *C. schottii*. The newest species was omitted, placed in synonymy, or simply not mentioned in the majority of subsequent, authoritative floristic treatments and checklists (Anderson 2001; Pinkava 2003; Bárcenas 2004; Hernandez et al. 2004; Hunt 2006).

Separate from the confusion over the two foundation taxa, a third club cholla, *Corynopuntia emoryi*, had been discovered to occur in western Texas in the late 1970s (Weedin & Powell 1978). More commonly known from southeastern Arizona, southern New Mexico, and adjacent Mexico, its small disjunct population in southern Presidio County is just upriver from the core distribution of the other CSC species (Fig 1 D). As a geographically peripheral CSC member, the tetraploid *C. emoryi* has not typically been involved in any of the associated taxonomic problems.

Despite the description of two new species, *Corynopuntia aggeria* and *C. densispina*, taxonomic relationships of the four "core" western Texas club chollas (*C. aggeria*, *C. densispina, C.*

grahamii, *C. schottii*) remained unclear in many ways: (1) contemporaneous and conflicting labels proliferate on more than a few herbarium sheets of each taxon, (2) published chromosome counts for vouchers identified as *C. schottii* (last summarized in Pinkava 2002) reflect continued disagreement regarding ploidy level (n = 11, 22, 33), (3) identities of chromosomal vouchers for *C. schottii* were considered ambiguous (Powell & Weedin 2004), (4) significant meiotic and pollen stainability irregularities were observed in populations assumed to be *C. schottii* (Ralston 1987; Powell & Weedin 2004), and (5) polyploid chromosome counts were made from populations that appeared morphologically to be *C. aggeria* despite its reportedly diploid nature (Powell & Weedin 2004). Perhaps most tellingly, incorrectly identified photos and specimens, omission of important characters (e.g., ease of disarticulation, chromosome number), and/or inaccurate descriptions have persisted even in recent authoritative literature (Pinkava 2003; Bárcenas 2004; Hunt 2006; SEINet 2014; USDA, NRCS 2014).

The current study aims to clarify species distinctions and relationships within the Big Bend club chollas via chromosomal, pollen stainability, and morphologic data. The long-standing confusion and inconsistent reports regarding species' morphologic characteristics and distributions are addressed, easy to use keys for both field and herbarium use are provided, and the incidence of hybridization between several species, potential novel taxa, and possible mechanisms for evolutionary development are examined. Several avenues showing promise for further investigation are also discussed.

MATERIALS AND METHODS

Chromosome counts. The majority of chromosome numbers were obtained through meiotic observations. Flower buds were removed from the plant and bisected longitudinally to view developing anthers for the appropriate size. If buds encountered were not sufficiently developed to yield the appropriate meiotic stage, the entire joint was harvested with bud still attached, kept indoors in a sunny location, then harvested after a few days of further growth. Immediately upon harvest buds were fixed in modified Carnoy's Solution (4:3:1) generally overnight. Anthers were then removed from buds with forceps and macerated in acetocarmine stain (Turner & Johnston 1961) and observed immediately. All counts were made by the author and/or A. Michael Powell, except for two meiotic and two mitotic counts provided by Marc Baker.

Pollen stainability. Pollen for stainability measurements was collected from either living or dried specimens. Anthers were collected in the field from open flowers, or joints with the most mature buds were harvested and placed in a sunny location until the flowers opened. Recently closed flowers were sampled rarely, when an individual or location was important to sample but no buds or open flowers were present. Herbarium specimens (when flowers were mounted with reproductive parts facing up) were an extremely valuable source for pollen analysis. Floral remnants in packets were preferentially sampled. Otherwise anthers were removed with forceps from mounted flowers. The standard sample size was four anthers from one flower. Rarely, when direct access with forceps was not possible, pollen was instead tapped out of partially closed, mounted buds or inconveniently-oriented mounted flowers. Pollen grains were stained and macerated in cotton blue in lactophenol following Powell et al. (1991) and left at least overnight before observation. Pollen stainability percents were based on a count of ca. 200 grains or, in cases of low pollen productivity, the total amount of pollen grains contained in the four-anther sample. As pollen grains sampled were derived from macerated anthers, the incidence of mixed pollen from other plants was considered to be insignificant for purposes of this study; non-Opuntiae pollen grains were noted in a handful of samples, identified easily by different size, shape, and surface projections. Low-staining pollen samples were those with a lower than 50% stainability result. High-staining samples were those with above 70% stainability.

Field observations, voucher specimens. Voucher specimens were open-air dried without the use of ETOH. Tepal samples from various populations across the species' ranges were collected and placed in plastic vials with silica gel, enabling future genetic study by interested researchers. All specimens and tepal samples, unless otherwise noted, are housed at SRSC. All five of the CSC taxa were observed in the field across their known ranges in the USA (excluding *Corynopuntia emoryi* populations outside of Texas). All key morphological characteristics (often not apparent once pressed and dried as a specimen) were recorded as label data including joint shape, ease of joint disarticulation, root morphology, joint growth origin, and filament color. Herbarium specimens of CSC taxa, in addition to some associated species in the southwestern USA and Mexico, were examined via loans from the following herbaria: ASC, NMSU, MICH, TEX-LL, UNM. Digital images of specimens were also utilized (SEINET 2014; JSTOR Plant Science 2014). Primary collector names are used to cite specimens; use of 'et al.' indicates that secondary collectors are listed in label data.

Collector abbreviations and names used frequently in this paper, including the appendices, are as follows: ADZ = Alan D. Zimmerman; AK = Ad Konings; AMP = A. Michael Powell; AS = Anna Strong; BER = Barbara E. Ralston; BGH = Barry G. Hughes; BHW = Barton H. Warnock; CJ = Chris Jackson; DB = Daniel Brailovsky; DJP = Donald J. Pinkava; DOK = Don O. Kolle; DW = Del Weniger; EUC = Elzada U. Clover; GCR = Gerald C. Raun; GW = Gil Wiens; JEH = Jean E. Hardy; JF = Joselyn Fenstermacher; JFS = James F. Scudday; JFW = James F. Weedin; JL = Janice Lewis; KHS = Karl H. Schwerin; LCH = Leon C. Hinckley; MAB = Marc A. Baker; ME = Michael Eason; MSA = Margery S. Anthony; PRM = Patricia R. Manning; RDW = Richard D. Worthington; RM = Roy Morey; SL = Shane Lee; TG = Tony Gallucci; TP = Tom Patterson; WW = Wendy Weckesser.

RESULTS

A total of 272 new collections were made and utilized as vouchers for cytologic studies as well as to provide populational and morphologic documentation. More than 75 potted specimens were used for cytologic and morphologic study as part of a living collection maintained at a Sul Ross State University greenhouse. Several individuals remain in cultivation at the Chino Valley, Arizona, garden of Marc Baker. Tepals from over 100 individuals are available for genetic study. Cursory measurements of stomata, pollen grain size, and average stomata density revealed no correlation with ploidy level.

Chromosome counts. New chromosome data are reported for 81 individuals representing four of the five CSC species and three putative hybrids (Appendix A); *Corynopuntia emoryi* was not counted. The results of the present study support the previously reported chromosome numbers for CSC species (Appendix B). Though *C. schottii* has been widely believed to be a tetraploid, the new hexaploid counts ($2n = 33$ II) reported here support one previously published hexaploid count reported for the species (Yuasa et al. 1973) though the data are unverifiable as no voucher exists (Govorounova, pers. com. 2015). Meiosis was observed to be consistently regular in *C. aggeria* whereas irregular meiosis, including univalents and multivalents, was observed in *C. densispina*, *C. grahamii*, and *C. schottii*. No collections of *C. aggeria* were meiotically sterile, i.e., having irregular and/or absent microsporocytes, whereas the remaining species demonstrated varying degrees of sterility (Table 1). The first pentaploid and triploid counts known for the genus were made from individuals identified as *C. grahamii*. Triploid counts were also made for putative hybrids of *C. aggeria* × *C. densispina* and *C. aggeria* × *C. grahamii*. Tetraploidy, as well as meiotic sterility, were observed in multiple putative *C. aggeria* × *C. grahamii* individuals. An additional putative hybrid, *C. grahamii* × *C. schottii*, proved to be meiotically sterile, i.e., microsporocytes were entirely absent in the sample.

Table 1. Incidence of absent or irregular microsporocytes in flower bud samples used for chromosomal analysis in the *Corynopuntia schottii* complex species. *C. emoryi* was not sampled for chromosomal analysis.

	C. aggeria	*C.densispina*	*C. emoryi*	*C. grahamii*	*C. schottii*
Proportion sterile samples: total samples	0:34	2:26	n/a	4:10	3:6
% sterile samples	0	8	n/a	40	50

Pollen stainability. Pollen stainability was measured from 185 individual flowers representing at least 147 individuals (Appendix C, D). For several voucher specimens, a populational sample of flowers was made additional to harvesting flowers directly from the vouchered individual. Average percent stainability differed somewhat between species (Fig. 2 A), but *Corynopuntia aggeria* and *C. densispina* had the greatest proportion of higher staining grains (Fig. 2 B) and the least proportion of pollen sterility (i.e., anthers lacked pollen entirely) compared to the other taxa (Fig. 2 A). Pollen sterility was observed in all taxa, most commonly in *C. grahamii* (Fig. 2 A). All species showed a range in fertility both within populations (Fig. 2) and across the geographic ranges (Appendix C). At least one sample from each of the CSC species contained two or more sizes of pollen grains, which were variously stained and unstained (Appendix C).

Some *Corynopuntia schottii* flowers observed in populations had few functional anthers with little pollen, yet stained at high percentage (*JF 2404, 2434*). Another individual sampled had flowers with smaller filaments/anthers and few, low-staining grains, as well as flowers with longer/larger anthers containing abundant pollen staining around 50% (*JF 2430*). Other *C. schottii* collections were found to lack pollen entirely (*BER 103*), or were noted as having abnormal meiocytes via chromosome sampling (*AMP 6248*); both vouchers also contain flowers with abundant and high-staining pollen (Appx. D).

Geographic/morphologic data. The known ranges of CSC species across Texas as well as southeastern New Mexico and northern Mexico are now better understood by plotting new collections and verified herbarium records (Fig. 3 A-B). Field observations and examination of herbarium specimens, bolstered by cytologic work, uncovered multiple characteristics that reliably distinguish the CSC species (Appendix E), summarized in the treatments below.   Despite the wide variability in *C. aggeria* spination, the characters recognized as taxonomically reliable for the Big Bend Opuntiae (Anthony 1956), i.e., habit of stem and root growth, joint shape, and form and color of spines as opposed to the size of joints and the length and number of spines, do appear to consistently distinguish Big Bend club chollas. Several collections, detailed below, are putatively identified as hybrids based on mixed morphologic characters relating clearly to sympatric taxa.   Additional collections from three geographic areas, the O2 flats in mid-Brewster County, Texas (*MSA 1174, 1304* MICH; *CJ 364, 310, 265* SRSC), south of Sierra Blanca in Hudspeth County, Texas (*KHS 4123/UNM 52089, 52508* UNM), and southwestern Otero County, New Mexico (*GW 3809-A, 3809B, 3811, 3843, s.n./UNM 67866, s.n./UNM 86355* UNM), have not been confidently identified because their characters represent non-sympatric taxa; details are given under the respective treatments below.

Notes on terminology used in species treatments below (important terms are in **bold**):
Orientation. Many terms can be employed in reference to a location above or below an imaginary horizontal line bisecting an areole or other cactus structure (e.g., chain of cladodes/joints, single joints, spines) in half (Fig. 4). For example, when facing an areole straight on, adaxial refers to the upper half of the areole; synonyms for adaxial include apical, distal, upper, and above. The term abaxial refers to the lower half of the horizontally bisected areole; synonyms for abaxial include
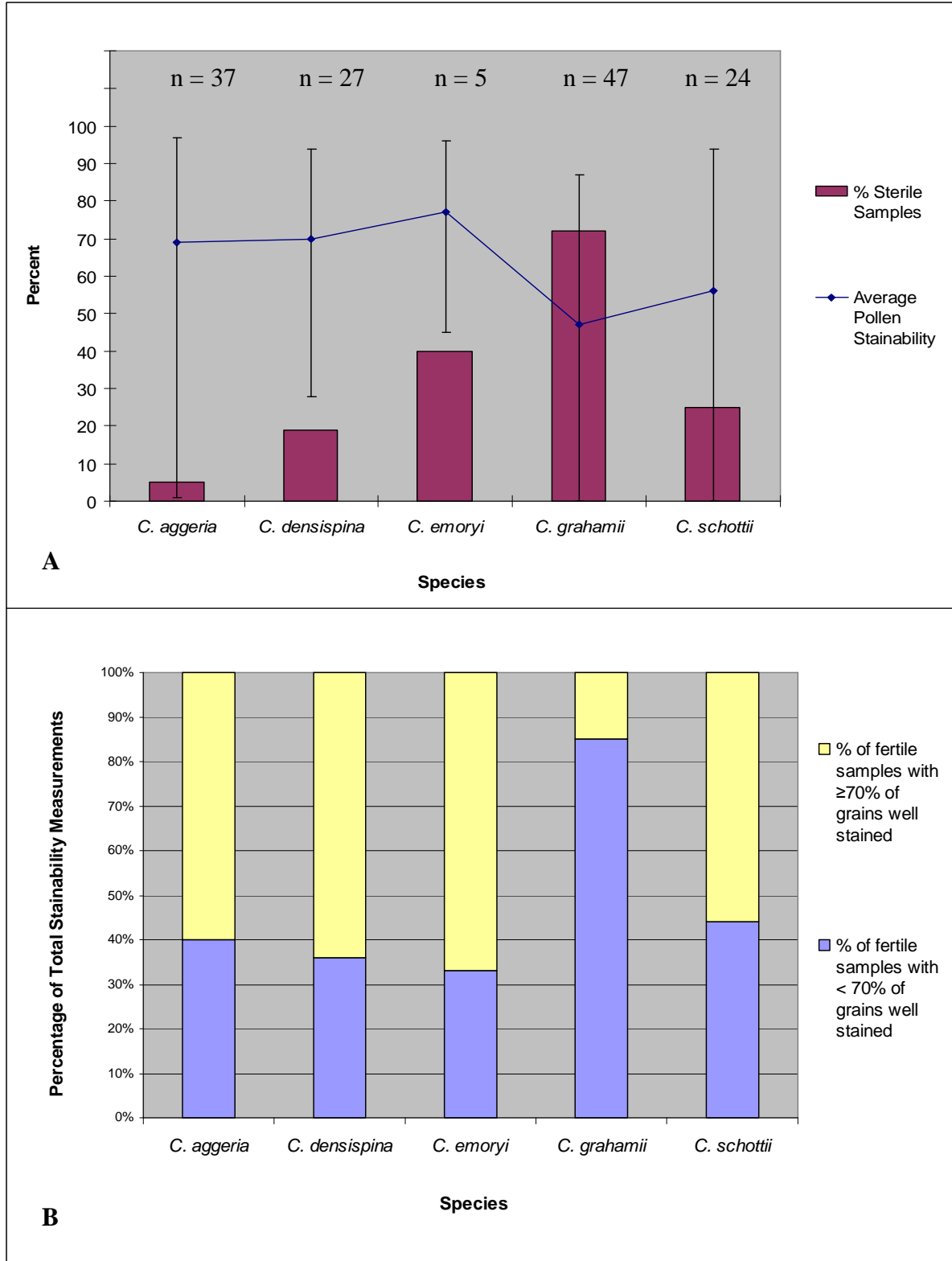
Figure 2. Pollen stainability in the *Corynopuntia schottii* complex. A. Average stainability relative to pollen sterility (lacking pollen entirely); error bars show range of stainability measured in each species; n is the total number of samples measured. B. Percent of fertile samples that were "well stained" (>70%) and "low staining" (<70%).
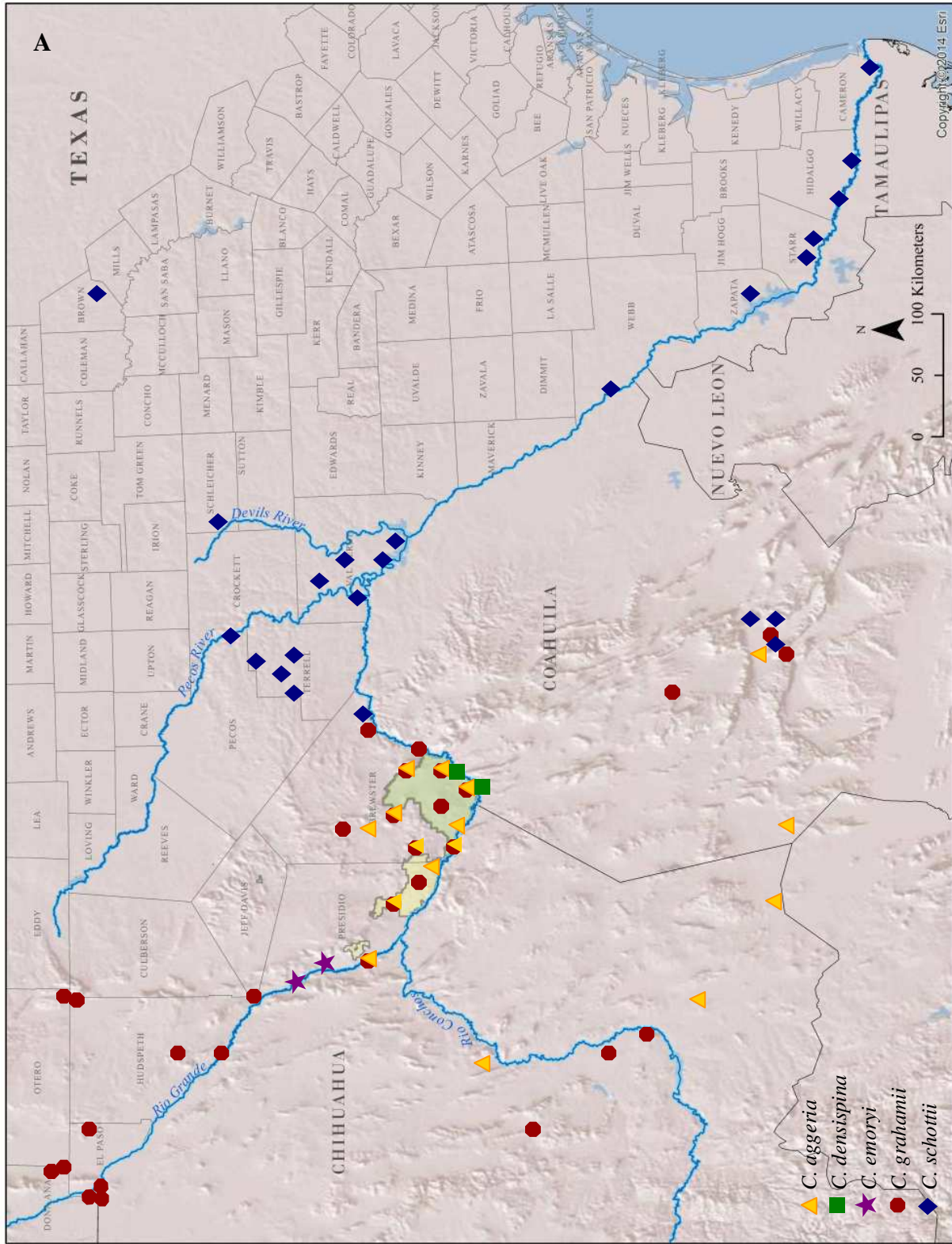
Figure 3. Representative voucher collection locations for the five *Corynopuntia schottii* complex species. A. Texas and adjacent Mexico.
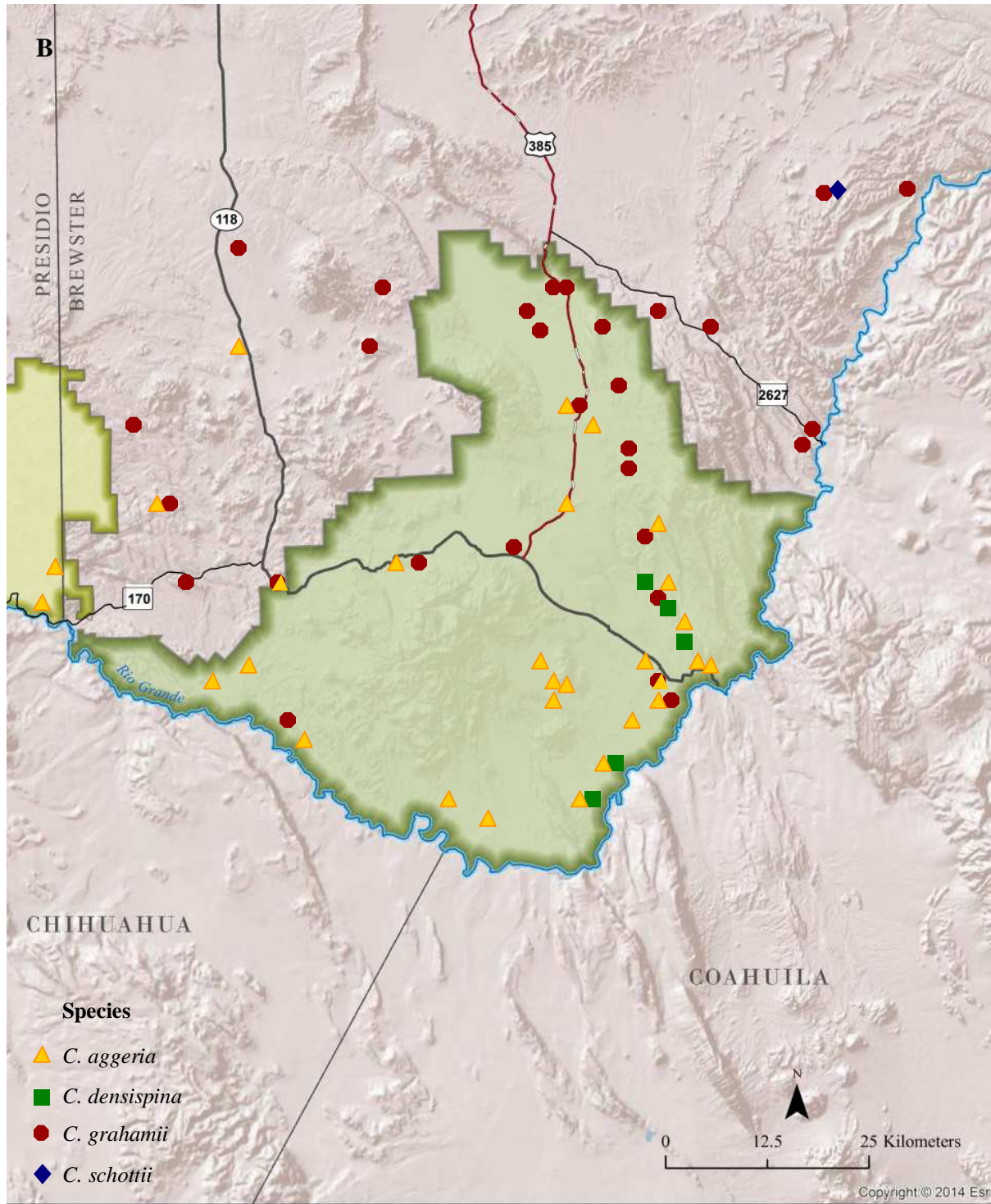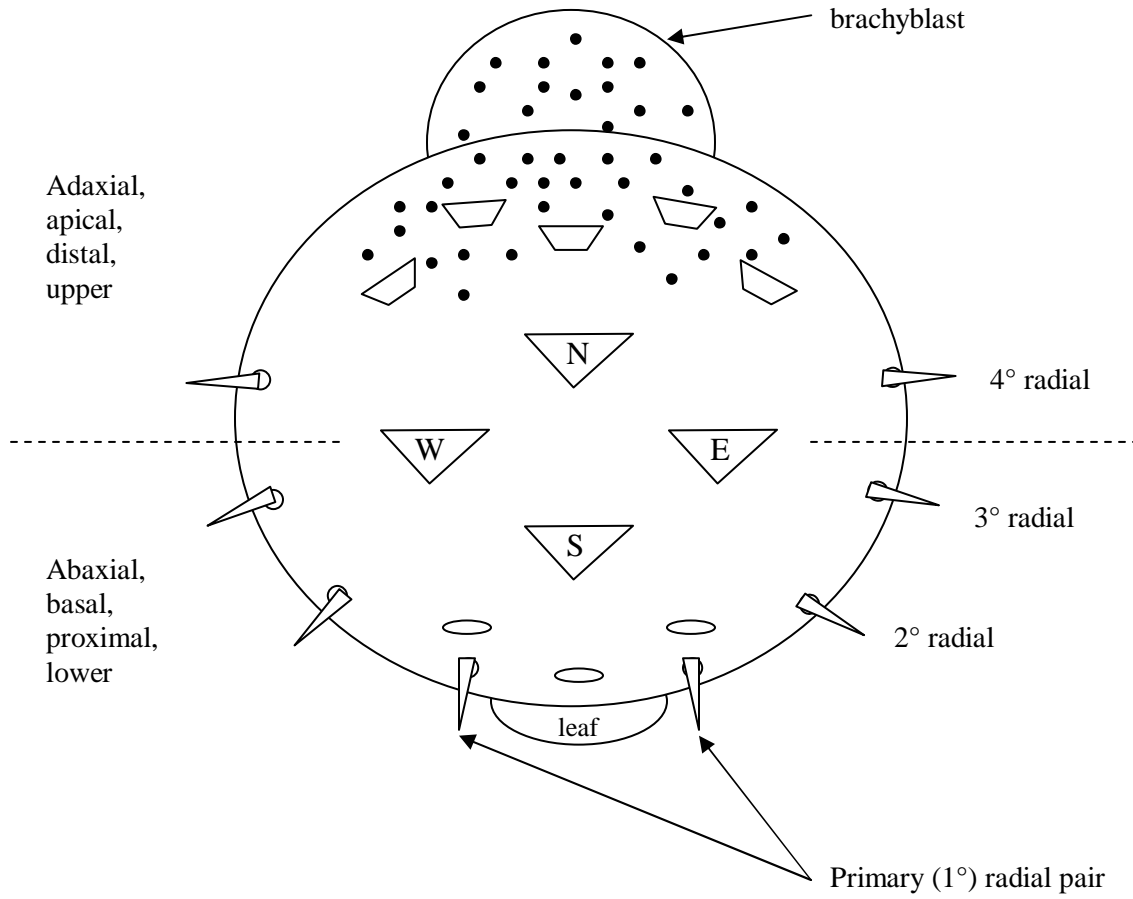
Figure 3. Representative voucher collection locations for the five *Corynopuntia schottii* complex species. B. Big Bend National Park, Texas, and environs.

brachyblast

Adaxial,
apical,
distal,
upper

N

W   E

S

4° radial

3° radial

Abaxial,
basal,
proximal,
lower

2° radial

leaf

Primary (1°) radial pair

Legend:

• = glochids

▽ = main central spine

= radial spines

⬯ = subcentral spine

⏢ = upper central spine

Figure 4. An idealized, representative areole of *Corynopuntia schottii* complex species showing all relevant structures, spine architecture, and orientation vocabulary. The four 'core' central spines are labeled N, S, E, W representing points of the compass for ease of individual identification.

basal, proximal, lower, and below. In structures larger than an areole, for example, apical would refer to the furthest-from-the-root portions of the plant, where basal refers to the closest-to-the-root but above-ground portions of a plant. Apical also refers to the tips of plant components such as spines or joints, and basal—as its opposite—refers to where those structures are attached.

Roots. Cacti are often described as having either "tuberous" or "fibrous" roots but more subtle designations are needed to accurately describe the variation in Big Bend club chollas. For the current study, **tuberous roots** are considered conic-fusiform shaped: those that are enlarged 2-3 cm broad or even wider, elongated (not round or turnip-shaped), and frequently constricted at the root origin but always constricted towards the distal end of the tuber. The creamy-white, fibrous interior of a tuberous root is covered with a papery, shedding, protective epidermal layer. Plants with tuberous roots may also grow relatively more diffuse roots, which can emanate from the tuber or adventitiously from stems at edges of mounds. These may or may not have thin, fusiform-shaped swellings, but in species described as having tuberous roots there will always be a central core of one or more thick, fusiform tubers as the main underground structure.

Diffuse roots do not contain any swellings, lumps, or bumps within or along the root tissue. Diffuse roots are always fibrous in nature and include both thickened and filiform roots. A **thickened root** refers to the existence of one central taproot which is clearly the widest and longest of the underground structures, and is either the same width along its length or tapers evenly towards the tip. Along with a thickened tap root, many other diffuse roots (2-4 mm wide) are usually present and are covered by a papery, shedding, epidermal layer, as are the thickened and tuberous roots. **Filiform roots,** are fine and hair-like in nature (<2 mm wide) and generally lack the papery epidermal layer, instead having a fuzzy covering of very fine root hairs to which fine particles of substrate often remain attached, regularly persisting and notable in prepared herbarium specimens.

Plant structures. Following Bárcenas (2004) the following structures are here defined: areoles on the green photosynthetic stems are called **axial areoles**; modified stem tissue surrounding the flower is the **pericarpel**; and areoles on the pericarpel are **pericarpelar areoles**. Newly termed here is the **pericarpel rim**: the junction of the pericarpel and the base of the tepals, best seen at the bud stage of flower growth (Fig. 5). **Inflated tubercles** are those with a rounded or humped abaxial profile and that, when dry as in an herbarium specimen, maintain a rounded and mammillate appearance (Fig. 6 A). Such tubercles are always clearly laterally compressed, and are raised in obvious relief from the central stem surface. **Deflated tubercles** have a relatively flattened abaxial profile, do not appear linear in shape nor laterally compressed when turgid, and when pressed and dried they appear flattened, as if lacking internal structure, and do not retain a rounded or mammillate appearance (Fig. 6 B).

Spination. Newly detailed here are two distinguishing characters for mature areoles of Big Bend area club cholla species: 1) the presence or absence of **subcentral spines** (Powell & Weedin 2004) — shorter and thinner, lower central spines (Fig. 4); and 2) the relative length of the **primary radial spine pair**, i.e., the two radial spines most abaxial in the areole. Spination has the potential to be very confusing in the CSC species, but there is an abiding core structure in the spine habit for all five species: central spines are oriented around a core group of usually four spines in a "crucifix" pattern, easily represented by the cardinal directions (N, S, E, W); radials occur along the areole periphery; and newer 'upper' central spines emerge at the apex of the areole intermixed with glochids (Fig. 4). When subcentrals are present, there are three of them and they are located below the main four central spines (Figs. 4, 7). A **diminutive subcentral** is a medial subcentral that is noticeably shorter, thinner, and lighter in color than the lateral subcentrals and markedly so in comparison to the central spine directly adaxial to it (Fig. 7 C-D).
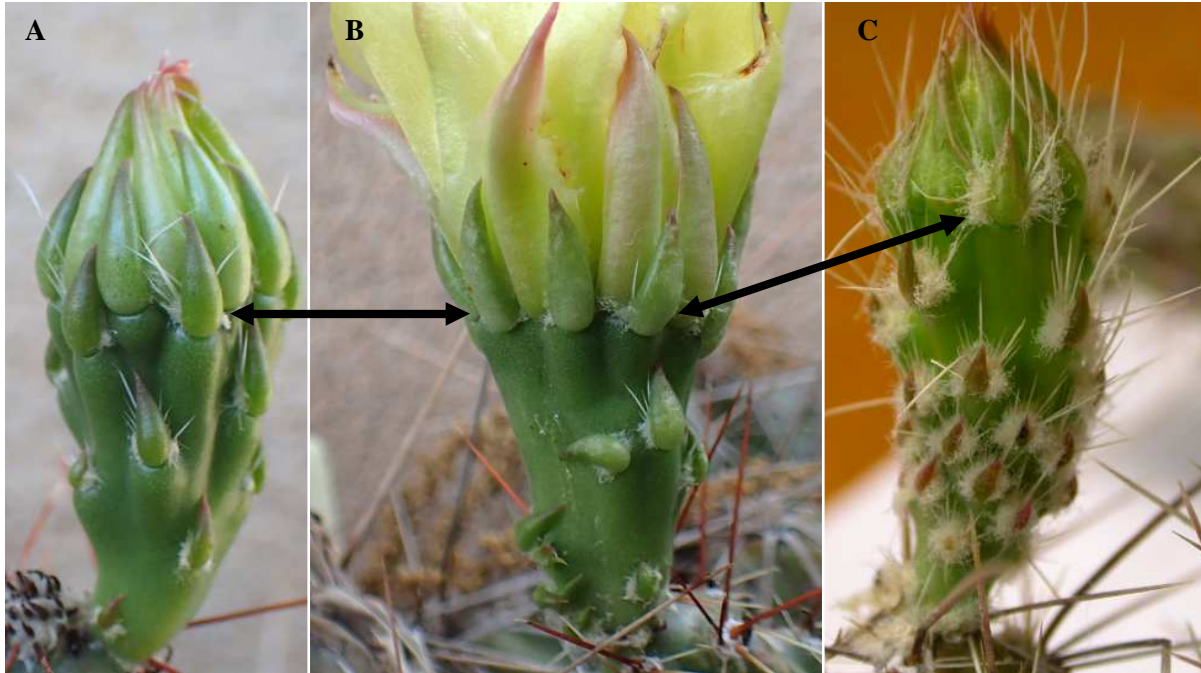
Figure 5. Pericarpel rim location, indicated by black arrows. A-B. *Corynopuntia aggeria.* C. *C. grahamii.* Note the difference between species regarding number of bristle spines at the pericarpel rim as well as the amount of wool in, and density of, pericarpelar areoles.
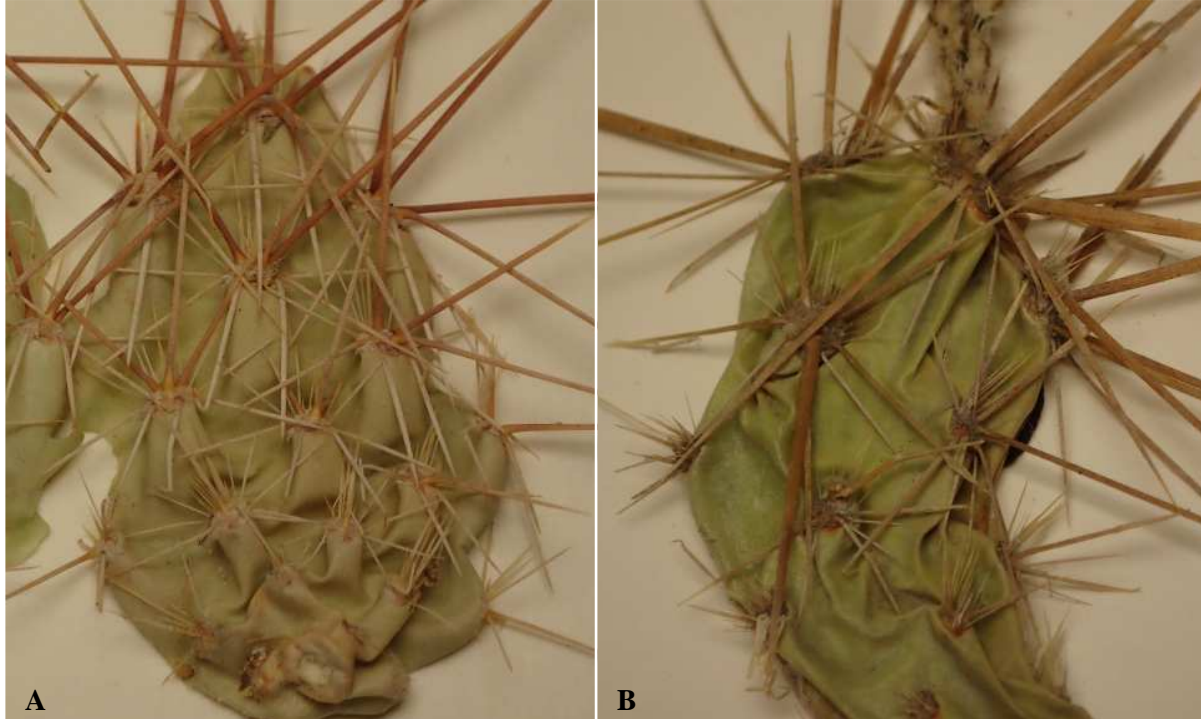

Figure 6. Examples of tubercle morphology types. A. Inflated, *Corynopuntia grahamii.* B. Deflated, *C. schottii.*
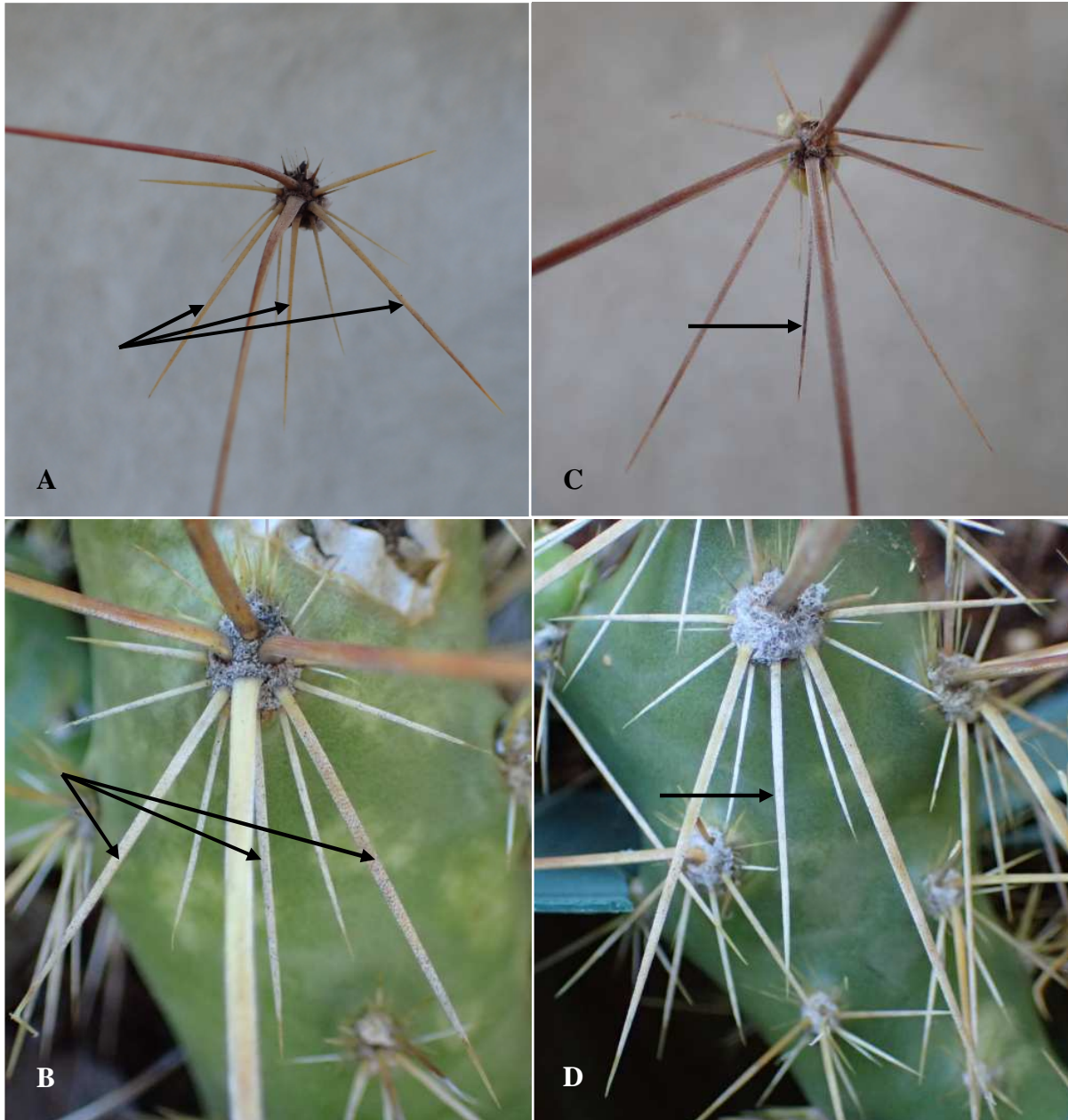
Figure 7. Subcentral spines in Big Bend *Corynopuntia*. A-B. Spine clusters of *C. emoryi* with arrows showing the three equal subcentrals. C-D. Spine clusters of *C. schottii* with arrows indicating the one diminutive subcentral spine.

Despite being slighter in size, the subcentrals are actually the oldest spines in the areole, apart from the primary pair of radials. Following the "mixed" sequence of spine maturation (Gibson and Nobel 1986), after the subcentrals emerge at the adaxial meristem of the areole, they are subsequently pushed downwards abaxially in the areole as they are eclipsed both in location and in robustness by the successively generated central spines (Fig. 8). Subcentrals, having been the first to develop, are thus situated below the main centrals, and the most recently emerged central spines—or "upper" centrals, are situated above the main centrals in mature spine clusters.
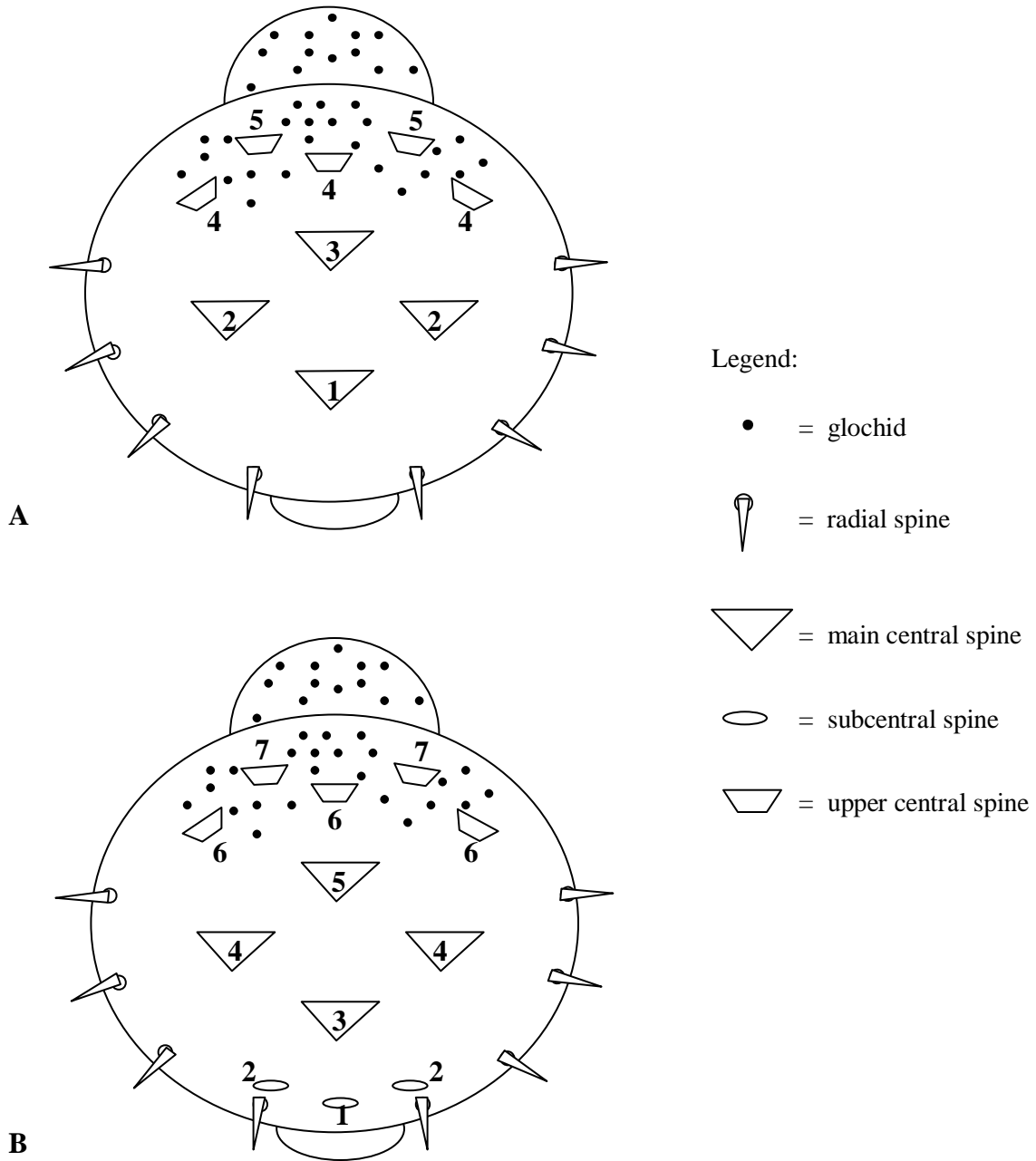
Figure 8. Central spine genesis order in *Corynopuntia schottii* complex species, with 1 being first i.e., oldest. A) Order when subcentral spines are not present. B) Order when subcentrals are present. After Gibson & Nobel (1986).

Generally, radial spines occur at the periphery of stem areoles, usually in the abaxial half of the areole. In the Big Bend club chollas radial spines are borne in a more descending or appressed orientation than the more globally-radiating central spines. Consistently across CSC taxa, radial spines occur in radially-symmetric "pairs." The first, primary, or 1° pair — the one that emerges earliest — is the longest and most basal in the areole, with successive pairs (i.e., 2°, 3°) ascending the periphery of areole to about the 3 o'clock/9 o'clock position, even as high as 1-2 o'clock/10-11 o'clock in *C. grahamii* (Figs. 4, 9). As the radials ascend the areole periphery they decrease in length with each pair.
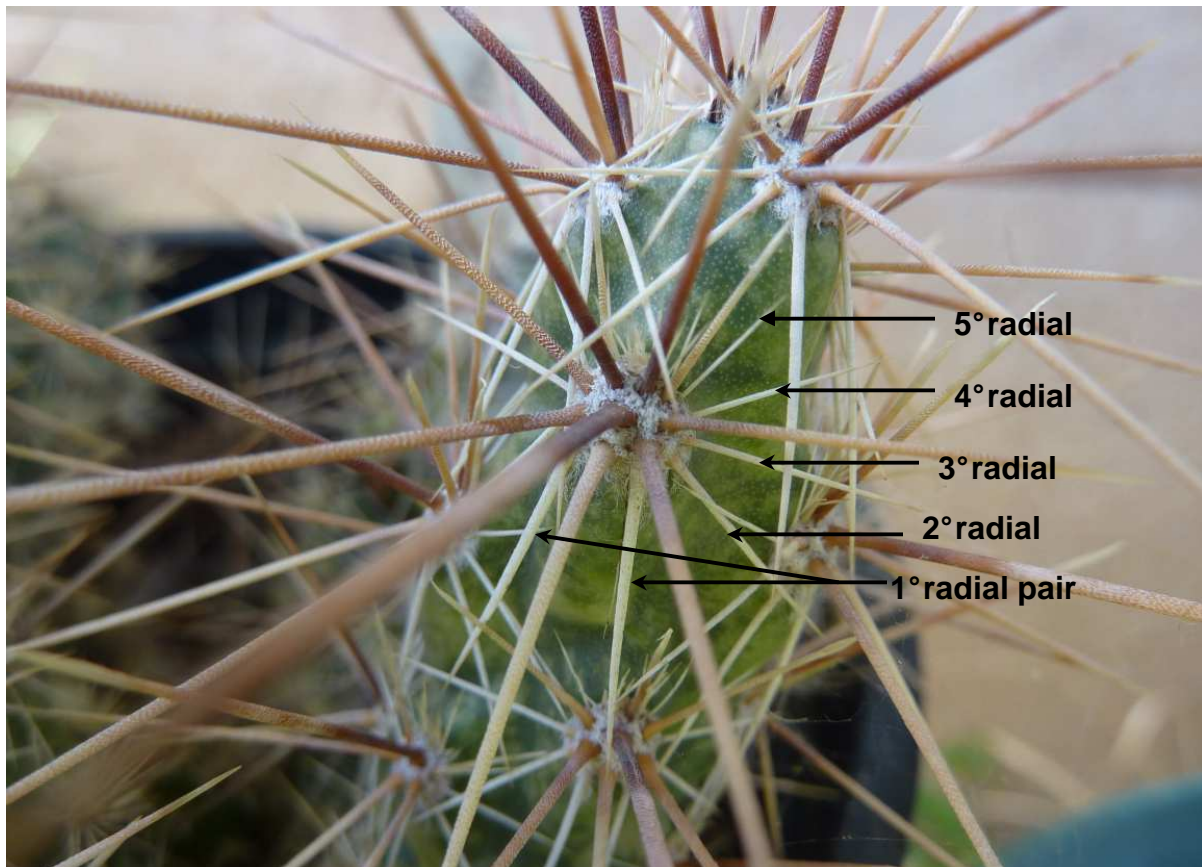

Figure 9. Example of radial spine aspect in Big Bend *Corynopuntia*. All species will have at least the primary (1°) pair of radials most abaxially in the areole whereas *C. grahamii*, especially those with 'classic' morphology as shown above, will often have three or more radial pairs.

Glochids in distal joints are borne in the upper third of mature axial areoles, sometimes mixing with incipient centrals. As described in Bárcenas (2004), stem and pericarpelar areoles of *Corynopuntia* [*Grusonia*] can have different shapes and spine arrangements. In the CSC species this includes occasional production of small apical **brachyblasts** (Fig. 4): raised, wooly structures in the most extreme adaxial areolar position that contain only glochids (Fig. 10). Several CSC species commonly also have **protruding basal areoles:** stem-tissue areoles in the lower-most parts of the plant just above the ground, which are raised significantly from the stem surface in part due to their abundant villous wool. Though these protruding basal areoles lack central spines they do contain abundant, usually radially-symmetric glochids (Fig. 11). In areoles of the pericarpel rim, of all CSC taxa, instead of glochids there are **bristle spines** occurring with conic leaves. Bristle spines are longer than glochids, more flexible and slender than central spines, have retrorsely-barbed tips, and are easily detached (e.g., Fig. 5 C).

Figure 10. Brachyblasts in areoles of Big Bend *Corynopuntia*. A) *C. aggeria*. B-C) *C. grahamii*.

Figure 11. Protruding basal areoles in *Corynopuntia aggeria*. Note radially-symmetric aspect of glochids and abundant wool.

Spine color and form. Coloration and form of spines have been suggested to be good taxonomic characters in opuntiads (s.l.), though both characters may exhibit some variability in different environmental settings (Anthony 1956). In CSC taxa, the color of central spines can be longitudinally **streaked** with white, usually with the amount of white increasing distally (Fig. 12 A). Alternatively, central spines can be **saturated** with color (i.e., no white streaking, Fig. 12 B). If saturated, the tone of color is often blotchy, i.e., having 3-5 subtly lighter and/or darker transverse bands along the lengthof the spine. The thickness of the spine epidermal layer influences spine color. Indicative of

Figure 12. Spine color characteristics in Big Bend *Corynopuntia*. A) Streaky central spines of *C. aggeria*. B) Saturated central spines of *C. grahamii*. C) Iridescent bulbous central spine bases of *C. grahamii*.

Corynopuntia, the layer of sclerified epidermal cells appears as a 'skin' or a 'sheath' covering the spine's fibrous core (Mauseth 2006), and is shed only at the tips of spines as they mature. The remaining indehiscent, tightly-attached epidermal cells affect the way spine color appears to the naked eye, especially in that they create differing surface topography and cell patterns. Thicker layers

of epidermal cells make the spine appear whiter as the cells increasingly obscure the underlying color, observable in radial spines of most species. Thinner, or even absent, cell layers allow more of the underlying color of the spine to appear; this is especially apparent in the iridescent and comparatively boldly-colored spine bases of *C. grahamii* (Fig. 12 C).

Differences in spine epidermal cells, epidermal cell patterns, and spine surface topography for club chollas were also noted by Bárcenas (2004); selected terms modified for use here include: **ridged** – irregular projections of the spine surface resembling appressed, sclerified trichomes which occur either singly, in pairs, or as several in a series which coalesce into rough slanted ridges, the "ridges and valleys" making the spine surface appear papillate to the naked eye (Fig. 13 A-C); **farinose** – thick, whitish or light-gray epidermal cells, often with microscopic black globular markings, the cells particularly thick at spine edges (Fig. 13 D); **longitudinally striate** – longitudinal grooves and microscopic black streaks not globules (Fig. 13 E).

FIELD KEY TO BIG BEND *CORYNOPUNTIA*

1. Joints (especially distal ones) weakly attached, readily disarticulating.

    2. Distal joints ovoid-obovate; new joints originating from apical areoles; central spines terete, pink to red-brown (no white); roots of one to several conic-fusiform tubers; central spines of mature areoles all of similar length; flowers yellow, occasionally dusky pink .... **Corynopuntia grahamii**

    2. Distal joints clavate, J-shaped; new joints originating from lateral areoles; central spines flattened, tan to red-brown, often with white margins; roots diffuse, the majority filiform (well-established plants may also have a slightly-thicker main taproot, possibly several times longer than the height of the plant); central spines of mature areoles include three subcentrals with the medial spine being shorter than the two lateral subcentrals and < 1/2 the length of the main central spine; flowers yellow .... **Corynopuntia schottii**

1. Joints firmly attached.

    3. Joint length usually exceeding 9 cm; central spines (medial and abaxial) flat, uppers often terete, with all spines tan-brown (no white) and evenly colored along the entire length of the spine; spine bases (centrals only) not bulbous nor differently colored than the rest of the spine; one main central spine (longest, broadest); subcentrals present, three, of generally equal length; near Candelaria or Porvenir in extreme southwestern Presidio County, Texas .... **Corynopuntia emoryi**

    3. Joint length usually less than 9 cm; central spines flattened and variously colored (including white, especially distally); spine bases (all) bulbous and differently colored than the rest of the spine; no clear dominant central spine; subcentrals absent; in southern Brewster and Presidio counties.

        4. Habit a well-defined, contiguous to patchy mound of tightly-associated stems; joints clavate and erect-oriented, growing from mostly lateral areoles; central spines 1-4(-7); primary radial spine pair (the most abaxial) less than half the length of central spines; roots conic-fusiform tuber(s) .... **Corynopuntia aggeria**

        4. Habit an open, sprawling mound of loosely-aggregated stems; joints clavate (often slightly J-shaped) and erect-oriented to sprawling in chains, growing from lateral areoles; central spines 7-11+; primary radial spine pair (the most abaxial) greater than half the length of the central spines; roots diffuse/adventitious, usually with a long, thickened, distally tapering tap root .... **Corynopuntia densispina**
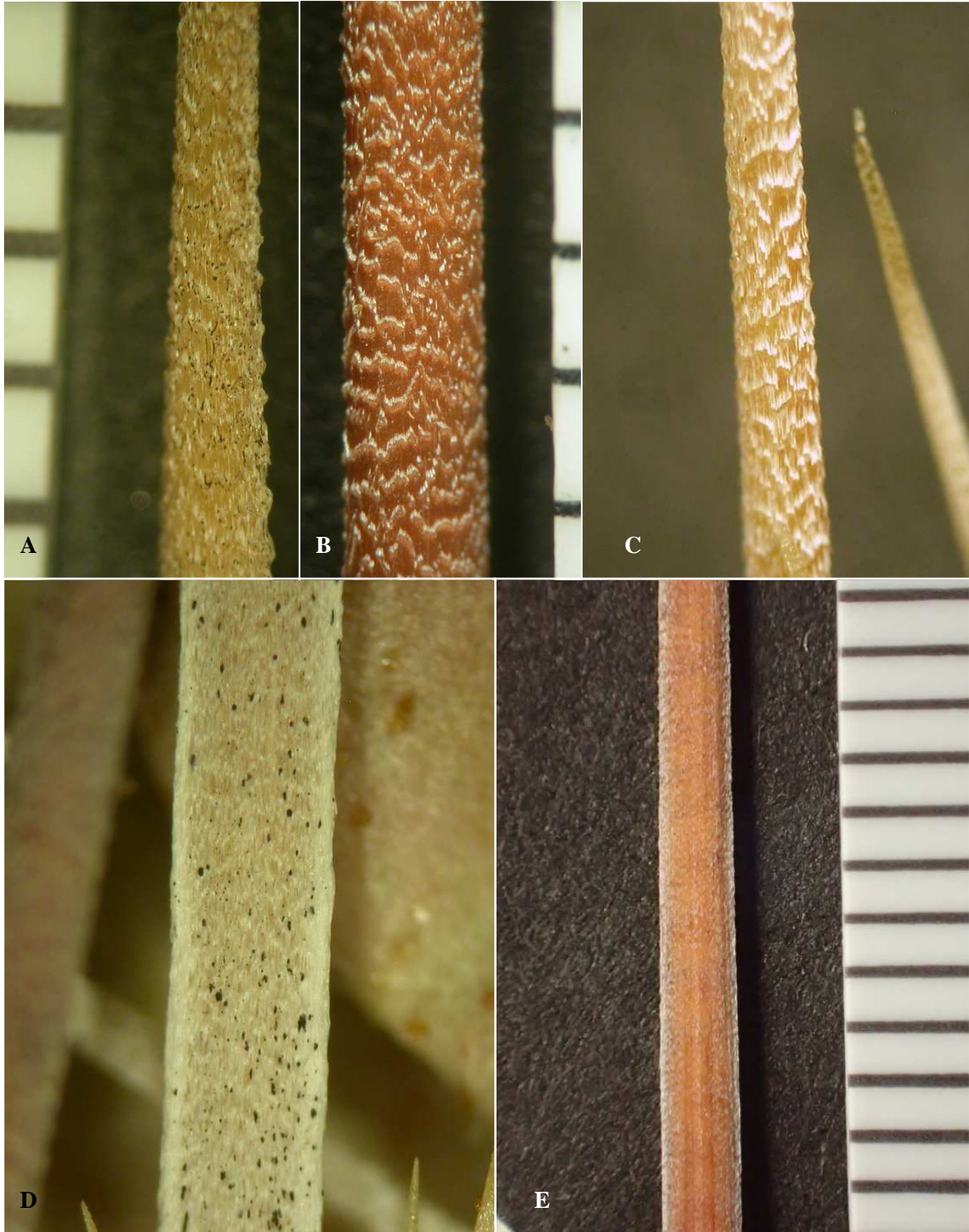
Figure 13. Central spine epidermal characters of Big Bend *Corynopuntia*. A-B) Ridged surfaces of *C. emoryi*. C) Ridged surface of *C. grahamii.* D) Farinose surface of *C. aggeria.* E) Smooth, longitudinally striate surface of *C. schottii*.

HERBARIUM KEY TO BIG BEND *CORYNOPUNTIA*

1. Joints ovate; central spines terete, less than 1 mm wide, numbering no less than 4, colored mauve, peach, or darker red, with saturated tone (no white) and with bulbous, iridescent bases; radial spines (4–)6 or more, terete, white, bulbous iridescent bases .... **Corynopuntia grahamii**
1. Joints clavate; central spines flattened, greater than or equal to 1 mm wide, of various numbers and colors; radial spines generally 2–4, flattened, white to tan, bases bulbous/iridescent or not.

   2. Central and radial spines the same color (tan-brown) and saturated, containing no white (rarely with lighter-colored margins in largest central spines) .... **Corynopuntia emoryi**
   2. Central spines variously colored but all with at least some white/gray in the most mature clusters; radial spines white or significantly lighter in color than central spines.

      3. Central spines tan, copper, or dark red-brown, and saturated, the only white being at the extreme margins of most mature central spines; diminutive lower central spine present; radial spines lighter in color than central spines .... **Corynopuntia schottii**
      3. Central spines colored variously but containing some white in addition to or other than along spine margins; diminutive lower central spine absent; radial spines white.

         4. First radial pair greater than or equal to half the length of lower central spines; central spines 7–11+; roots diffuse perhaps with one thickened, distally-tapering taproot ....**Corynopuntia densispina**
         4. First radial pair less than half the length of the central spines; central spines 1–4(-6–7); roots conic-fusiform tuber(s) .... **Corynopuntia aggeria**

TAXONOMIC TREATMENTS

CORYNOPUNTIA AGGERIA (Ralston and Hilsenb.) M.P. Griff., Haseltonia 9: 91. 2002. *Opuntia aggeria* Ralston & Hilsenb., Madroño 36: 226. 1989. *Grusonia aggeria* (Ralston & Hilsenb.) E.F. Anderson, Cact. Succ. J. (Los Angeles) 71: 324. 1999. **TYPE**: **USA**. **Texas**. Brewster Co.: Big Bend National Park, Tornillo Flats, 2800 ft., Jul 1948, *M.S. Anthony 856* (holotype: MICH!). AGGLOMERATED CLUB CHOLLA. Figs. 14-15.

Plants of *Corynopuntia aggeria* are most abundantly found in upper Cretaceous, gypsiferous and/or clay-containing limestone soils on gravelly alluvial slopes and hummocks. *Corynopuntia aggeria* is commonly found in mixed or closely associated populations of *C. grahamii* as well as sympatrically with *C. densispina* (Fig. 3; B), although *C. aggeria* appears to occur in slightly more elevated locations than *C. densispina*. *Corynopuntia aggeria* is consistently diploid despite wide morphologic variation, especially in spine color, abundance, and form, within and between populations.

In addition to chromosome number, *Corynopuntia aggeria* is distinguished from other species by the following: (1) habit of discrete, cushion-like mounds, (2) taproots conic-fusiform-tuberous, from which may emerge a few fibrous-tuberous roots, all with a shedding papery-cork epidermal layer, (3) stems ascending, without clear above-ground central point of growth, (4) joints clavate, laterally-growing, firmly-attached, tightly-associated, (5) central spines flat adaxially and angled abaxially, containing white coloration especially distally, (6) radial spines four or less and relatively short, and (7) filaments red/pink (recorded as green in Ralston & Hilsenbeck 1989, though original type description stated red, Anthony 1956). The pericarpelar areoles *C. aggeria* are less dense, have fewer glochids, and have fewer bristle spines on the pericarpel rim than the often co-occurring *C. grahamii*. Also, *C. aggeria* is earlier to bud and flower than *C. grahamii* and *C. densispina*, although their flowering seasons do overlap.
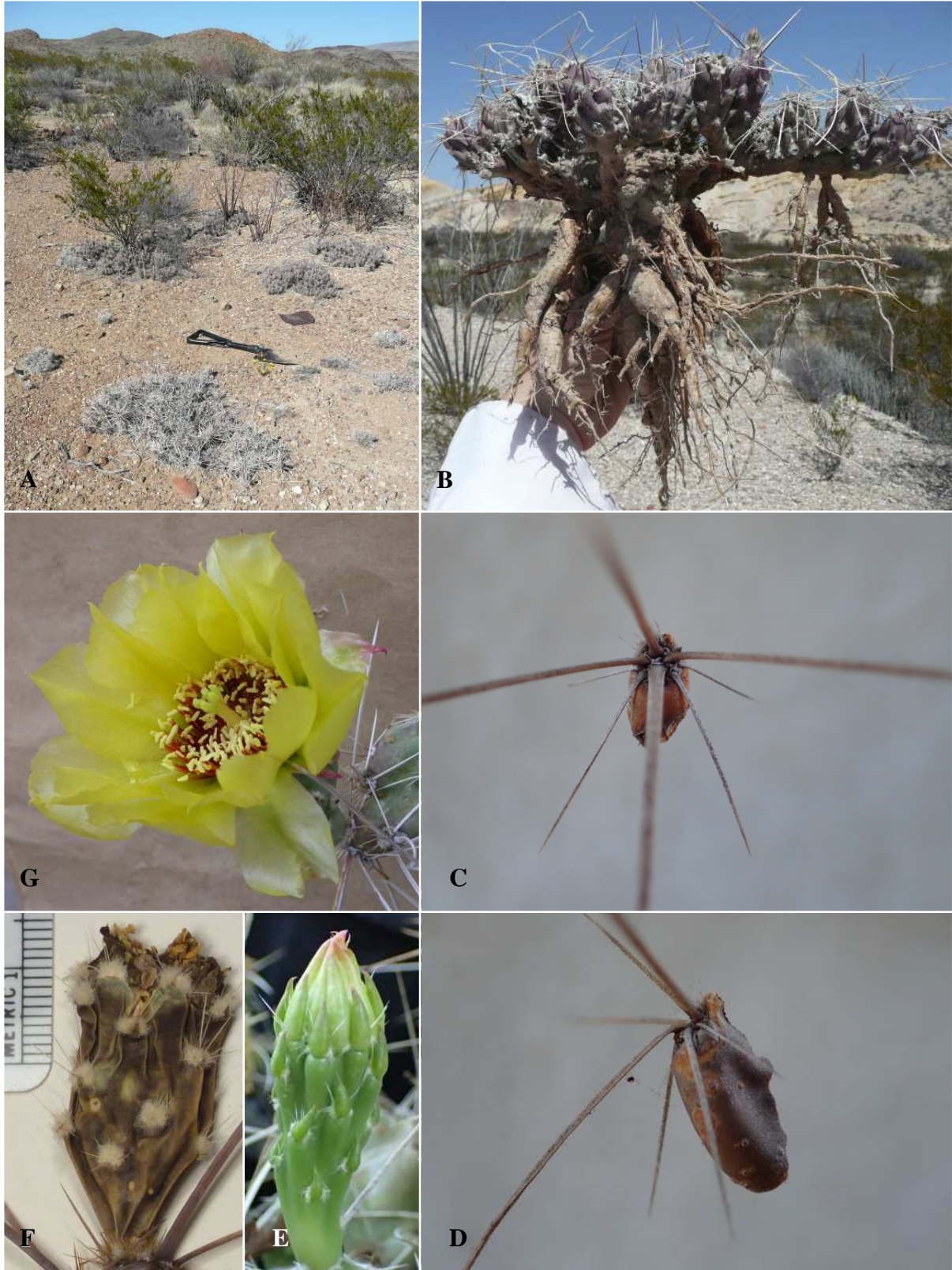
Figure 14. *Corynopuntia aggeria.* Clockwise from top left. A. Habitat. B. Root and joint habit. C. Spine cluster, front view. D. Spine cluster, profile view. E. Bud. F. Fruit. G. Flower.

Figure 15. *Corynopuntia aggeria* morphotypes. A. Dense. B. Decurved. C. Boquillas. D. Gochidiate. E-F. Sparse.

Several basic morphotypes of *Corynopuntia aggeria* are common in its populations (Fig. 15), generally graded by robustness of joints and central spine number/character. One population along the Boquillas Canyon road in Big Bend National Park, in addition to including basic morphotypes, also contained diploid individuals with elongated clavate-cylindric joints, long thin spines, and roots apparently all thickened-fibrous, i.e., no clearly tuberous taproot (e.g., *JF 1563, 2344, 2345*). One herbarium specimen matching many characteristics of *C. aggeria* (clavate joints, few spines, red filaments) has been collected approximately 161 kilometers east of El Paso, which appears to be just west of Van Horn (*Neuman s.n.* DES); attempts to relocate this population have been unsuccessful and because the locality is significantly outside the known range for the species, a confident identification is difficult without root or joint attachment information.

CORYNOPUNTIA DENSISPINA (Ralston & Hilsenb.) J. Fenstermacher, **comb. nov.** *Opuntia densispina* Ralston & Hilsenb., Madroño 39: 281, fig.1. 1992. *Grusonia densispina* (Ralston & Hilsenb.) Pinkava, J. Arizona-Nevada Acad. Sci. 34: 45. 2002. **TYPE**: **USA**. **Texas**. Brewster Co.: Big Bend National Park, on River Road ca. 5.3 mi E of Mariscal Mine [erroneously recorded as Solis Ranch in the original description] near Solis junction, May 1989, *B.E. Ralston 200* (holotype: SRSC!; isotype: SRSC!, TEX). DENSELY-SPINED CLUB CHOLLA. Fig. 16.

Previously known only from the isolated type locality with its low-lying, extremely clay-rich soils, new populations were found during this study that expand the known range by ca. 26 kilometers and the habitat to include low-lying, gravelly, fine-sandy loam as well as higher, tighter, rockier limestone. *Corynopuntia densispina*, in all known populations, occurs sympatrically with *C. aggeria* (Fig. 3; B) but *C. densispina* is more abundant in lower-lying areas with high clay content.

Corynopuntia densispina is consistently tetraploid across its range, and is additionally distinguished from other species by 1) habit of loosely-aggregated, sprawling mounds, 2) roots consisting of one long, slender, tapering taproot with many straggly, diffuse roots adventitiously growing from lateral stems, all roots with a shedding papery-cork epidermal layer, 3) stems ascending-to-prostrate without a clear above-ground central point of origin, 4) joints clavate, laterally-growing, firmly attached, robust, 5) central spines ≥7, flat adaxially, angled abaxially, 6) primary radial spines relatively long, and 7) filaments red, pink, or green. At a distance, sunlight reflection from some mounds of *C. densispina* appears as a silvery sheen due to the higher number of relatively thin and long, grey- to straw-colored central spines. This can help distinguish *C. densispina* from mounds of nearby *C. aggeria* in some locations. The morphologic similarity of the tetraploid *C. densispina* to the denser-spined, more robust morphotype of the diploid *C. aggeria*, along with their contiguous distributions (and often ecologic segregation) across several populations, suggest that *C. densispina* is an autopolyploid derived from *C. aggeria*.

CORYNOPUNTIA EMORYI (Engelm.) M.P. Griff., Haseltonia 9: 91. 2002. *Opuntia emoryi* Engelm., Proc. Amer. Acad. Arts 3: 303. 1857. *Grusonia emoryi* (Engelm.) Pinkava, J. Arizona-Nevada Acad. Sci. 32: 50. 1999. *Opuntia stanlyi* Engelm. ex B.G. Jacks., Notes of a Military Reconnaissance, 7. 1848. *Grusonia stanlyi* (Engelm. ex B.D. Jacks.) H. Rob., Phytologia 26: 176. 1973. *Corynopuntia stanlyi* (Engelm. ex B.D. Jacks.) F.M. Knuth, Kaktus ABC, 114. 1936. **LECTOTYPE** (Bárcenas et al. 2012): **MEXICO**. **Chihuahua**. Arid soil south and west of El Paso, especially between the Sand hills and Lake Santa Maria, *J.M. Bigelow s.n.* (MO! sheet 178185; isolectotype: NY). Other original materials: *Engelmann s.n.*, MO; *Parry+ s.n.*, NY!; *Wright s.n.,* MO). DEVIL CLUB CHOLLA. Fig. 17.

Corynopuntia emoryi has a limited range in the western Big Bend, occurring in rocky, silty-sandy soils near the Rio Grande communities of Porvenir and Candelaria in Presidio County. It is highly likely that *C. grahamii* occurs sympatrically with *C. emoryi*, based on distribution both
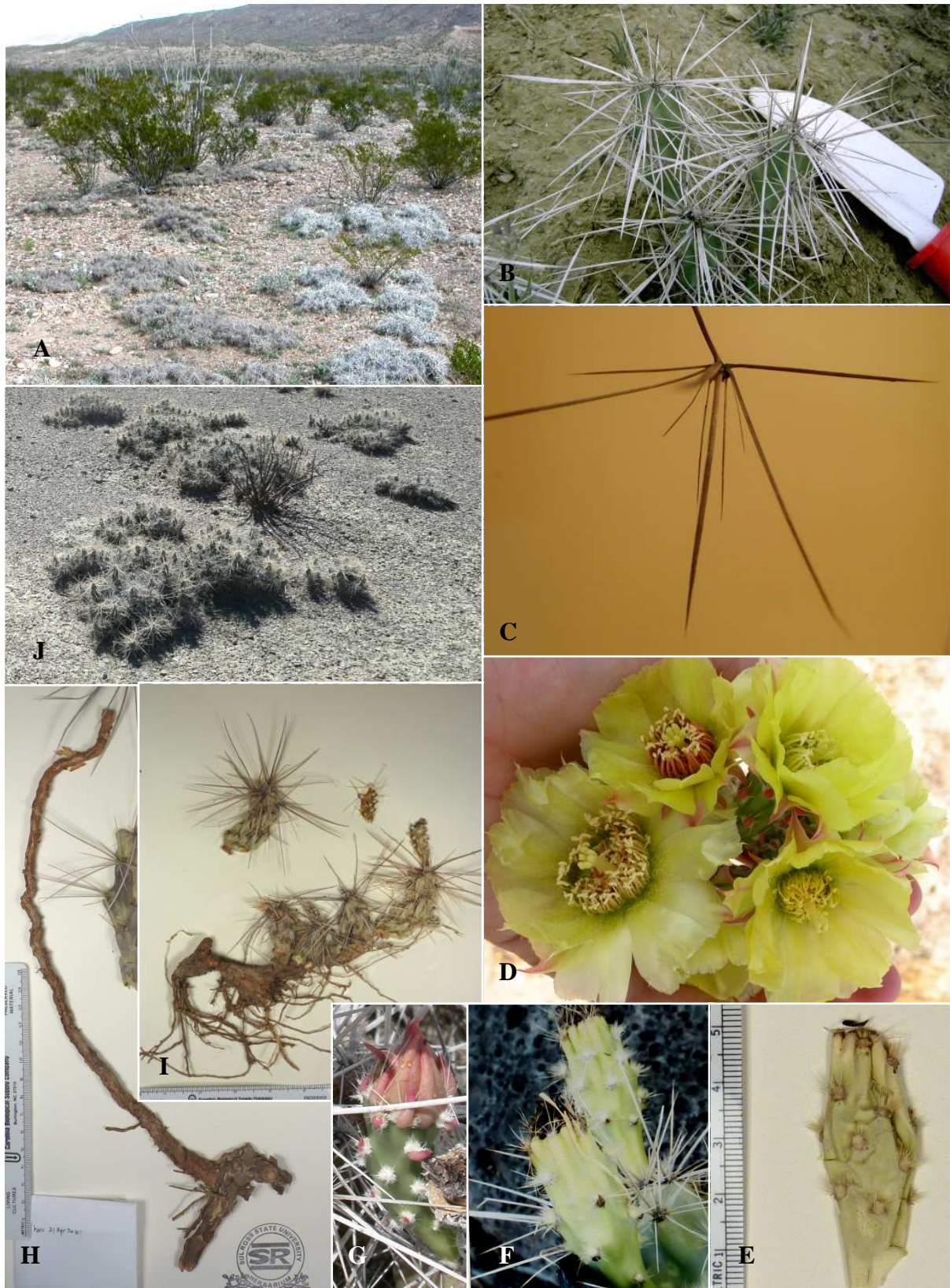
Figure 16. *Corynopuntia densispina.* Clockwise from top left. A. Mound habit. B. Joints. C. Spine cluster.
D. Flowers. E-F. Fruit. G. Bud. H-I. Roots. J. Mound habit.

Figure 17. *Corynopuntia emoryi* from Candelaria, Texas, population. Clockwise from top left. A. Habitat and habit. B. Joint habit. C. Spine cluster. D. Bud. E. Fruits. F-G. Flowers. H. Roots.

downriver and upriver from the *C. emoryi* populations (Fig. 3; A), but this is not yet scientifically documented.

Distinguishing characteristics of *Corynopuntia emoryi* include (1) habit of open clumps to mats, (2) roots diffuse, filiform, adventitious, and generally of a fragile or delicate nature lacking a papery-cork epidermal layer, (3) stems erect, in larger mats without clear above-ground central point of origin; 4) joints clavate, laterally-growing, firmly-attached, long, robust, (5) central spines flattened (not angled abaxially), shorter/sparser relative to joint size in comparison with other Big Bend species, one main central spine and three smaller subcentrals, all evenly colored tan with no white, (6) radial spines essentially equal in color to central spines, and (7) filaments green. Specimens of Big Bend area plants are less robust and spiniferous in comparison to material of the same species from Arizona and New Mexico. While not typically confused with other CSC species, one specimen (consisting of two individual joints) had been to that point misidentified as *C. schottii* (*BER 112*).

CORYNOPUNTIA GRAHAMII (Engelm.) F.M. Knuth, Kaktus ABC, 116. 1935. *Opuntia grahamii* Engelm., Proc. Amer. Acad. Arts 3: 304. 1857. *Opuntia schottii* var. *grahamii* (Engelm.) L.D. Benson, Cact. Succ. J. (Los Angeles) 41: 124. 1969. *Grusonia grahamii* (Engelm.) H. Rob, Phytologia 26: 176. 1973. **LECTOTYPE** (Bárcenas et al. 2012): **USA**. **Texas**. [El Paso Co.]: Sandy soil in the bottom of the Rio Grande, near El Paso, and for a distance of about 100 miles along the river, 1851, *C. Wright 10* (MO sheet 2015356!; epitype: *Palmer 386* MO sheet 2511550; isoepitypes: K, NY, US; other material: *Wright s.n.* GH!). GRAHAM'S CLUB CHOLLA. Figs. 18-19.

Corynopuntia grahamii occurs in sandy to rocky limestone soils across its range and often in soils with some clay content in the central/southern Big Bend region. Populations of *C. grahamii* in Brewster and Presidio counties are frequently mixed with or closely associated with *C. aggeria* (Fig. 3; B). *Corynopuntia grahamii* is marginally associated with *C. densispina* in a limited area of southern Brewster County. *Corynopuntia grahamii* and *C. schottii* appear to be sympatric in eastern Brewster County (*MSA 977, 981* MICH); both species are sympatric with *C. aggeria* in Mexico near Cuatro Cienegas, nearly 325 km directly south from the area of sympatry in eastern Brewster County (*DJP 5279, 5714; MAB 12817* ASC). Plants of *C. grahamii* across their geographic range are consistently tetraploid and exhibit a high percentage of sterility (e.g., *JF 694*, *2342, 2352*; Appx. A, C).

Plants of *Corynopuntia grahamii* with typical morphology, i.e., individuals similar to those found near the type locality, are readily distinguished from other species by (1) habit of open clumps to small mounds, (2) roots of conic-fusiform tubers with shedding papery-cork epidermal layer, (3) stems erect-ascending, emanating from a clear, above-ground central core of the plant, (4) joints ovate, apically-chaining, readily-disarticulating, openly-associated, (5) central spines terete, with iridescent bulbous bases, colored pink to red-brown, saturated with no white, (6) radial spines six or more, terete, white, and with differently-colored bulbous bases, and (7) filaments green.

In *Corynopuntia grahamii*, the higher number of central and radial spines combined with generally smaller joints can give the plants a particularly bristly appearance making it difficult to see the epidermal surface of joints. Flowers are usually yellow; rose to salmon-pink tepals are an uncommon but consistent feature in populations across the range. During the spring season, new joint growth in *C. grahamii* develops at the same time as buds are produced in populations of *C. aggeria*; in mixed populations the phenologic stages can be an additional identification aid.

Corynopuntia grahamii in the Big Bend region are often more robust than the typical morphology found near the type locality (Fig. 19). Robust Big Bend *C. grahamii* have central spines — terete to flattened above and angled below — that are often white-streaked and/or with deeper red

Figure 18. *Corynopuntia grahamii*. Clockwise from top left. A. Habitat and habit; note apically-chaining, erect stems. B. Roots and joint shape. C. Spine cluster. D. Bud. E. Typical bloom with yellow tepals. F. Occasional pink-tepal bloom. G. Stem/joint habit of robust Big Bend form; note fewer central spines and radials but consistent apical chain and globose joint shape.
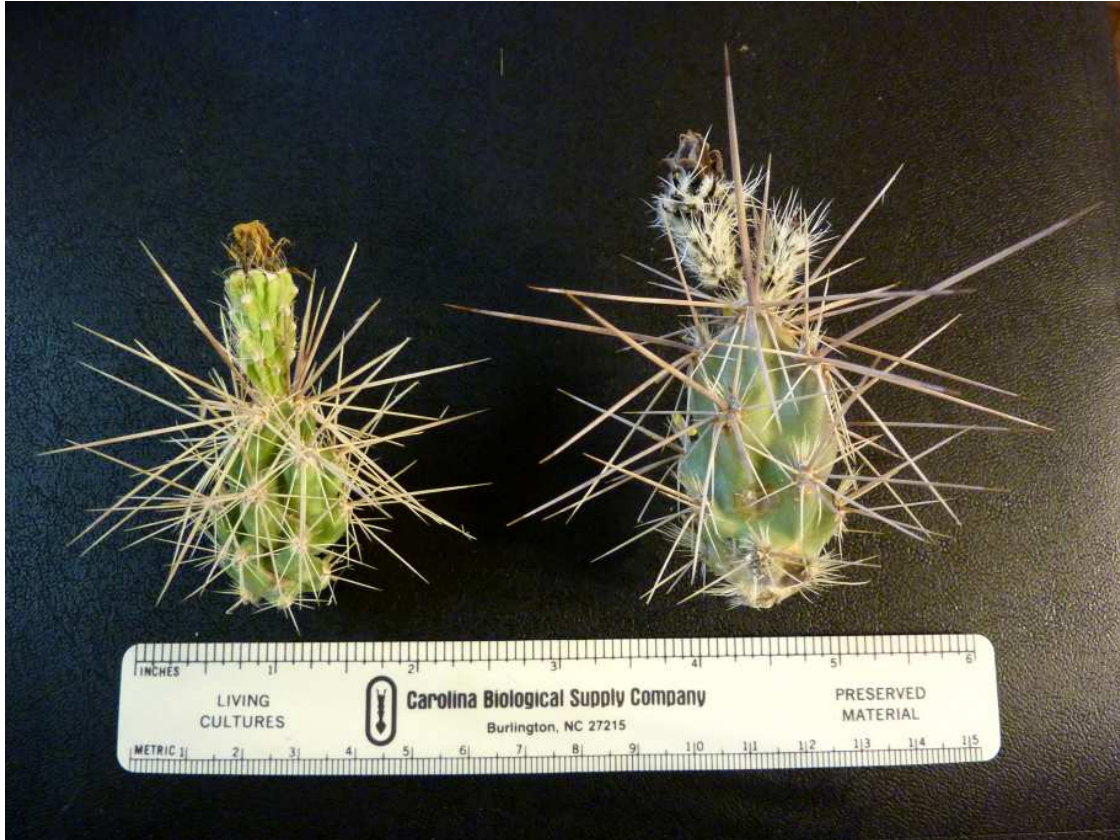
Figure 19. Morphologic comparison between western *Corynopuntia grahamii* (left) and Big Bend area (right) plants. Note smaller joint size, denser tubercles, higher spine number of the western morph and the increased glochids, fewer radial spines, and more robust habit of the Big Bend morph.

coloration as opposed to the saturated, paler mauve/peach-pink color consistently seen in western populations. Most Big Bend *C. grahamii* also tend to have fewer spines ($\leq$ 6 centrals, $\leq$ 4 radials), may show more growth from lateral areoles, and may exhibit some atypical clavate joint morphology, while maintaining ease of disarticulation, tuberous roots, apically-chaining obovate joints, and tetraploid chromosome number (e.g. *JF 2415*, *AMP 6152*). Two *C. grahamii*-like collections (*JF 2325, JF 1558/MAB 17814*) were documented as tetraploids and have typical robust morphologies as seen in the Big Bend region, but roots were scraggly and diffuse, not containing any tubers. The typical morphology of smaller joints and more numerous spines can be found in the Big Bend — it is just not as widespread as the robust morph.

CORYNOPUNTIA SCHOTTII (Engelm.) F.M. Knuth, Kaktus ABC, 114. 1935. *Opuntia schottii* Engelm., Proc. Amer. Acad. Arts 3: 304. 1857. *Grusonia schottii* (Engelm.) H. Rob., Phytologia 26: 176. 1973. **LECTOTYPE** (Benson 1982): **USA**. **Texas**. [Val Verde Co.:] Arid hills near the Rio Grande, between the San Pedro and Pecos rivers, 1853, *A. Schott s.n.* (MO sheet 2015355!; isotype: NY sheet 00688043!; other original material: *Schott 80*, F!; *Schott s.n.*, NY sheet 00688042! (> *C. grahamii*); *Schott s.n.*, NY sheet 00688042!; *Wright 227*, MO). CLAVELLINA. Fig. 20.

Corynopuntia schottii occurs most abundantly in deeper, loamy-silty soils, although it can also be found in rockier locations with shallower soils. The only co-occurring species is the marginally sympatric *C. grahamii*, occurring at the extreme western extent of the *C. schottii* range both in the
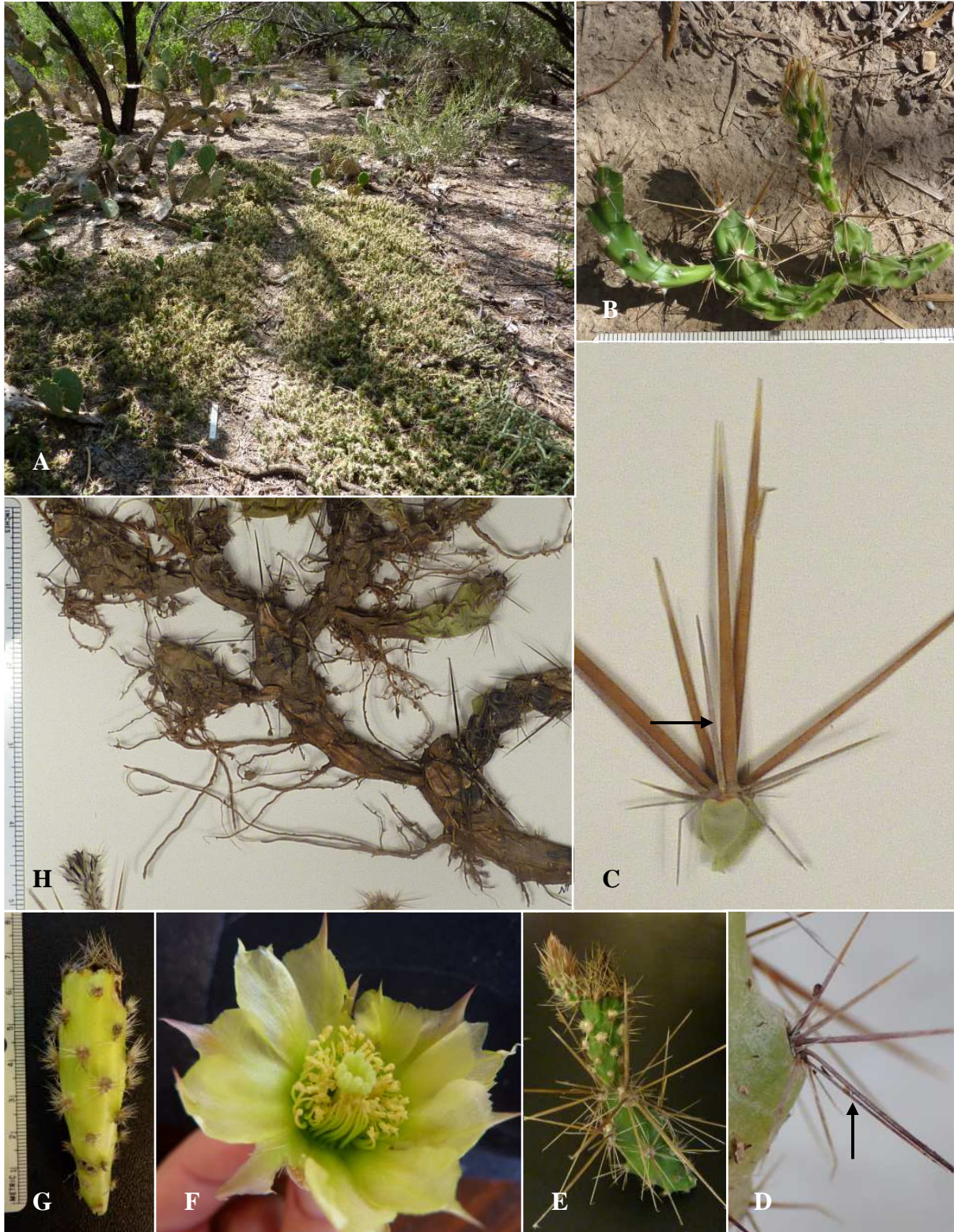
Figure 20. *Corynopuntia schottii*. A. Habitat and habit (south Texas). B. Stem habit; note bud origin on medial joint. C. Spine cluster; arrow indicates diminutive subcentral; note origination at base of larger, main central. D. Spine cluster, profile; arrow highlights tight association of diminutive subcentral and adaxial central spine. E. Bud proliferation. F. Flower. G. Ripe fruit. H. Root habit.

USA (Fig. 3; B) and Mexico, although *C. aggeria* was collected within 10 km of a *C. schottii* population at Cuatro Cienegas, Mexico (*DJP 5714; MAB 12817* ASC). Plants of *C. schottii* are hexaploid at both the eastern and western USA extents of its range.

Aside from chromosome number, *Corynopuntia schottii* is quickly distinguished from other species by (1) a habit of ground-hugging stems that can form dense, extensive mats, (2) roots diffuse, filiform, adventitious, generally more fragile or delicate without shedding papery-cork epidermal layer, (3) stems prostrate and creeping, developing into mats without an obviously central, above-ground origin, (4) joints clavate or J-shaped, laterally-chaining, readily-disarticulating, (5) central spines flat/angled abaxially, colored copper/red/dark-brown with many mature spines having white margins and abruptly narrowing at the barbed tips, medial subcentral central spine diminutive and lighter in color than other central spines, (6) radial spines lighter in color than centrals, and (7) filaments green. When compared side-by-side, typical stems of *C. schottii* and *C. grahamii* are truly distinctive based on the above listed characters (Fig. 21).

Figure 21. Joint comparison between *Corynopuntia schottii* (left) and *C. grahamii* (right). Note in *C. schottii*: (1) clavate/J-shaped joint, (2) broad, ill-defined tubercles, (3) relatively long, copper-colored, erect main central spines in the top third of stem areoles, (4) descending subcentral spines, (5) few radials, (6) few glochids, (7) abundant, persistent spine sheaths, and (8) abundant bristle spines at the pericarpel rim. This contrasts with *C. grahamii*: (1) ovate/globose joint shape, (2) laterally-compressed, inflated tubercles, (3) thinner (terete) peach-colored, central spines in at least the top half of stem areoles, (4) lack of subcentral spines, (5) numerous radial spines, (6) abundant glochids, (7) fewer and less obvious persistent spine sheaths, and (8) fewer pericarpel-rim bristle spines.

Additional distinct characters apart from all other species of the CSC include (1) stem tubercles commonly appearing deflated when dry (Fig. 6; B), with flattened abaxial profiles and not laterally compressed when turgid, (2) flower buds appearing on joints two or three more basal than the terminal joint of a stem as opposed to the four other species where buds appear on only terminal joints, buds also commonly proliferating from pericarpelar areoles (not documented in the other CSC species), and (3) pericarpal rim areoles having longer conic leaves and more bristle spines than in the other four species. The fruits of *Corynopuntia schottii* are similar to those of *C. emoryi* (and differ from *C. aggeria*, *C. densispina*, and *C. grahamii*) in that they turn yellow when mature, are more elongate-fusiform shaped, less tuberculate, and have globose areoles with radiating glochids. However, as noted in Powell and Weedin (2004), unlike in *C. emoryi*, mature fruits of *C. schottii* persist on the plants often into the next reproductive season.

Some *Corynopuntia schottii* plants collected in the western part of its range (e.g., Terrell Co., *AMP 6248, BER 107, JF 2406, Lee 30*; Val Verde Co., *JF 2404*) show slightly modified stem and root morphology from the more typical traits encountered in south Texas. Modified traits of the western plants include (1) roots of smaller, clumpy plants slightly thickened and centralized, neither tuberous nor filiform, (2) both ovate and clavate/J-shaped joints, and (3) joints with inflated tubercles and joints with deflated tubercles occurring in the same individual.

Putative hybrids (see map, Fig. 22)

Corynopuntia aggeria ✕ *C. grahamii*

Putative hybrids between *Corynopuntia aggeria* and *C. grahamii* were found in numerous locations across the southern Big Bend area (Fig. 22) and several proved to be sterile, i.e., either producing malformed meiocytes, or meiocytes entirely lacking, (e.g., *JF 2334a, 2341a, 2341b, 2359, 2368b*). One putative hybrid of *C. aggeria* and *C. grahamii* was triploid (*JF 2334*). The putative *C. aggeria* ✕ *C. grahamii* hybrids do not seem to fit one consistent morphologic profile; instead each individual displays varying degrees of parental traits. For example, one individual encountered (*JF 697*) has clavate, laterally-growing joints that easily disarticulate plus terete, dark-red central spines; another (*JF 2353b*) has ovate, robust joints that grow both laterally and apically, sometimes disarticulating with more effort than is typical for *C. grahamii*, with 3 or 4 short flat stout white central spines and only one pair of radials, and perhaps even pink tepals and red filaments. Frequently the tuberous roots of putative hybrids of *C. aggeria* and *C. grahamii* appear to be more slender than typical of either parent species. Flowers with red filaments and abundant pollen, as well as flowers with green filaments lacking pollen are both found in putative hybrids. Near the Maverick Road in BBNP and in the Cedar Springs area of Terlingua Ranch, plants with red-filamented flowers had fruits that seemed to lack developing seeds, while plants with green-filamented flowers had maturing fruits with well-formed seeds. Red filaments also appear to be associated with more robust plants that have fewer overall spines, whereas green filaments seem to be associated with smaller-sized joints.

Corynopuntia aggeria ✕ *C. densispina*

One chromosome-documented putative hybrid from the Ernst Tinaja area, BBNP (i.e., n=14-16; *JF 635*), demonstrates the following mixed traits: (1) 4–6 central spines broader than *Corynopuntia densispina* and similar to some robust *C. aggeria* morphotypes, (2) primary radial spines longer than in *C. aggeria* but shorter than typical in *C. densispina*, (3) tuberous roots, (4) unusually abundant glochids at the apex of terminal joints, and (5) bud production much earlier than in surrounding *C. densispina*. Early bud production was how this putative hybrid individual was initially noticed. Other putative hybrid vouchers (*JF 702, 703*) were made from a mixed population of *C. densispina* and *C. aggeria* in the Solis area, BBNP, with various buds yielding chromosome formations that suggested triploidy and tetraploidy with multivalents.
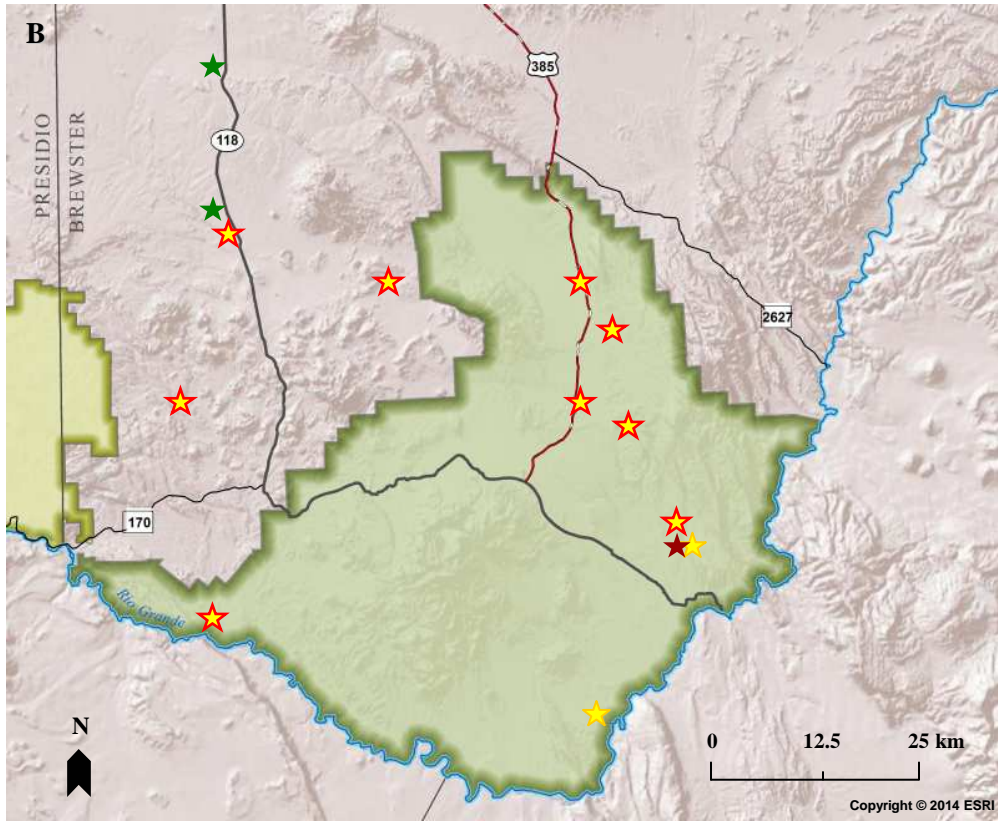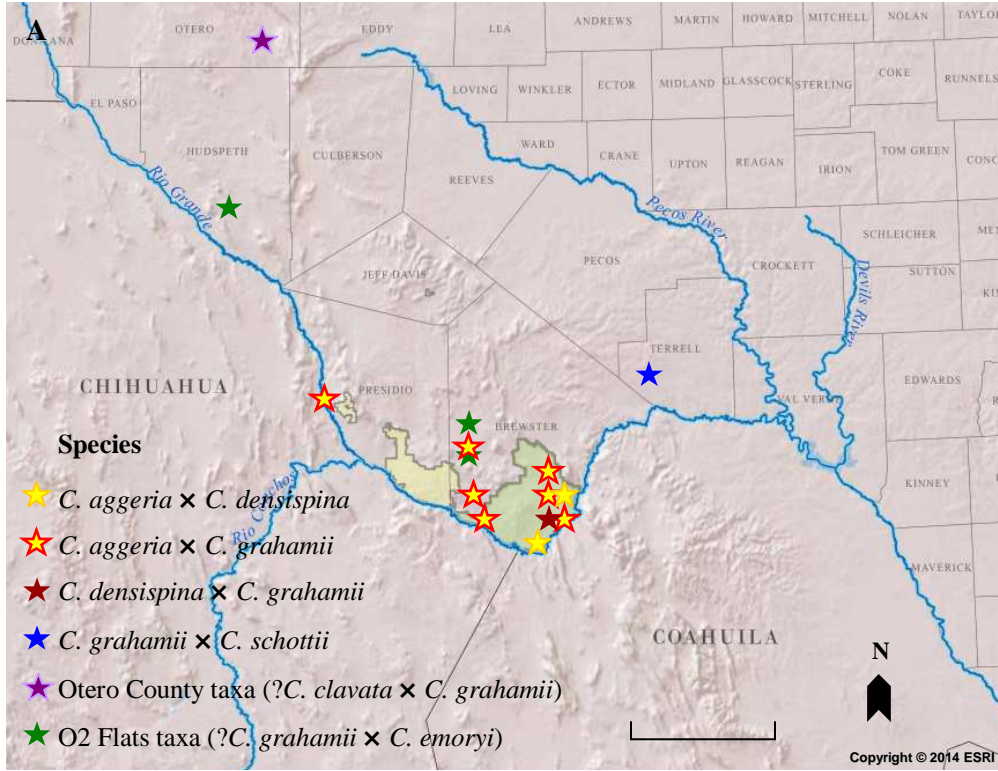
Figure 22. Hybrid voucher collections of *Corynopuntia schottii* complex species. A. Texas, adjacent New Mexico, adjacent Mexico. B. Big Bend National Park, Texas, and environs.

Corynopuntia densispina ✕ *C. grahamii*

Individuals were collected from two different locations within 1 km of each other (*JF 2355, 2390, 2391*); both locations were also in the vicinity of populations of both parent species. Putative hybrids of *Corynopuntia densispina* and *C. grahamii* stood out as clearly distinct, in comparison to the surrounding plants (individuals of *C. densispina*), by virtue of the following mixed traits: 1) thickened taproots as well as abundant, straggly, diffuse roots, 2) robust joints, both clavate and ovoid shaped, with most growing apically and disarticulating relatively easily, 3) long, flat, white (one individual with terete and mauve) central spines, 4) relatively long 1° radial pairs, 5) protruding basal areoles with radiating glochids, 5) striking fuchsia-pink flowers (*JF 2391*).

Corynopuntia grahamii ✕ *C. schottii*

The collection made in Terrell County, Texas (*JF s.n.*) is within the range expected for *Corynopuntia schottii* (Fig. 1 B) and slightly further east than expected for *C. grahamii*. The voucher displays mixed morphologic characters. Traits reminiscent of *C. grahamii* include (1) ascending, apically-chaining stem habit, (2) ovate joint shape, (3) inflated tubercles, and (4) terete central spines. Traits reminiscent of *C. schottii* include (1) diffuse roots, (2) lateral growth, (3) flat, deep-red-colored central spines, (4) diminutive subcentral spines, and (5) bud proliferation. The one bud collected for chromosomal analysis was meiotically sterile.

Unidentified populations of *Corynopuntia* in the Big Bend region (see map, Fig. 22)

Brewster and Hudspeth counties, Texas

Several specimens collected Brewster County, in Green Valley ("O2 Flats," ca. 42 miles south of Alpine), do not fit the profile of any one CSC species but rather a mixture of traits attributable to four of the CSC species: *Corynopuntia aggeria*, *C. grahamii*, *C. emoryi*, and *C. schottii*. Two recent collections (*CJ 285, 310*) align most closely with *C. grahamii* in their (1) cylindric joints, (2) thin, terete, papillate, saturated-peach central spines, (3) multiple radials, and (4) bulbous/iridescent spine bases. However *CJ 285* and *310* also exhibit subcentral spines (as in *C. emoryi* and *C. schottii*) as well as diffuse roots (as in *C. emoryi* and *C. schottii*), tightly attached stems (as in *C. aggeria*, *C. emoryi*), and some lateral growth (as in *C. aggeria*, *C. emoryi*, *C. schottii*).

An additional recent collection in the same area (*CJ 364*, Fig. 23) includes mixed characters suggesting *Corynopuntia aggeria*, *C. grahamii*, and *C. emoryi*: (1) thick, clavate-cylindric joints, (2) large tubercles similar to *C. emoryi*, (3) wide, flat areoles with short, felt-like wool as in *C. emoryi* or *C. schottii*, (4) central spines of varying shapes/aspects including (a) flat, erect, and robust like *C. schottii*, (b) some areoles with upper centrals terete and one main, flat lower central like in *C. emoryi*, and (c) some central spines streaked with white like in *C. aggeria*, but with most colored a saturated dark red-brown seen in *C. grahamii* and *C. schottii*, and (5) numerous radials like in *C. grahamii*. The collection *CJ 364* also exhibits a novel trait as yet unobserved in CSC species: at least five subcentral spines — one medial subcentral and two pairs of lateral subcentrals — which is more than the one pair of lateral subcentral spines known in *C. emoryi* and *C. schottii*. The position of these additional subcentrals are analogous to the pattern of 1° and 2° pairs of radial spines (Fig. 9) but are clearly situated in an intermediate aspect overlying the surrounding radials yet underneath the main central spines (Fig. 23 C).

Historic collections from the O2 flats (*MSA 1174, 1304* MICH) similarly show affinity to multiple CSC species, mostly strikingly in that some central spines have white margins as seen in *Corynopuntia schottii*, and in that the radial spines have bulbous and iridescent bases as in *C. grahamii* (despite their flattened, not terete, shape). Also present in *MSA 1174* and *1304* are decurved main central spines and central spines streaked with white, thus far known only in *C. aggeria*/*C. densispina*. A similar mixed-character specimen from Hudspeth County, south of Sierra Blanca (*KHS 4123* UNM), sharing characters from what could be considered the "*C. schottii*/*C. emoryi* cohort"

Figure 23. Unidentified *Corynopuntia* from the O2 flats, Brewster County, Texas (*CJ 364*). A–B) Habit. C) Spine cluster; arrows indicate the relatively robust yet still diminutive subcentral spine, plus 1° and 2° subcentrals. The position of these subcentrals is clearly intermediate, overlaying the white, thin radial spines and underneath the thicker, more robust main central spines.

(one flat lower central spine, terete uppers, subcentral spines) as well as the "*C. grahamii*/*C. aggeria* cohort" (protruding basal areoles, saturated-papillate, terete, upper centrals with bulbous iridescent bases, abundant glochids).

Otero County, New Mexico

A second unidentified *Corynopuntia* population consists of several collections from southeastern Otero County, NM (*GW 3809A, 3809B, 3811, 3843, s.n./UNM 67866, s.n./UNM 86335* UNM). These collections have characters known from *C. clavata* in addition to some of the CSC species (Fig. 24). Diffuse roots, robust habit, laterally chaining clavate stems, and kinked or twisted radials suggest *C. densispina* or *C. aggeria*. Additional characters suggest *C. clavata*, known from northern Otero County, and *C. grahamii,* known from SW Otero County (e.g., *GW 3829* UNM), and possibly *C. schottii*. The specimens do not consistently exhibit the exact same morphology but generally the *C. clavata* characters include (1) diffuse roots, (2) laterally chaining, robust, short-clavate joints, (3) robust, numerous, flat/broad, longitudinally striate, whitish central spines with only one main central spine being the widest and whitest, (4) robust radial spines, and (5) long, robust glochids. Characters suggesting *C. grahamii* include (1) protruding basal areoles, (2) saturated, peach-colored central spines, (3) terete, upper central spines with bulbous iridescent bases, and (4) numerous radial spines. Characters that could be considered *C. schottii* traits include strongly J-shaped clavate joints and central spines that abruptly narrow at the tips, though these traits are also seen in *C. clavata*.

DISCUSSION

The current study significantly expands the breadth and depth of all CSC species concepts, and helps resolve the persistent confusion between the CSC species. Perceptions of widespread intermediacy, genetically-mediated variability, and poor/incomplete/limited study specimens all contributed to the historic lack of clarity. The variation in characters that was once attributed to widespread hybridization between *Corynopuntia grahamii* and *C. schottii* was provisionally explained by the discovery of a separate species, *C. aggeria*, and is now well documented through broadly based field observations and vouchered chromosome counts. *Corynopuntia aggeria* is a distinct, consistently diploid species displaying extremely varied morphology both within and between populations. The lack of clarity between species concepts was likely due not only to the plasticity of *C. aggeria* across its range but also the now-documented and apparently widespread introgression of *C. grahamii* with *C. aggeria*. Moving east from its type locality, the progressively more robust morphology of *C. grahamii*, in addition to multiple instances of mixed populations, true hybrid morphologies, and triploid and tetraploid counts within populations of *C. grahamii*, provide evidence that the variations are not environmental nor are they the result of a plastic phenotype as in *C. aggeria*. Hybrids are known between other species but in very localized areas and are unlikely to have contributed to the historic perception of widespread intermediacy.

Viewing plants in isolation, especially prepared specimens, may have increased the possibility of confusion between some species. The original published description of *Corynopuntia aggeria* (Ralston & Hilsenbeck 1989) states the filaments as green. The type specimen (*MSA 856* MICH) does not contain floral material; the original type description (Anthony 1956) states filament color as red. It is not clear whether the Ralston and Hilsenbeck description of filament color was derived from subsequent collections or field observations. During the current study, all filaments in *C. aggeria* observed were pink at minimum, but most were deep maroon-red. Bárcenas (2004) reported that the majority of *Corynopuntia* [*Grusonia*] species, including the five CSC species, have red stigma lobes. However the coloration noted by Bárcenas may have been an artifact of the drying process; during the present study all live flowers of CSC species observed in the field or in cultivation had yellow or cream colored stigma lobes, which in the subsequent dried specimens actually appear light pink.

Figure 24. Unidentified *Corynopuntia* from the Brokeoff Mountains, southeastern Otero Co., New Mexico. A-B) *Weins 3809* UNM: few, short central spines including one broad, main central spine, plus terete, bulbous-based upper centrals. C-D) *Weins s.n./UNM 67866* UNM: numerous, long central spines with iridescent bulbous bases.

Lack of context appears to be why *Corynopuntia densispina* was for so long disregarded as a distinct species. Two specimens collected by Margery Anthony in 1948 were identified at the time as *C. schottii* (*MSA 273, 1137*). They are in fact *C. densispina* and are now considered the first known collections of that species. Commingling these distinct individuals into one broadly inclusive species concept helped propagate much subsequent taxonomic confusion throughout the CSC history.

Superficial similarities, namely clavate joint shape and diffuse roots, do exist between *C. densispina* and *C. schottii*. This likely contributed to the fact that *C. schottii* has been widely cited as a tetraploid (Yuasa et al. 1973; Weedin & Powell 1978; Pinkava et al. 1985; Ralston & Hilsenbeck 1989; Weedin et al. 1989; Powell & Weedin 2001, 2005; Pinkava 2002). After most of these voucher specimens were reassigned based on improved morphologic and chromosomal understanding, by 2004 there was only one remaining chromosome count attributed to *C. schottii* (Powell & Weedin 2004; *DOK 53*). Now, the morphology displayed by that remaining tetraploid voucher specimen, bolstered by chromosome counts showing *C. schottii* to be hexaploid, both suggest the voucher *DOK 53* is actually *C. densispina*. Even if disregarding the difference in ploidy level, the clear distinctions involving disarticulation, spination, habitat, and distributions between *C. densispina* and *C. schottii* eliminate the possibility that they are the same species.

Future Research

As a result of the present study, more coherent definitions for CSC species now exist to help guide future explorations of these and related taxa within *Corynopuntia*. The details of morphology, habitat, distribution, and chromosome number discussed above already clearly demonstrate the distinctness of each species. Many unresolved issues, however, were uncovered in the course of study, including potentially new identifying characters, taxa with unknown chromosome numbers, and possible new species/taxa. These all warrant further study; several topics are offered below to inspire continued study of the CSC and the *Corynopuntia* genus as a whole.

Spine surface characteristics. Bárcenas (2002) and I note that the spine surface character consistently differs between some CSC species, from the abundantly farinose surfaces of *Corynopuntia aggeria* and *C. densispina* to the variously ridged surfaces and appressed/sclerified trichomes in *C. emoryi* and *C. grahamii*, as opposed to the relatively smooth spine surfaces in *C. schottii*. Similar interspecific differences in epidermal micro-morphology have been documented in at least one other Cactaceae genus (*Turbinicarpus*, Mosco 2009). Additionally, I have observed that the rudimentary spine sheaths, occurring only at the tips of central spines, persist much longer on *C. grahamii* and *C. schottii* than in the other three CSC species. SEM analysis has been used to demonstrate some differences in spine morphology between Opuntioid (s.l.) genera (Robinson 1974), but the study lacked infrageneric comparisons and analysis of central spine tips. Perhaps targeted morphologic analysis within *Corynopuntia* species would not only better document the above-mentioned micro-morphological differences but explore a possible structural basis for my extensive anecdotal experience that both glochids and central spines of *C. grahamii* and *C. schottii* puncture and lodge more readily and securely into shoes and skin than do glochids and central spines of *C. aggeria*, *C. densispina*, or *C. emoryi*. More robustly-barbed spine tips in readily disarticulating species would be consistent with adaptations for increased effectiveness of vegetative propagation via mammalian vectors, especially considering *C. grahamii* and *C. schottii* showed the lowest pollen stainability percentages (i.e., lower fertility) among CSC species in the current study.

Disarticulation. Ease of joint detachment has long been an inconsistently recorded and/or appreciated character state for CSC species. The manifestation of this character appears to be consistent across USA populations of CSC species, but perhaps not in Mexico. According to Davide Donati (pers. comm.), there may be a seasonal or perhaps rainfall-correlated relationship affecting disarticulation in some species.

Secondary compounds. Freshly cut stems of *Corynopuntia aggeria* release a strong odor which was not observed in freshly cut stems of other CSC species (JF pers. observ.). Many different chemicals are known in Cactaceae and there seems to be some level of differentiation between alkaloids found in some *Corynopuntia* species (Trout 2014). In one example, mucilage flavor was cited as a character distinguishing *Corynopuntia* from *Grusonia* and *Cylindropuntia* (Hamilton 1970).

Perhaps a targeted study of secondary compounds of all *Corynopuntia* species would help elucidate infrageneric relationships.

Extra-floral nectaries/spine secretions. Extra-floral nectaries (EFNs) have been observed in *Corynopuntia emoryi*, *C. invicta*, and *C. wrightiana* as well as spine tip secretions — and associated interest by ants — in *C. emoryi* and *C. schottii* (Felger et al. 2014). In my Alpine, Texas, research collection I also observed liquid droplets at the tips of emergent central spines in *C. emoryi* and *C. schottii* (Fig. 25; A-C). Similar to the related reports in Felger et al. (2014), I also observed in my collection non-native rover ants (*Brachymyrmex patagonicus*), multiple times during two spring seasons (2014-15), visiting areoles of new stem growth and performing "spine grooming" behavior (i.e., rapid paddling of antennae) on the tips of emergent central spines of *C. schottii*, *C. emoryi*, *C. aggeria*, and of *C. aggeria* × *C. grahamii* and *C. grahamii* × *C. schottii* putative hybrids (Fig. 25; D-E). In south Brewster County (near Lajitas and in Big Bend National Park, June 2015) I observed workers of a different, presumably native, ant species in abundance on in situ *C. aggeria* plants, visiting and performing spine grooming behavior in areoles of newly growing stems. In addition, in my Alpine research collection, I observed over two seasons (spring 2014, 2015) numerous prickly pear cactus bug nymphs (*Chelinidea vittiger*) in and among the tubercles of the above-mentioned putative hybrids, often with their probosci embedded in the areolar wool (Fig. 25; F).

Breeding systems. Widespread lack of pollen and/or withered anthers in *Corynopuntia grahamii*, in addition to lack of fruits across its range, suggests reproductive dysfunction rather than a nascently-evolving cryptic breeding system. However cryptic fertility cannot be ruled out in *C. schottii* or *C. emoryi*. In the south Texas *C. schottii* populations, fruits are uncommon yet still present in the densely-matted, extensive colonies. No clear pattern of perfect and pistillate-flowered individuals was immediately apparent in the field, but pollen stainability did seem to segregate evenly to higher and lower levels in *C. schottii* (Fig. 2), suggesting a possible evolution toward differential floral fertility. One *C. emoryi* specimen examined (*MAB 11638*) includes flowers with no pollen (Appx. C) but also a fruit with seeds; a separate *C. emoryi* specimen (*AZ 2348*) includes flowers with abundant and high-staining pollen (Appendix C) as well as label data noting fruits were observed in the population. These inconsistencies may indicate more than simple sampling error. Subdioecy is correlated with polyploidy and is known in Cactaceae (Ashman et al. 2013). Recently, another report was made of gynodioecy in *Cylindropuntia* (Baker & Cloud-Hughes 2014), adding to the five other gynodioecious species in the genus (Rebman 1998); as yet gynodioecy is undocumented in *Corynopuntia*. Different levels of fertility within a population would be expected especially in the hexaploid *C. schottii* but data collection for the current study was not designed to draw definitive conclusions regarding fertility levels. The possibility of cryptic dioecy or agamospermy in both *C. schottii* and *C. emoryi* should be investigated.

Chromosomal studies. The unexpected discoveries of various ploidy levels in Big Bend *Corynopuntia* populations should encourage more attention to this line of inquiry, both to support investigations into regional polyploid evolution as well as to further elucidate lesser understood, regional *Corynopuntia* species. The Mexican *C. vilis*, known from Coahuila to San Luis Potosí, is uncounted. Highly similar in features to the tetraploid *C. grahamii*, *C. vilis* is distinguished most obviously by its purple-pink flower. This makes the occasional but consistent presence of salmon-orange pink flowers in typical *C. grahamii* populations across its USA range especially intriguing. Flower color and extreme morphologic similarity suggest the possibility that *C. grahamii* is an autotetraploid derivative of a diploid *C. vilis*. The Mexican diploid *C. moelleri*, despite being regularly included as an extant member of the Chihuahuan Desert club cholla cohort (Bravo-Hollis 1978; Anderson 2001; Bárcenas 2004; Hernández et al. 2004; Hunt 2006), had long been documented by only one chromosome count in the literature (Pinkava & Parfitt 1982) and with only a brief literature description based solely on what could be considered unrepresentative, cultivated material

Figure 25. Extra-floral nectaries and spine secretions in Big Bend *Corynopuntia*. Arrows indicate apparent spine-tip secretions from emergent central spines in A) *C. emoryi* (*PM s.n.*) and B–C) *C. schottii* (*TP s.n.*). D) *Chelinidea vittiger* nymph with proboscis in areolar wool of *C. grahamii* (*JF 2302*). E–F) *Brachymyrmex patagonicus* "grooming" spine tips with antennae on *C. grahamii* (*JF 2302*). 9 July 2014, cultivated plants in pots, Alpine, Texas.

(Bravo-Hollis 1978; Wright 1932). Donati (2011) reexamined the taxon in the field and concluded via chromosome analysis, morphology, and geography, that *C. moelleri* is a well defined species that — despite having various morphotypes — does exclude character overlap with especially *C. bulbispina*, yet is similar in aspect to the northern diploid *C. clavata*. The existence of uncounted morphotypes in *C. moelleri*, as well as its sympatry and past confusion with various other *Corynopuntia* species including the little known and uncounted *C. guccini* and *C. nigrispina* (Donati 2010, 2012), support the need for further study.

Hybridization. Unreduced gametes are believed to account for most of the origins of polyploid *Opuntia* (s.l.) (Pinkava et al. 1998) and are implicated in *Cylindropuntia* hybridization (Baker & Pinkava 1987). Evidence for the existence of unreduced gamete production in Big Bend *Corynopuntia* is suggested by multiple observations: (1) the existence of triploid individual within a *C. densispina* population (*JF 635*), (2) observation of heteromorphic bivalents and univalents in samples from a *C. densispina* population, (3) a suggested triploid meiotic pairing in a sample from a mixed population of *C. aggeria* and *C. densispina* (*JF 703*), (4) observations of two sizes of pollen grains within a single pollen grain sample, most often noted in samples from *C. aggeria* and *C. densispina*, and (5) a pentaploid *C. grahamii* individual (*JF 2416*). The formation of autopolyploids such as *C. densispina* via the triploid bridge mechanism (Ramsey & Schemske 1998) is a likely scenario, where triploids form in a diploid population by the production of an unreduced gamete and then either self-fertilize or backcross to a diploid, either of which results in a tetraploid.

The Big Bend area, with its high desertic temperature extremes and frequent drought conditions, may be a particularly well-suited location for the production of unreduced gametes as they occur more frequently as a result of environmental stress (Ramsey & Schemske 1998). There are now more vouchers suggesting gene exchange between Big Bend *Corynopuntia* species, but the true extent of hybridization and/or introgression between *C. grahamii* and *C. schottii* is unknown. So too is the extent and/or mechanism and significance of the apparent widespread introgression between *C. grahamii* and *C. aggeria*. Additionally, unidentified specimens (discussed below) that do not align with any one known species concept raise the distinct possibility of additional hybrid evolutions; these taxa require further study.

Novel taxa. The more robust character descriptions developed herein for the CSC species resulted in several specimens defying definitive identifications. The collections from mid-Brewster and northern-Hudspeth counties show affinities to multiple CSC species, and those from the Brokeoff Mountains in southeastern New Mexico contain characters suggestive of *C. clavata* and *C. grahamii*. In addition, I encountered two unusual *C. emoryi* specimens from southeastern Arizona (*Puente 1624*, *Rebman 1850*, DES) that suggest an affinity to *C. schottii* in that the joints were strongly J-shaped, with long spines relative to the shorter/smaller joints (the opposite is true in typical *C. emoryi*), as well as copper-colored central spines with white margins. Further documentation of these mixed-morphology populations will help inform possible evolutionary connections between these species. Hybrids have not only been documented in areas disjunct form parental taxa (Pinkava et al. 1998) but taxa resulting from the introgression of three parental genomes is not impossible (Soltis & Soltis 2009). Discoveries of as-yet unknown taxa, including situations similar to the long-unacknowledged *C. densispina*, are a significant possibility (e.g., Donati 2014; Nesom 2015) as more of the geographic range of the genus is explored and more extant specimens are reviewed, utilizing the most up-to-date species characterizations.

Biogeographic context, evolutionary relationships. The true relationship between CSC species and Mexican *Corynopuntia* is unknown. Newly described species like *C. guccini* from southern Coahuila with its striking red flowers (Donati 2010), as well as new data (Donati 2011) that enrich the species concept of *C. bulbispina* and re-energize the protologue-only concept of *C.*

agglomerata (Berger 1929), are exciting additions to the regional pool of *Corynopuntia* genomes. Further, the similar morphology of the latter two species to *C. grahamii* and *C. vilis* (ovate joints, tuberous roots, terete spines) suggest some level of genome connection. An additional indication of possible gene exchange involves the occurrence of red filaments.   In the USA populations of *Corynopuntia*, maroon-red filaments are a true, consistent character of only *C. aggeria*.   Fully maroon-red filaments are occasionally seen in *C. densispina*, but this could be considered unsurprising for an autopolyploid-derived taxon. Red filaments are also known in some individuals resembling *C. grahamii* but only in populations with robust morphologies, i.e., introgressed with *C. aggeria*.   In Mexican club cholla species, red filaments are reported for *C. bulbispina* and *C. agglomerata* (Donati 2011) but apparently also as a consistent character of *C. grahamii* (Donati pers. com.).

Following the above and other character traits through populations may yet add new depth to existing species concepts as well as lead to the discovery of new *Corynopuntia* species, especially in northern Mexico where the cactus diversity is high (reviewed in Hernández et al. 2004) and geographical rarity is common (Hernández & Gómez-Hinostrosa 2005; Hernández et al. 2010). There, habitat divergence and genetic isolation results from regional climatic patterns and topographically separated basins (Hernández & Bárcenas 1995), though area biodiversity was likely initially influenced by virtue of being an environmental refugium during the last glacial maximum (Van Devender 1986, 1990; Betancourt et al. 1990; Fenstermacher et al. 2008).

Similarly, the southwest desert of the USA has also been suggested as a Pleistocene refugium — and as such serving as a hub for post-glacial expansion of *Opuntia* (s.s.) diversity (Majure et al. 2012b, c). Recalling some *Opuntia* (s.l.) species' propensity for disarticulation, this expansion of range and/or diversity may have been aided by the movements of Pleistocene megafauna (Majure 2012c) as well as humans and related domestic animals during their long history of migration across the northern Chihuahuan Desert region (Keller 2005). Perhaps the CSC is a young, localized remnant of the proposed post-glacial diversification event, considering the relatively small species ranges and sympatric distribution of diploid and polyploids (Stebbins 1971).

Molecular systematics.   There is much potential to further elucidate relationships within *Corynopuntia*. Bárcenas et al. (2011) showed resolution of two *Corynopuntia* clades, each containing a diploid — *C. parishii* and *C. moelleri*. These two clades separate well based on both morphologic and geographic qualifications. Western USA club cholla species trend towards having one main spine, numerous centrals, and less morphological distinctions between radial and central spines — incidentally all characteristics of *Cylindropuntia*. Southern/eastern species, including the CSC, have fewer central spines and distinctly different radial and central spine morphologies as well as locations in the areole. The subcentral spines of *C. emoryi* and *C. schottii* seem to exist in an intermediate state between the two otherwise-separated clades.

Bárcenas et al. (2011) did not include the other known diploids of *Corynopuntia*, *C. aggeria* and *C. clavata*, in the molecular analysis so it is still unknown if more clades may be shown in the genus.   The likelihood of reticulate evolution in *Corynopuntia* poses challenges to ultimate infrageneric resolution, however methods exist to elucidate this influence (Griffith 2003). Recent, strongly field-based studies in the Opuntioideae, especially Cylindropuntiae and Corynopuntiae, are resulting in species concept revisions (Majure 2012b; Felger et al. 2014), amendments (Donati 2011), and even new species discoveries and descriptions (Rebman 2006; Donati 2010, 2011, 2012; Baker and Cloud-Hughes 2014). It is hoped that the current study provides inspiration towards more such efforts.

ACKNOWLEDGEMENTS

LITERATURE CITED

Anderson, E. 2001. The Cactus Family. Timber Press, Portland, Oregon.

Anthony, M.S. 1949. An Ecologic and Systematic Analysis of the Genus *Opuntia*, Miller in the Big Bend Region of Texas. Ph.D. dissertation, Univ. of Michigan, Ann Arbor.

Anthony, M.S. 1954. Ecology of the Opuntiae in the Big Bend region of Texas. Ecology 35: 334–347.

Anthony, M.S. 1956. The Opuntiae of the Big Bend region of Texas. Amer. Midl. Naturalist 55: 225–256.

Ashman, T.-L., A. Kwok, and B.C. Husband. 2013. Revisiting the dioecy-polyploidy association: alternate pathways and research opportunities. Cytogenet. Genome Res. 140: 241–255.

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

Baker, M.A., J.P. Rebman, B.D. Parfitt, D.J. Pinkava, and A.D. Zimmerman. 2009. Chromosome numbers in some cacti of western North America VIII. Haseltonia 15: 117–134.

Baker, M.A. and M.A. Cloud-Hughes. 2014. *Cylindropuntia chuckwallensis* (Cactaceae), a new species from Riverside and Imperial counties, California. Madroño 61: 231–243.

Bárcenas, R.T. 2004. Systematics of *Grusonia* F. Rchb. ex Britton & Rose (Opuntioideae: Cactaceae). Ph.D. dissertation, University of Reading, United Kingdom.

Bárcenas, R.T. 2015. A molecular phylogenetic approach to the systematics of Cylindropuntiae (Opuntioideae, Cactaceae). Cladistics. doi: 10.1111/cla.12135.

Bárcenas, R.T., C. Yeson, and J.A. Hawkins. 2011. Molecular systematics of the Cactaceae. Cladistics 27: 1–20.

Bárcenas, R.T., J.A. Hawkins, and F. Chiang. 2012. Typification of four North American club-chollas: The names of four Engelmannian species from Mexico and southwestern United States. Haseltonia 17: 66–69.

Benson, L. 1969. The cacti of the United States and Canada — new names and nomenclatural combinations. Cact. Succ. J. (Los Angeles) 41: 124–234.

Benson, L. 1982. The Cacti of the United States and Canada. Stanford Univ. Press, Stanford, California.

Berger, A. 1929. Kakteen. Eugen Ulmer, Stuttgart, Germany.

Betancourt, J., T.R. Van Devender, and P. Martin (eds.). 1990. Packrat Middens: The Last 40,000 Years of Biotic Change. Univ. of Arizona Press, Tucson.

Bravo-Hollis, H. 1978. Las Cactáceas de México (ed. 2). Univ. Nacional Autónoma de México, Ciudad Universitaria, México, D. F., México.

Breslin, P. and D. Donati. 2014. Vizcaino mystery: A tale of *Corynopuntia robertsii*. Cact. Succ. J. (Los Angeles) 86: 70–75.

Britton, N.L. and J.N. Rose. 1919. The Cactaceae, Descriptions and Illustrations of Plants of the Cactus Family. The Carnegie Institution of Washington, 248(1). Washington, D.C.

Correll, D.S. and M.C. Johnston. 1970. Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner.

Donati, D. 2010. Una nuova eccezionale specia appartenente al genere *Corynopuntia* Knuth: *Corynopuntia guccinii* D. Donati sp. nov. Piante Grasse 30: 115–119.

Donati, D. 2011. Nuovo studio sul gruppo *Clavata* del genere *Corynopuntia* Knuth: riscoperta di *C. agglomerata* e descrizione di *C. bulbispina* subsp. *basileocephala* subsp. nov. Piante Grasse 31: 2–18.

Donati, D. 2012. A new species belonging to the genus *Corynopuntia* Knuth: *Corynopuntia nigrispina* D.Donati sp. nov. Piante Grasse 32: 2–7.

Donati, D. 2014. Technical and taxonomic notes on *Corynopuntia robertsii*. Cact. Succ. J. (Los Angeles) 86: 73-75.

Engelmann, G. 1856. Synopsis of the Cactaceae of the territory of the United States and adjacent regions. Proc. Amer. Acad. Arts 3: 259–311.

Engelmann, G. 1859. Cactaceae of the Boundary, From the Report of the U.S. and Mexican Boundary Survey and the Order of Lt. Col. W.H. Emory, Maj. 1st Cav. and U.S. Commissioner. Vol. 2, pt. 1, 1–78. Washington, D.C.

Evans, D.B. 1998. Cactuses of Big Bend National Park. Univ. of Texas Press, Austin.

Felger, R.S., S. Rutman, J. Malusa, and M.A. Baker. 2014. Ajo Peak to Tinajas Altas: A flora in southwestern Arizona. Part 7. Eudicots: Cactaceae – Cactus Family. Phytoneuron 2014-69: 1–95.

Fenstermacher, J., A.M. Powell, J. Sirotnak, and M. Terry. 2008. Annotated vascular flora of the Dead Horse Mountains, Big Bend National Park, Texas, with notes on local vegetation communities and regional floristic relationships. J. Bot. Res. Inst. Texas 2: 685–730.

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

Griffith, M.P. 2002. *Grusonia pulchella* classification and its impacts on the genus *Grusonia*: Morphological and molecular evidence. Haseltonia 9: 86–93.

Griffith, M.P. 2003. Using molecular evidence to elucidate reticulate evolution in *Opuntia* (Cactaceae). Madroño 50: 162–169.

Griffith, M.P. and J.M. Porter. 2009. Phylogeny of Opuntioideae (Cactaceae). Internatl. J. Plant Sci. 170: 107–116.

Hamilton, M.W. 1970. The comparative morphology of three Cylindropuntias. Amer. J. Bot. 57: 1255–1263.

Hernández, H.M. and R.T. Bárcenas. 1995. Endangered cacti in the Chihuahuan Desert. I. Distribution Patterns. Conserv. Biol. 9: 1176–1190.

Hernández, H.M., C. Gómez-Hinostrosa, and B. Goettsch. 2004. Checklist of Chihuahuan Desert Cactaceae. Harvard Pap. Bot. 9: 51–68.

Hernández, H.M. and C. Gómez-Hinostrosa. 2005. Cactus diversity and endemism in the Chihuahuan Desert Region. *In* J.L. Cartron, G. Ceballos, and R. Felger (eds.). Biodiversity Ecosystems and Conservation in Northern Mexico. Oxford Univ. Press, New York.

Hernández, H.M., C. Gómez-Hinostrosa, and G. Hoffmann. 2010. Is geographical rarity frequent among the cacti of the Chihuahuan Desert? Rev. Mex. Biodiv. 81: 163–175.

Hernández-Hernández, T., H.M. Hernández, J.A. De-Nova, R. Puente, L.E. Eguiarte, and S. Magallon. 2011. Phylogenetic relationships and evolution of growth form in Cactaceae (Caryophyllales, Eudicotyledonae). Amer. J. Bot. 98: 44–61.

Hunt, D. (compiler). 2006. The New Cactus Lexicon. DH Books, Milborne Port, England.

JSTOR Plant Science. 2014. JSTOR Plant Science/Global Plants. <http://plants.jstor.org/> Accessed October 2014.

Keller, D.W. 2005. Below the Escondido Rim: A History of the O2 Ranch in the Texas Big Bend. Center for Big Bend Studies, Occasional Papers No. 10. Sul Ross State University, Alpine, Texas.

Konings, A. and G. Konings. 2009. Cacti of Texas in their Natural Habitat. Cichlid Press, El Paso, Texas.

Majure, L.C. and G.N. Ervin. 2008. The Opuntias of Mississippi. Haseltonia 14: 111–126.

Majure, L.C. and E. Ribbens. 2012. Chromosome counts of *Opuntia* (*Cactaceae*), prickly pear cacti, in the midwestern United States and environmental factors restricting the distribution of *Opuntia fragilis*. Haseltonia 17: 58–65.

Majure, L.C., R. Puente, and D.J. Pinkava. 2012a. Miscellaneous chromosome numbers in Opuntiae DC. (Cactaceae) with a compilation of counts for the group. Haseltonia 18: 67–78.

Majure, L.C., W.S. Judd, P.S. Soltis, and D.E. Soltis. 2012b. Cytogeography of the Humifusa clade of *Opuntia* s.s. Mill. 1754 (Cactaceae, Opuntioideae, Opuntiae): Correlations with Pleistocene refugia and morphological traits in a polyploid complex. Comp. Cytogen. 6: 53–77.

Majure, L.C., R. Puente, M. P. Griffith, W.S. Judd, P.S. Soltis, and D.E. Soltis. 2012c. Phylogeny of *Opuntia* s.s. (Cactaceae): Clade delineation, geographic origins, and reticulate evolution. Amer. J. Bot. 99: 1–18.

Mauseth, J.D. 2006. Structure-function relationships in highly modified shoots of Cactaceae. Ann. Bot. 98: 901–926.

Mosco, A. 2009. Micromorphology and anatomy of *Turbinicarpus* (Cactaceae) spines. Rev. Mex. Biodiv. 80: 119–128.

Nesom, G.L. 2015. Taxonomy of *Galactia* (*Fabaceae*) in the USA. Phytoneuron 2015-42: 1–54.

Nyffeler, R. 2002. Phylogenetic relationships in the cactus family (Cactaceae) based on evidence from *trnK/ matK* and *trnL-trnF* sequences. Amer. J. Bot. 89: 312–326.

Pinkava, D.J. 2002. On the evolution of the continental North American Opuntioideae (Cactaceae). Pp. 59– 98, <u>in</u> D. Hunt & N. Taylor (eds.). Studies in the Opuntioideae (Cactaceae). Succ. Pl. Res., Vol. 6.

Pinkava, D.J. 2003. Cactaceae, Subfamily Opuntioideae. Pp. 102–150, <u>in</u> Flora of North America North of Mexico, Vol. 4. Oxford Univ. Press, New York and Oxford.

Pinkava, D.J. and B.D. Parfitt. 1982. Chromosome numbers in some cacti of western North America. IV. B. Torrey Bot. Club 109: 121–128.

Pinkava, D.J., M.A. Baker, B.D. Parfitt, and M.W. Mohlenbrock. 1985. Chromosome numbers in some cacti of western North America—V. Syst. Bot. 10: 471–483.

Pinkava, D.J., J.P. Rebman, and M.A. Baker. 1998. Chromosome numbers in some cacti of western North America—VII. Haseltonia 6: 32–41.

Powell, A.M., A.D. Zimmerman, and R.A. Hilsenbeck. 1991. Experimental documentation of natural hybridization in Cactaceae: Origin of Lloyd's hedgehog cactus, *Echinocereus* × *lloydii*. Pl. Syst. Evol. 178: 107–22.

Powell, A.M. and J.F. Weedin. 2001. Chromosome numbers in Chihuahuan Desert Cactaceae. III. Trans-Pecos Texas. Amer. J. Bot. 88: 481–485.

Powell, A.M. and J.F. Weedin. 2004. Cacti of the Trans-Pecos and Adjacent Areas. Texas Tech Univ. Press, Lubbock.

Powell, A.M. and J.F. Weedin. 2005. Documented Chromosome Numbers 2005:2. Counts from western Texas, mostly Trans-Pecos cacti. Sida 21: 1665–1668.

Powell, A.M., J.F. Weedin, and S.A. Powell. 2008. Cacti of Texas: A Field Guide, With Emphasis on the Trans-Pecos Species. Texas Tech Univ. Press, Lubbock.

Ralston, B.E. 1987. A Biosystematic Study of the *Opuntia schottii* Complex (Cactaceae) in Texas. M.S. thesis, Sul Ross State University, Alpine, Texas.

Ralston, B. E. and R. A. Hilsenbeck. 1989. Taxonomy of the *Opuntia schottii* complex (Cactaceae) in Texas. Madroño 36: 221–231.

Ralston, B.E. and R.A. Hilsenbeck. 1992. *Opuntia densispina* (Cactaceae): A new club cholla from the Big Bend Region of Texas. Madroño 39: 281–284.

Ramsey, J. and D.W. Schemske. 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. Ann. Rev. Ecol. Syst. 29: 467–501.

Rebman, J.P. 1998. A new cholla (Cactaceae) from Baja California, Mexico. Haseltonia 6: 17–21.

Rebman, J.P. 2006. A new club cholla, *Grusonia robertsii* (Cactaceae) from Baja California Sur, Mexico. Madroño 53: 278–281.

Rebman, J.P. and D.J. Pinkava. 2001. *Opuntia* of North America: An overview. Fla. Entomol. 4: 474–483.

Robinson, H. 1974. Scanning electron microscope studies of the spines and glochids of the Opuntioideae (Cactaceae). Amer. J. Bot. 61: 278–283.

Schulz, E.D. and R. Runyon. 1930. Texas cacti, a popular and scientific account of the cacti native to Texas. Proc. Texas Acad. Sci., Vol. XIV. Texas Academy of Science, San Antonio.

SEINET. 2014. Southwest Environmental Information Network. Managed at Arizona State Univ., Tempe. <http://swbiodiversity.org/seinet/index.php> Accessed November 2009 – September 2014.

Soltis, P.S. and D.E. Soltis. 2009. The role of hybridization in plant speciation. Ann. Rev. Plant Biol. 60: 561–588.

Stebbins, G.L. 1971. Chromosomal Evolution in Higher Plants. Edward Arnold Ltd., London, UK.

Stuppy, W. 2002. Seed characters and generic classification of Opuntioideae. Succ. Pl. Res. 6: 25–58.

Trout, K. (ed.). 2014. Cactus Chemistry by Species. Mydriatic Productions, Better Days Publishing. <http://www.largelyaccurateinformationmedia.com/LAIM/C10.html >

Turner, B.L. and M.C. Johnston. 1961. Chromosome numbers in the Compositae. III. Certain Mexican species. Brittonia 13: 64–69.

USDA, NRCS. 2014. The PLANTS Database. National Plant Data Team, Greensboro, North Carolina. <http://plants.usda.gov> Accessed November 2009–September 2014.

Van Devender, T.R. 1986. Pleistocene climates and endemism in the Chihuahuan Desert flora. Pp. 1–19, in J.C. Barlow, A.M. Powell, and B.J. Timmerman (eds.). Second Symposium on Resources of the Chihuahuan Desert Region, United States and Mexico, Chihuahuan Desert Research Institute, Alpine, Texas.

Van Devender, T.R. 1990. Late Quaternary vegetation and climate of the Chihuahuan Desert, United States and Mexico. Pp. 104–133, in J. Betancourt, T.R. Van Devender, and P. Martin (eds.),

Packrat Middens: The Last 40,000 Years of Biotic Change,. University of Arizona Press, Tucson.

Wallace, R.S. and S.J. Dickie. 2002. Systematic implication of chloroplast DNA sequence variation in subfam. Opuntioideae (Cactaceae). Succ. Pl. Res. 6: 9–24.

Weedin, J.F. and A.M. Powell. 1978. Chromosome numbers in Chihuahuan Desert Cactaceae. Trans-Pecos Texas. Amer. J. Bot. 65: 531–537.

Weedin, J. F., A.M. Powell, and D.O. Kolle. 1989. Chromosome numbers in Chihuahuan Desert Cactaceae. II. Trans-Pecos Texas. Southwest. Nat. 34: 160–164.

Weniger, D. 1988. Cacti of Texas and Neighboring States. Univ. of Texas Press, Austin.

Wright, Y. 1932. *In* E.M. Baxter (ed.), Notes on "The Cactaceae." Cact. Succ. J. (Los Angeles) 4: 281–282.

Yuasa, H., S. Shimizer, S. Kashiwai, and N. Kondo. 1973. Chromosome numbers and their bearing on the geographic distribution in the subfamily Opuntioideae (Cactaceae). Rep. Inst. Breed Res., Tokyo Univ. Agric. 4: 1–10.

Appendix A. New or previously unpublished meiotic chromosome counts for the *Corynopuntia schottii* complex. Unless otherwise indicated, counts were made by the author and/or AMP, collection localities are within Texas, and vouchers are housed at SRSC. See Methods and Materials for names associated with collector abbreviations. Symbols: † univalents observed; ‡ multivalents and/or tetravalents observed; * count by MAB; ** mitotic count, by MAB.

Corynopuntia aggeria

n = 11. USA. TEXAS. **Presidio Co.** Ruidosa/Pinto Canyon Road, *BER 130* [previously unpublished, count by BER]. **Brewster Co.** Terlingua, Saltgrass Draw, *JF 2329a, 2329b, 2329c*. Big Bend National Park: West Entrance, *JF 2330, 2332*; Glen Spring Road, *JF 409, 2321, 2322*; River Road, 22.9 mi E of Castolon, *BER 123*; River Road, Solis, *JF* 2350; Rooney's Place, *ADZ 2449*; Rt. 11: mi. 6.7, *JF 2334b*; Rt. 11 mi. 7, *JF 2353a*; Rt. 12 mi. 15, *JF 2312a, 2312f, 2314*; Dagger Flat Rd, *JF 2339*; Old Ore Rd. (OOR), Telephone Canyon trailhead, *JF 1620*; OOR, La Noria jct., *JF 2343*; OOR, Ernst Tinaja jct., *JF 640, 641*; OOR, Candelilla campsite area, *JF 630, 631, 632, 633*; Boquillas Canyon Road (BCR), flats in first mile, *JF 2351d*; BCR, N of Barker House, *JF 1574a, 1574b, 1576, 2344a, 2344b, 2344e, 2345a, 2345b*; BCR, first Boquillas overlook, *JF 1562, 1563*.

Corynopuntia densispina

n = 22. USA. TEXAS. **Brewster Co.** Big Bend National Park: River Road, Solis jct., *JF 2397b, 2399, 2212**; River Road, 1.9 mi. E of Solis jct., *JF 2349a, 2349b.1, 2349b.2, 2349d‡, 2349d.1‡*; Old Ore Rd. (OOR), Carlotta Tinaja, *JF 32380a, 2380b, 2385, 2387*; OOR, N of La Noria jct., *JF 2382g, 2382i, 2382k‡*; OOR, La Noria jct., *JF 2392‡*; OOR, Ernst Tinaja jct., *JF 691‡, 2393a, 2393b‡, 2394‡, 2395a, 2395b*; *MAB 17815 / JF 2218a** *(SRSC, ASC); OOR, Candelilla campsite area, *JF 2378, 2378b, 2378c‡*.

Corynopuntia grahamii

n = 22. USA. TEXAS. **Brewster Co.** Elephant Mtn. Wildlife Mgmt. Area: southern wildlife viewing area, *JF 2372*. Big Bend National Park: West Entrance, *MAB 17814 / JF 1558*** *(SRSC, ASC); Nine Point Draw campsite, *JF 2415*; North Rosillos Road mi. 1, *JF 2338b*; Rt. 11 mi. 19.7, *JF 2336*; River Road, Gravel Pit jct., *JF 2361‡*.

n = 24 – 31. USA. TEXAS. **Presidio Co.** Marfa: Casa Piedra Rd., 36.8 mi S of Marfa, *JF 2416*.

Corynopuntia schottii

n = 33. USA. TEXAS. **Val Verde Co.** Langtry, *JF 2404†‡*. **Starr Co.** S of Escobares, *MAB 17635 / AS s.n.** *(SRSC, ASC, US). Eastern edge of Rio Grande City, *JF 2430*. **Hidalgo Co.** Mission, adjacent to The Nature Conservancy Chihuahua Woods Preserve, *JF 2434*.

Corynopuntia aggeria × C. densispina

n = 14 – 16. USA. TEXAS. **Brewster Co.** Big Bend National Park (BBNP): Old Ore Rd., Ernst Tinaja *JF 635†‡*.

n = 16 – 22. USA. TEXAS. **Brewster Co.** BBNP: River Road, Solis, *JF 703a‡*; *JF 703b‡*. Hybrid identification based on morphological intermediacy as well as chromosome count.

Corynopuntia aggeria × C. grahamii

n = 14 – 16. USA. TEXAS. **Brewster Co.** Big Bend National Park, Rt. 11 mi. 6.7, *JF 2334c*.

n = 22. USA. TEXAS. **Brewster Co.** Saltgrass Draw, *JF 2325*; near Agua Fria Rd. entrance to Hwy 118, *JF 2360a*; Big Bend National Park, Rt. 11 mi. 7, *JF 2353*. Hybrid identification based on morphological intermediacy not chromosome count.

Corynopuntia densispina × C. grahamii

n = 20 – 22. USA. TEXAS. **Brewster Co.** Big Bend National Park, Old Ore Rd., Ernst Tinaja, *JF 2355*.

Appendix B. Previously published somatic chromosome numbers for the *Corynopuntia schottii* complex, based on the summary in Pinkava (2002) with my updated determinations indicated, see symbols below. Unless otherwise noted, collection locations are within Texas and specimens are housed at SRSC. Where relevant, species names under which the counts were originally published are included in brackets; any additional annotations are subsequently listed in chronologic order. Symbols: [1] = specimen does not exist at SRSC, location unknown, reassignment based on chromosome count; [2] = updated determination from last publication (Pinkava 2002); [3] = locality unreported in literature; [4] = corrected collection number from last publication (Pinkava 2002); [5] = locality unreported in literature, now known as "Mexico" (Govorounova, pers. com. 2015*).

Corynopuntia aggeria
  22 Baker et al. 2009. **Mexico, Chihuahua.** *MAB+ 12390, MAB 15667* (ASC).
  22 Pinkava et al. 1985, Baker et al. 2009. **Brewster Co.** *RDW 9714* (UTEP, ASC) [*Opuntia schottii* var. *schottii*].
  22 Powell and Weedin 2001. **Brewster Co.** *AMP 5216, AMP+ 6006.*
  22 Ralston and Hilsenbeck 1989. **Brewster Co.** *AMP 5216, 5383; BER 114, 118, 120, 128, 135, 136, 152.*
  22 Weedin et al. 1989. **Brewster Co.** *JFW 1152* [*O. schottii var. schottii*][1].
  22 Weedin and Powell 1978. **Brewster Co.** *AMP 3074a, b* [*O. schottii* var. *grahamii*][2].

Corynopuntia densispina
  44 Ralston and Hilsenbeck 1992. **Brewster Co.** *BER 200* (SRSC, ASC, TEX).
  44 Weedin et al. 1989. **Brewster Co.** *DOK 53* [*O. schottii*][2].

Corynopuntia emoryi
  22 Yuasa et al. 1973. Y-72-402-020 [*O. stanlyi* (sic)].[3]
  44 Baker et al. 2009. **Arizona, Graham Co.** *MAB 11638* (ASC).
  44 Pinkava et al. 1985. **Arizona, Pinal Co.** *MAB+ 4645* [ASC, as *O. stanleyi* var. *stanleyi*].
  44 Powell and Weedin 2001. **Presidio Co.** Candelaria, *AMP+ 5996*[4].
  44 Ralston and Hilsenbeck 1989. **Presidio Co.** Capote Creek, *BER 113.*
  44 Weedin and Powell 1978. **Presidio Co.** Candelaria, *DOK 9* [*O. stanleyi*].

Corynopuntia grahamii
  44 Pinkava et al. 1985. **El Paso Co.** El Paso, *RDW 6910.5* (UTEP, ASU) [*O. schottii > O. grahamii*].
  44 Powell and Weedin 2005. **Brewster Co.** Heath Canyon, *AMP+ 6152* [*O. schottii* var. *schottii*].

Corynopuntia schottii
  44 Yuasa et al. 1973. [**Mexico**]. Y 68-402-090 [*O. shotii* (sic.)].[5]
  66 Yuasa et al. 1973. [**Mexico**]. Y-72-402-019 [*O. shotii* (sic.)].[5]

C. aggeria ✕ C. grahamii (putative)
  44 Weedin and Powell 1978. **Brewster Co.** BBNP, La Noria, *JFW+ 237* [*O. grahamii*, *O. schottii*, *O. aggeria*][2].
  44 Powell and Weedin 2001. **Brewster Co.** Terlingua, *GGR 93-52* [*O. schottii*][2].

*Locality unreported in original publication of count (Yuasa et al. 1973), but via a translator Yuasa was contacted and asked about the collection location of these specimens; apparently the plants were in cultivation at the Izu Shaboten Park, Ito, Shizuoka Prefecture, with original material (possibly seeds) having come from Mexico. Email conversation with Elena Govorounova, May 2015.

Appendix C. Pollen stainability data for the *Corynopuntia schottii* complex including putative hybrids.

	C. aggeria	*C. densispina*	*C. emoryi*	*C. grahamii*	*C. schottii*	*C. aggeria* x *C. densispina*	*C. aggeria* x *C. grahamii*	*C. densispina* x *C. grahamii*	*C. grahamii* x *C. schottii*
Total samples measured	37	27	5	47	24	1	42	2	1
# samples containing pollen	35	22	3	13	18	1	13	1	0
Average % stainability	69	70	77	47	56	26	43	93	0
# samples lacking pollen	2	5	2	34	6	0	29	1	1
% samples lacking pollen	5	19	40	72	25	0	69	50	100
Range in stainability %	1-97	28-94	45-96	0-87	0-94	n/a	0-98	n/a	n/a
% stained grains ≥ 70%	60	64	67	15	56	0	15	100	-
% stained grains ≥ 80%	54	41	67	15	39	0	15	100	-

Appendix D. Pollen stainability measurements of the *Corynopuntia schottii* complex. Percentages for each flower sampled per voucher are listed in brackets. Stainability was measured by the author and vouchers are housed at SRSC unless otherwise noted. Underlined collection numbers indicate chromosome number vouchers. See Methods and Materials for names associated with collector abbreviations. Symbols: n/a = pollen sterile (i.e., flower lacked pollen entirely); * = sample showed two or more sizes of pollen grains.

Corynopuntia aggeria
USA. TEXAS. **Presidio Co.** Ruidosa, 4.3 mi NE on Pinto Canyon Rd., *BER 130* [91]; Marfa, 39.5 mi S on FM 169/Casa Piedra Rd, *JF 2417* [96]*. **Brewster Co.** Lajitas, 0.5 mi. N, *AMP 6006* [94]. Terlingua, Saltgrass Draw, *JF 2327* [50], *2329a* [14], *2329b* [93], *2329c* [87], *2329d* [n/a], *2329e* [93], *2329f* [86]. Terlingua Ranch, 14 mi. E on Terlingua Ranch Rd., *BER 127* [75]. Big Bend National Park: West Entrance, *JF 2330* [93], *2332* [96]; Maverick Rd., *BER 120* [36]; River Road, 12 mi E of Castolon, *BER 128* [n/a]; 20 mi E of Castolon, *BER 152* [22]; River Road, Solis jct., *JF 2350* [88]; Glen Spring Rd. (GSR), Juniper Canyon jct., *JF 392* [33]; GSR, Black Gap jct., *JF 409* [93]; GSR, S of Glen Spring, *JF 2321* [19], *2322* [1]; GSR, N of River Road jct., *JF 2370g* [85], *2370i* [92]; Rt. 11, mi. 6.7, *JF 2334b* [77]; Rt. 11, mi. 7, *JF 2353a* [94]; Rt. 12, mi. 13.6, *BER 118* [93]; Old Ore Rd. (OOR), La Noria jct., *JF 2343* [89]*; OOR, Ernst Tinaja area, *JF 640* [27], *641* [44]; OOR, Candelilla campsite area, *JF 630* [54], *631* [42]; Boquillas Canyon Rd. (BCR), flats in first mile, *JF 2351d* [68]; BCR, N of Barker House, *JF 2344a* [58], *2344b* [97]*, *2344e* [92], *2345a* [52, 85]*, *2345b* [13, 54].

Corynopuntia densispina
USA. TEXAS. **Brewster Co.** Big Bend National Park: River Road, 5.3 mi NE of Solis Ranch, *BER 200* [73]*; River Road, Solis jct., *JF 2397b* [52], *2399* [90], *2400* [n/a]; River Road, 2.8 mi W of Glen Spring Rd. jct., *JF 2349a* [74], *2359d* [67], *2396* [n/a, 84]; Old Ore Rd. (OOR), Carlotta Tinaja, *JF 2380a* [92], *2380b* [86]; OOR, S of Carlotta Tinaja, *JF 2382g* [28], *2382i* [35]*, *2382j* [n/a], *2382k* [85], *2385* [49], *2387* [75]; OOR, N of La Noria jct., *JF 2392* [n/a]; OOR, Ernst Tinaja trailhead parking, *JF 691* [85], *2393b* [50]*, *JF 2218a/MAB 17815* [55]; OOR., Ernst Tinaja jct. area, *JF 637* [n/a], *638* [94], *2394* [53], *2395a* [72]; OOR, Candelilla campsite area, *JF 2378* [90]*, *2378b* [88], *2378c* [73].

Corynopuntia emoryi
USA. ARIZONA. **Graham Co.** 6km SW of Gila Peak, *MAB 11638* [n/a]
USA. NEW MEXICO. **Hildalgo Co.** NW of Lordsburg, 13 mi. NW of Hwy 90 jct., *AZ 2348* [96].
USA. TEXAS. **Presidio Co.** Porvenir, along the river, *BHW 47473* [n/a]; Chamber's Ranch, .6 mi N of Capote Creek, *BER 113* [45]*; Candelaria, 1.2 mi SE of village, *AMP 5996* [89]*.

Corynopuntia grahamii
MEXICO. CHIHUAHUA. 52 mi S of Ciudad Chihuahua, *DJP 13374* [87].
MEXICO. COAHUILA. Cuatro Cienegas, *DJP 5279* [0].
USA. NEW MEXICO. **Doña Ana Co.** SW base of Bishop's Cap Mtn, *AK s.n* .[n/a, n/a, n/a, n/a, n/a, n/a, n/a].
USA. TEXAS. **Hudspeth Co.** Indian Hot Springs, *GGR 98-49* [n/a]; Sierra Blanca, .5 mi S of I10 on FM 1111, *JF 2429* [n/a]. **Presidio Co.** Marfa, 36.8 mi S on FM 169/Casa Piedra Rd., *JF 2416* [65]. **Brewster Co.** Elephant Mtn. Wildlife Mgmt. Area, southern wildlife viewing area, *JF 2372* [n/a, n/a, n/a, n/a, n/a, n/a, n/a], *AMP 6291* [n/a]; Terlingua Ranch, just NW of Cedar Springs Rd. and Marathon Road jct., *JF 2420* [n/a]; Big Bend National Park: N Rosillos Road, 0.5 mi W of Rt. 11, *JF 2338a* [0], *2338b* [n/a], *2338c* [n/a]; N Rosillos Road, 1 mi W of Rt. 11, *JF 2338c* [0]; Nine Point Draw campsite, *JF 694* [33], *2337* [n/a], *2401* [52], *2415* [n/a]; Dagger Flat Road (DFR), 2.3 mi E of Rt. 11, *JF 2352* [n/a]; DFR, 5.5 mi E of Rt. 11, *JF 783* [n/a]; Rt. 11

mi. 20, *JF 695* [64]*; Rt. 11 mi. 19.7, *JF 2336* [n/a, n/a, n/a, n/a, 46, 53, 83]; River Road, 0.3 mi N of Gravel Pit jct., *JF 2346* [n/a]; *JF 2361* [n/a]; Old Ore Rd. (OOR), mid-way, *JF 2403* [44]; OOR, SW of Ernst Tinaja jct., *JF 692* [n/a]; OOR, Ernst Tinaja spur road, *JF 2354* [n/a]; OOR, at La Noria jct., *JF 2342* [n/a]; OOR, 4 mi S of N end, *JF 696* [n/a]. Heath Canyon Ranch: near La Linda crossing, *BER 111* [43]; just N of airstrip, *AMP 6152* [47].

Corynopuntia schottii
MEXICO. COAHUILA. Cuatro Cienegas, *DJP 5714* [75]*; *JL 75413* [0].
USA. TEXAS. **Terrell Co.** N of Sanderson, E of 285 on FM 2400: 13 mi., *JF 2406* [n/a]; 15 mi., *JF 2407* [n/a]; 16 mi., *BER 106* [n/a]; 17 mi., *JF 2408* [n/a], *BER 107* [n/a, n/a, 0]; 17.6 mi., *BER 108* [78]; 30 mi. S of Sheffield on Hwy 349, *SL 26* [0]. **Val Verde Co.** Langtry: *AMP 6248a* [82]; at entrance off Hwy 90, *JF 2404* [n/a, 71, 84, 94], *JF 2405* [77, 87, 93]; 1.4 mi S of Hwy 90, *BER 103* [n/a, 94]. Pandale: 13 mi. N of Hwy 90 on 1024, *BER 101* [82]; 2 mi. E of Pandale on 1024, *BER 102* [89]; 9 mi. N of Hwy 90 on 1024, *BER 100* [1]. **Starr Co.** Rio Grande City: East of downtown on Hwy 83, *JF 2430* [44]; N of Escobares, *AS s.n./MAB 17635* (SRSC, ASC, US) [30]*. **Hidalgo Co.** Mission: Chihuahua Woods Preserve, *ME s.n.* [61]; adjacent to Chihuahua Woods Preserve, *JF 2434* [64].

Corynopuntia aggeria × C. densispina
USA. TEXAS. **Brewster Co.** Big Bend National Park, Old Ore Rd., Ernst Tinaja jct., *JF 635* [26].

Corynopuntia aggeria × C. grahamii
USA. TEXAS. **Brewster Co.** Hwy 118: 0.5 mi W on Agua Fria Rd, *JF 2360a* [0, 50, 64], *2360b* [38, 69]; Terlingua, South County Rd. 8 mi. N of FM 170, *JF 2325* [59], *2368a* [n/a], *2368b* [n/a]; Terlingua Ranch, Red Bluff Hill, *JFS 820* [n/a], *821* [98]; just NW of Cedar Springs Rd. and Marathon Rd. jct., *JF 2421* [n/a], *2428* [n/a]. Big Bend National Park: Maverick Rd, 0.8 mi N of southern terminus, *JF 2356* [0, n/a]; Rt. 11 mi. 6.7, *JF 2334a* [5]*, *2334c* [n/a], *2334e* [n/a, n/a, n/a, n/a, n/a]; Rt. 11, mi 17, *JF 2335a* [n/a], *2335b* [24], *2353b* [n/a, n/a, n/a, 47]; Old Ore Rd., Roy's Peak jct., *JF 697* [83]; *698* [53]; *699* [n/a] *700* [n/a], *2340* [n/a], *2340a* [n/a, n/a], *2341a* [n/a, n/a, n/a], *2341b* [n/a, n/a, n/a, n/a, n/a].

Corynopuntia densispina × C. grahamii
USA. TEXAS. **Brewster Co.** Big Bend National Park: Old Ore Rd., N of La Noria, *JF 2391* [n/a]; Old Ore Rd., SW of Ernst Tinaja jct., *JF 2355* [93].

Corynopuntia grahamii × C. schottii
USA. TEXAS. **Terrell Co.** North of Dryden, *JF s.n.* [n/a].

Appendix E. Character comparison of the *Corynopuntia schottii* complex in the Big Bend region. Unless otherwise noted, measurements given in cm. Descriptions, especially spine characters, refer to the most mature or developed structures of the plant.

	C. aggeria	*C. densispina*	*C. emoryi*	*C. grahamii*	*C. schottii*
Chromosome number (*n*)	11	22	22	22	33
Plant habit	Tight mound	Open mound	Clumps / mound / mat	Small clumps	Small clumps to vast mats
Root habit	Tuberous	Diffuse, thickened	Diffuse, hair-like	Tuberous	Diffuse, hair-like
Adventitious roots common	No	Yes	Yes	No	Yes
Plant width	30 – 60	30 – 150	30 – 150+	15 – 30	15 – 300+
Plant height	15 – 30	10 – 30	10 – 30+	10 – 20	5 – 12
Joint attachment	Strong	Strong	Strong	Weak	Weak
Joint growth origin	Lateral	Lateral	Lateral	Apical	Lateral
Joint length	3.5 – 8	6 – 9	9 – 15	2 – 5	2 – 8
Joint size ratio	2-3x long as broad	2-3x long as broad	≥ 3x long as broad	1-2x long as broad	≥ 3x long as broad
Joint shape	Clavate, elongated	Clavate, elongated	Clavate, elongated	Obovate to cylindric	Clavate, J-shaped
Tubercle shape, abaxial profile	Rounded/ inflated	Rounded/ inflated	Rounded/ inflated	Rounded/ inflated	Flat/ deflated
Areolar wool habit; where most abundant	Protruding, villous; basally	Protruding, villous; basally	Flat/short, felt-like; apically	Protruding, villous; basally	Flat/short, felt-like; apically
Central spine no.	1 – 4 (6 – 9)	(4) 7 – 11 (+)	6 – 8	7 – 8	6 – 8 (10+)
Central spine shape: adaxial/ abaxial	Flat / angled	Flat / angled	Flattened but no angles, oval profile	Terete (rare: slight angle below)	Flat / angled; thinned margins

Appendix E, continued. Character comparison of the *Corynopuntia schottii* complex in the Big Bend region. Unless otherwise noted, measurements given in cm. Descriptions, especially spine characters, refer to the most mature or developed structures of the plant.

	C. aggeria	*C. densispina*	*C. emoryi*	*C. grahamii*	*C. schottii*
Central spine color; tone	Various, with white/gray; streaked	Yellowish (pinkish), white/gray; streaked	Tan/golden brown; saturated	Peach to red-brown; saturated, blotchy	Tan to red-brown, white margins; saturated, blotchy
Central spine base shape / color	Bulbous / differently colored	Flared to bulbous / diff. colored	Flared (uppers flared to bulbous)	Bulbous / diff. colored, iridescent	Undifferen-tiated, hidden by wool
Central spine epidermis	Smooth, farinose, especially distally	Smooth, farinose, especially distally	Variously ridged, thin appressed trichomes	Lateral ridges, robust appressed trichomes	Smooth, longitudinal striations
Main central spine present	No	No	Yes	No	No
Central spines often twisted	Yes	Yes	No	No	No
Subcentrals present	No	No	Yes	No	Yes
Diminutive subcentral	No	No	No	No	Yes
Location of most mature spine clusters in joint	Upper half to third	Upper half	Upper half	$\geq$ Upper $^3/_4$	Upper half
Radial spine color	Bright white; bases different	Bright white/gray; bases various	Light tan	White; bases different, iridescent	Cream-tan
Radial spine number (pairs)	1 – 2 (3)	2 – 3	2 (3)	3 – 4 (5+)	2 – 3
Radial spine aspect (esp. lowest pair)	Appressed and decurved at base	Appressed and decurved at base	Descending	Appressed to decurved at base	Descending

Appendix E, continued. Character comparison of the *Corynopuntia schottii* complex in the Big Bend region. Unless otherwise noted, measurements given in cm. Descriptions, especially spine characters, refer to the most mature or developed structures of the plant.

	C. aggeria	*C. densispina*	*C. emoryi*	*C. grahamii*	*C. schottii*
Long 1° radial pair	No	Yes	No	Various	No
Glochids in brachyblasts	Common	Common	Rare	Common	Rare
Glochid/areole habit towards base of plant	Often increased, radiating, protruding	Often increased, radiating, protruding	No pattern	Often increased, radiating, protruding	No pattern
Location of joints with flower buds	Terminal	Terminal	Terminal	Terminal	Medial
Conic leaf length, pericarpel rim areoles (mm)	< 5	< 5	≤ 5	< 5	> 5
Bud proliferation common	No	No	No	No	Yes
Flower color	Yellow	Yellow	Yellow	Yellow (pink)	Yellow
Filament color	Red, pink	Green, red, pink	Green/clear	Green/clear	Green/clear
Stigma lobe color	Green	Green	Cream	Green	Green
Fruit color, at maturity	Green	Green	Yellow	Green	Yellow
Phenology	(Feb-)Mar–Apr(-May)	(Mar-)Apr–May	May–June	(Mar-)Apr–May	(May-)Jun(-Jul)
Woody old growth	Yes	Yes	Yes	Yes	No

Appendix F. Specimens used to populate range dot map, additional to those already referenced in this report. Specimens were either reviewed via the SEINet portal online, annotated as a loan, or via photo request (MO, US). Underlined collection numbers indicate the specimen is also a chromosome number voucher. See Methods and Materials for abbreviation explanations.

Corynopuntia aggeria
MEXICO. CHIHUAHUA. 25 km NE of Escalon, *MAB 15667* (ASC).
MEXICO. COAHUILA. SE of Torreón, *MAB 12819* (ASC); Bolsón de Mapimí *DJK K-8126* ASC);
    16.8 mi N of Aldama *EL L22846* (ASC); 10 km WSW of Cuatro Cienegas *MAB 12817* (ASU,
    DES).
USA. TEXAS. **Presidio Co.** N of Ruidosa, *BER 130*. **Brewster Co.** Terlingua, *WW 476*; Big Bend
    National Park, N of Talley Mtn, *MSA 83* (MICH); S of Chilicotal Mtn, *MSA 21* (MICH); Dagger
    Flat, *AMP 5223*; Old Ore Rd., *AMP 6078*; River Rd, *BER 126*.

Corynopuntia emoryi
USA. TEXAS. **Presidio Co.** Porvenir, *BHW 47473*; near Candelaria, *BER 113*, *SL 3*.

Corynopuntia grahamii
MEXICO. CHIHUAHUA. 5 km NW of La Cruz and Rio Conchos, *MAB 15662* (ASC); 54 mi S of
    Chihuahua City on Rt 45, *DJP P-13374* (ASC); Ciudad Juarez, *RDW 11680* (ASC); 2 km W of
    Juarez, *RS 11798* (UTEP).
MEXICO. COAHUILA. N of Ocampo, *MAB 15672* (ASC); 106 km E of Torreón, *DJP P-13875*
    (ASC); Cuatro Cienegas Basin, *DJP 5279* (ASC).
MEXICO. DURANGO. 20 mi S Leon Guzman Plaza, Rt. 40, *DJP P-13458* (ASC); ca. 19 air mi W
    Torreón, *DJP P-13866* (ASC); 21 air mi SW Torreón, *DJP P-13864* (ASC).
USA. NEW MEXICO. **Doña Ana Co**. Franklin Mtns, *Champie 3934* (UNM); Bishop's Cap Mtn.,
    GW 3422 (UNM). **Otero Co.** Brokeoff Mtns, *GW 3829* (UNM).
USA. TEXAS. **El Paso Co.** El Paso, *AZ 2631* (DES), *RDW 32137* (UTEP); Franklin Mtns, *Ferguson
    149* (UTEP); Hueco Mtns, *RDW 19354* (DES, UTEP). **Jeff Davis Co.** 96 Ranch on the Rio
    Grande, *PRM s.n.* **Hudspeth Co.** Indian Hot Springs, *GGR 89*-49. **Presidio Co.** N of Ruidosa,
    MSA 1074 (MICH); Solitario, *JEH 702* (SRSC)*; RDW 23061* (UTEP). **Brewster Co.** Nine Point
    Mesa, *PRM 988* (SRSC), *MSA 909* (MICH); Terlingua, *PRM 960,* BBNP, River Rd, *BER 121*,
    BBNP, Lone Mtn, *MSA 827* (MICH), BBNP, Chilicotal Mtn *MSA 21* (MICH); FM 2627 near La
    Linda, *BER 119*; Reagan Canyon, *BHW 47449* (SRSC), *MSA 977, 1005* (MICH).

Corynopuntia schottii
MEXICO. COAHUILA. Cuatro Cienegas Basin, *Lewis ASU59091*, *DJP P-5539*, *DJP 5714*, *DJP
    4123-A* (*ASC*).
USA. TEXAS. **Brewster Co.** Reagan Canyon, *MSA 981* (MICH). **Pecos Co.** FM 2400, *BER 104*.
    Terrell Co. FM 2400, *BER 109*; E of Langtry, *Trelease DES54522* (DES); Hwy 90 at Pecos
    River bridge, *AMP 6244*. **Val Verde Co.** N of Dryden, *SL 30*; near Comstock, *BER 101*, *DW 40*
    (UNM); Lake Amistad, *AMP 3436*. **Schleicher Co.** W of Eldorado, *JFW 1103*. **Brown Co.**
    Brownwood, *Palmer 11121* (MO). **Webb Co.** W of Laredo, *DW W478* (UNM)*,* near Laredo,
    DW 221 (UNM). **Zapata Co.** 5 mi. E of Zapata, *LV 2782* (UNM). **Starr Co.** W of Rio Grande
    City, *TP s.n.* **Hildalgo Co.** Near Reynosa, *EUC 1884* (MICH). **Cameron Co.** Brownsville,
    Runyon s.n. (US!).

Corynopuntia aggeria × C. grahamii
USA. TEXAS. **Brewster Co.** Terlingua Ranch, *JFS 821*; BBNP, Dagger Flat Rd. *AMP 5223;* BBNP,
    SE of Castolon, *MSA 11* (MICH).

Appendix G. Comments on, and corrected erratum for, previously published photographs of *Corynopuntia schottii* complex species.

Anderson 2001
p. 347. Identified as *C. schottii* however the red filaments, tightly bunched habit, and long white-containing central spines indicate *C. aggeria*.

Anthony 1956
p. 241, Fig. 10. Identified as *C. schottii*, however based on the locality and tightly mounded habit the photo shows *C. aggeria*. Fig. 12 is correct as identified. Fig. 13 shows *C. aggeria*.

Benson 1982
p. 369, Fig. 367. Identified as *C. schottii*, though considering the tightly bunched habit, flat white/light-colored central spines, and apparently darker-colored filaments, as well as reported locality of Tornillo Creek, Big Bend National Park, this photo shows *C. aggeria*.
p. 370, Fig. 368. The drawing of *C. schottii* includes some typical characters such as lateral growth, clavate joints, thin pericarp with longer conic leaves, flattened central spine, and what could be construed as diminutive central spines, though the spine cluster depiction is not exactly representative. The fleshy mature fruit (Fig. 368, 4) is atypical, normally being more swollen-spindle-shaped, tubercles not apparent, with stellate glochids from protruding areoles.
p. 371, Fig. 369. Rather than showing only characters representative of *C. grahamii* as identified, this drawing represents characters known in *C. schottii* (diminutive central spines, fruit) as well as *C. aggeria* (tuberous roots; lateral stem growth; elongate-clavate stems; long, decurved central spines; few central spines; basally-abundant glochids,), and *C. grahamii* (tuberous roots; apical stem growth; small, ovate stem shape (Fig. 369, 2); rounded tubercles; numerous radial spines; basally-abundant glochids). Drawing taken from original species publication in Engelmann (1859).

Evans 1998
p. 58: Identified as *C. grahamii*, however the tightly packed stems, white-grey flat spines, and pink-red filaments indicate *C. aggeria*.
p. 70: Identified as *C. schottii*, however the tightly mounded stems, spines decurved and white, plus numerous buds and flowers indicate *C. aggeria*.

Hunt et al. 2006
p. 479, 479.1: *C. aggeria* correct as identified, clearly showing red filaments, sparse spines, and bunched habit. 479.4: *C. emoryi* correct as identified, with its relatively short centrals and robust stems; this plant was in cultivation in Alpine, TX, resulting in the discordant background of volcanic rocks and fallen oak leaves. 479.5: Identified as *C. emoryi* however the apical stem growth, terete central spines, and abundant glochids, are traits associated with *C. grahamii*. 479.6: *C. grahamii* correct as identified.
p. 481, 481.3: Identified as *C. schottii* however the red filaments, purple-white central spines with iridescent bulbous bases, and bunched habit indicate *C. aggeria*. 481.4: Identified as *C. schottii* however it is likely an *C. aggeria* morphotype due to the red filaments, white central spines, and abundant glochids

Konings 2009
p. 164: Background photo is of *C. schottii*, as identified, showing its typical matted habit in south Texas. Pictures 2 and 3 (upper and lower right corners) are likely of a hybrid between *C. grahamii* (prominent wool in the globose new stem growth, some terete and pink/brown central

spines) and *C. aggeria* (lateral stem growth, some flat white central spines, abundant buds, pink filaments, fertile fruits).

p. 165: *C. grahamii* correct as identified, by its apical stem growth, numerous terete central spines, isolated mounded habit as opposed to extensive, matted growth.

Powell and Weedin 2004, Powell, et al. 2008

Plate 34, 35: *C. schottii* correct as identified, especially regarding the yellow ripening fruit, but perhaps introgressed with *C. grahamii* as it is lacking broad tan-brown central spines with white margins, and obviously clavate, J-shaped stems.

Plate 36: *C. grahamii* correct as identified, especially regarding the apically-chaining stems at top center of photo; however flowers appear to have darker, perhaps pink-red filaments which would indicate a degree of introgression with *C. aggeria*. Plants are in cultivation thus the atypical habitat of volcanic rocks and fallen oak leaves.

Weniger 1988

p. 318: Likely *C. grahamii* as identified, however atypical with elongate cylindric joints, white and tan-red central spines, and tightly associated stems. Not pictured in natural habitat.

p. 320: *C. schottii* correct as identified with the typical clavate stems, broad and brown central spines with white margins, and yellow ripening fruits. Not pictured in natural habitat.

p. 321: *C. emoryi* (*C. stanlyi*) correct as identified.