DONALD PINKAVA'S STUDIES ON THE VASCULAR FLORA OF THE BOLSÓN DE CUATRO CIÉNEGAS IN THE CHIHUAHUAN DESERT, UPDATES, AND TAXONOMIC INFORMATION ON ACANTHACEAE IN THE REGION

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ABSTRACT

In 1967 Donald Pinkava began botanical exploration of the then little-studied Bolsón de Cuatro Ciénegas in the east-central portion of the Chihuahuan Desert. This closed (i.e., internally drained) basin contains an unusual assemblage of biotic communities in a relatively small region. Following 10 years of field studies, between 1979 and 1984 Pinkava published catalogs of the vascular flora of his 2,000 km^2 study area, and documented 860 species in 456 genera from 114 families. He also recognized and summarized eight "vegetation zones" in the study area: aquatic and semiaquatic habitats, gypsum dunes, basin sacaton grasslands, a transition zone, desertscrub, chaparral, oak-pine and oak woodlands, and montane conifer forests. Some updates and discussions are offered relative to both the flora and vegetation of the basin area. The botanical richness of this region is illustrated by Acanthaceae. A key to and synopsis of the 13 species in six genera of that family occurring there are provided. Lists comparing Acanthaceae in the Sonoran and Chihuahuan deserts are also appended. Pinkava's pioneering botanical inventory in and around the Bolsón de Cuatro Ciénegas was both timely and has had a significant impact on subsequent efforts to preserve this precious natural resource of international significance.

RESUMEN

Donald Pinkava comenzó en 1967 la exploración botánica del 'Bolsón de Cuatro Ciénegas' (poco estudiada en ese momento) en la parte centro-este del Desierto Chihuahuense. Este bolsón cerrado (es decir, con drenaje interno) contiene un conjunto inusual de comunidades bióticas en una región relativamente pequeña. Después de 10 años de estudios de campo, entre 1979 y 1984 Pinkava publicó catálogos de la flora vascular de su área de estudio de 2.000 km2 y documentó 860 especies en 456 géneros de 114 familias. También reconoció y resumió ocho "zonas de vegetación" en el área de estudio: hábitats acuáticos y semiacuáticos, dunas de yeso, pastizales de sacaton del bolsón, una zona de transición, matorral desértico, chaparral, bosques de robles-pinos y robles, y bosques montanos de coníferas. Se ofrecen algunas actualizaciones y discusiones relativas tanto a la flora como a la vegetación del área del bolsón. La riqueza botánica de esta región está ilustrada por Acanthaceae. Se proporcionan una clave y una sinopsis de las 13 especies en seis géneros de esa familia que se encuentran allí. También se adjuntan listas que comparan Acanthaceae en los desiertos de Sonora y Chihuahua. El inventario botánico pionero de Pinkava en y alrededor del Bolsón de Cuatro Ciénegas fue oportuno y ha tenido un impacto significativo en los esfuerzos posteriores para preservar este precioso recurso natural de importancia internacional.

INTRODUCTION

In 1967 Donald J. Pinkava, director of the Arizona State University Herbarium, was invited by the well-known ichthyologist Wendell L. Minckley to study the rich yet poorly documented flora of the Bolsón de Cuatro Ciénegas in the east-central portion of the Chihuahuan Desert in the Mexican state of Coahuila. Minckley had been studying the basin and its aquatic biota, especially the highly endemic fish fauna (e g , Minckley 1969), and invited his ASU colleague to accompany him on an expedition there. The University's growing herbarium was focused on plants from the Sonoran Desert, in the northern reaches of which the school is located, and this was potentially a good opportunity to add collections from another major arid region of North America. Additionally, the prospect of seeing, collecting, and studying Cactaceae from a very different desert undoubtedly appealed to Pinkava's interest in the taxonomy of that family.

Over the next decade, Pinkava and co-collectors undertook six trips to the Bolsón de Cuatro Ciénegas to study the vegetation and collect plants in both the basin and surrounding mountains (BCC). These took place in the following years (months/co-collectors): 1967 (August/G. Cole, W. Minckley), 1968 (June/D. Keil, E. Lehto), 1969 (April/D. Keil, J. LaBounty, E. Lehto, J. Lewis, E. Meyer), 1973 (March), 1975 (August/T. Reeves),

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1976 (June/L. McGill, T. Nash, T. Reeves). The fieldwork, identification of collections, and analyses resulted in five publications between 1977 and 1984 that dealt specifically with the vegetation and flora of a ca. 2,000 km^2 study area in and around the BCC. The first of these (Pinkava 1978) consisted of a general description of the region, a preliminary classification of the vegetation with discussions of each of the eight zones recognized, and early estimates of the numbers of plant taxa. A revised vegetation scheme and the first portion of the floristic catalogue (Selaginellaceae–Orchidaceae) soon followed (Pinkava 1979). Pinkava (1980) continued the floristic catalogue (Casuarinaceae–Loasaceae), which he completed in 1981 (Pinkava 1981; with Cactaceae–Asteraceae). A summary of the vascular plants revealed 111 families, 429 genera, 796 species, and 28 additional infraspecific taxa (824 species + infraspecific taxa). Over the next several years, the accumulation of new records, corrections/updates to identifications, and changes in nomenclature resulted in a revised catalogue (Pinkava 1984). In this final installment on plants of the region, 114 families, 456 genera, 860 species, and 19 additional infraspecific taxa (879 species + additional infraspecific taxa) were documented. In addition, portions of the BCC were revealed to be the type localities for at least 49 taxa of plants, 23 of which were noted to be endemic there. The largest plant families (number of species) in the region were: Asteraceae (125), Poaceae (76), Cactaceae (50), and Fabaceae (47); each of these families except Poaceae contains one or more species endemic to the Bolsón de Cuatro Ciénegas. Pinkava's two subsequent publications on the BCC focused on conservation of the region (Pinkava 1987; Pinkava & Villarreal-Quintanilla 1997). Four species from the BCC have been named for Pinkava: *Abutilon pinkavae* Fryxell, *Ancistrocactus pinkavanu*s García-Mor. et al., *Erigeron pinkavii* B.L. Turner, and *Euphorbia pinkavana* M.C. Johnst.

THE BOLSÓN DE CUATRO CIÉNEGAS

The Chihuahuan Desert region (CDR), as delimited by Henrickson and Straw (1976) and accompanying maps (García 1976), extends from southeastern Arizona through southern New Mexico and the Trans-Pecos region of western Texas southeastward through northern Mexico to a small area south of the city of San Luis Potosí bordering the state of Guanajuato. The region occupies a plateau between the Sierra Madre Oriental and the Sierra Madre Occidental with a basin and range landscape. The CDR of ca. 507,000 km^2 includes desertscrub, grasslands, and more temperate biotic communities at higher elevations on many of the mountain ranges (sierras) within its borders. The CDR has been acknowledged as the most biologically diverse desert in the Western Hemisphere (Bell et al. 2014), with some 3,382 plant species, and at least 826 species, infraspecific taxa, and hybrids endemic or nearly endemic there (Villarreal-Quintanilla 2017).

Among several biodiverse hotspots within the CDR, the BCC was described in some detail by Minckley (1969). Floristically, it is one of the better-known of these hotspots, owing largely to the pioneering work of Pinkava (1984:23), who offered a compelling portrayal of the BCC, "Towering limestone sierras capped by conifer forests overlook a broad desertic valley studded with playas, streams, subterranean tubes, artesian wells and ciénegas." That is a fitting description in a nutshell of the BCC, with its juxtaposition of wetlands and arid desert (Fig. 1). Along with the scenic beauty of this geologically unusual region, it also possesses a rich and fascinating biological diversity with an array of endemic organisms. Extensive studies of the region over the past ca. 60 years have revealed much about its fragile ecosystems (e.g., Minckley 1969; Marsh 1984; Mandujano et al. 2020).

The BCC is an internally drained (until recent historic times) basin near the eastern edge of the CDR surrounded, and partially bisected, by sierras of varying heights (Fig. 2). Its most distinctive feature is the presence of both subterranean and epigeal water at the basin's floor. Much of this water originates from cool or thermal springs emerging from subterranean tubes as "pozos" (essentially sinkholes), which can enlarge or elongate via slumping into "lagunas" or channels/streams (Fig. 1). Because the water is highly mineralized, especially with calcium sulfate, evaporation during dry periods results in the crystallization of gypsum salts along shores; when dry, these crystals can be blown by winds to form gypsum dunes. Mountains surrounding the basin floor rise up via arroyo-dissected bajadas that are soon replaced by limestone slopes harboring various plant communities depending on elevation, exposure, and precipitation.

Fig. 1. Bolsón de Cuatro Cienégas and surrounding mountains. **A.** Stream/channel on basin floor, photo by and © Evan Carson, used with permission. **B.** Don Pinkava and Elinor Lehto, collecting in the BCC in 1968, photo by and © David Keil, used with permission. **C.** Gypsum dunes, © 2013 4M4T3URdC4CTU5-via Wikimedia Commons (CC BY-NC-SA 3.0). **D.** View of basin from NW end of Sierra San Marcos looking across basin floor to Sierra de la Madera, photo by TFD. **E.** Aerial view of the Pozos Azules complex, gypsum sands, and sierras, photo by and © David Jaramillo, used with permission. **F.** Pozo, photo by TFD.

The stated boundaries of Pinkava's ca. 2,000 km^2 study area of the BCC are somewhat vague, but include the 700 or more km^2 portion of the valley floor shown on his map (Pinkava 1984), and at least the adjacent, basin-facing slopes of most of the various surrounding sierras (Fig. 2). He specifically excluded the Sierra de la Fragua for lack of collections from there, but at least the basin-facing slopes of this sierra should be considered as part of the basin. I calculate the areas of those regions as ca. 2,000 km^2. However, Pinkava and others also made numerous collections on the outer slopes of surrounding mountains, and these are included in his floristic account. The elevation of the basin floor varies from 839 meters in the northwest to 681 in the northeast, and averages ca. 730 meters throughout (based on my sampling in Google Earth Pro). The highest of the surrounding sierras, the Sierra de la Madera, attains an elevation of ca. 3,020 meters. Within this region, Pinkava (1979, 1984) recognized eight "vegetation zones" as follows (taxon names and authors as provided by Pinkava in 1984):

Aquatic and Semi-aquatic Habitats: in and around the pozos, lagunas, streams/channels connecting them, and the marshes associated with these water bodies; typical plants include: sedges, grasses, *Ludwigia octovalis* (Jacq.) Raven, *Nymphaea ampla* (Salisb.) DC , *Utricularia obtusa* Sw., *Anemopsis californica* (Nutt.) Hook. & Arn , *Najas marina* L., and *Potamogeton nodosus* Poir.

Basin Sacaton Grasslands: on the ± saline basin floor with dominants including: *Sporobolus airoides* (Torr.) Torr., *S. spiciformis* Swallen, *S. wrightii* Munro ex Scribn., *Distichlis stricta* (L.) Greene, and *Monanthochloe littoralis* Engelm.

Gypsum Dunes: active or stabilized dunes several meters tall on the basin floor support *Prosopis glandulosa* Torr., *Acacia greggii* A. Gray, *Yucca treculeana* Carrière, and *Varilla mexicana* A. Gray; the dunes and gypsum flats are also particularly rich in gypsum endemics (gypsophiles), several putatively endemic to the BCC including: *Gaillardia gypsophila* B.L. Turner, *Machaeranthera restiformis* B.L. Turner, and *Phacelia marshalljohnstonii* N.D. Atwood & Pinkava.

Transition Zone (between grasslands and bajadas): islands or hammocks ("mogotes") of shrubs and trees around the basin including: *Condalia warnockii* M.C. Johnst., *Suaeda palmeri* (Standl.) Standl., *Atriplex canescens* (Pursh) Nutt., *Acacia greggii*, and *Prosopis glandulosa*.

Desertscrub: bajadas, lower montane slopes, and arroyos support characteristic species of the Chihuahuan Desert, including: *Larrea tridentata* (DC.) Coville, *Agave lecheguilla* Torr., *Jatropha dioica* Cerv., *Euphorbia antisyphilitica* Zucc , *Parthenium incanum* Kunth, *Flourensia cernua* DC , and many cacti.

Chaparral: often dense, shrub and small tree formation generally at elevations above desertscrub and dominated by various oaks (e.g., *Quercus hypoxantha* Trel.), and with *Arbutus texana* Buckley, *Arctostaphylos pungens* Kunth, *Rhus aromatica* Aiton, *Sophora secundiflora* (Ortega) Lag., *Fraxinus greggii* A. Gray, and *Nolina cespitifera* Trel.

Oak-pine and Oak Woodlands: woodlands in protected canyons and on higher and moister slopes, with various oaks (e.g., *Quercus gravesii* Sudw.), *Pinus johannis* M.-F. Robert (previously listed as *P. cembroides* Zucc.), *Juniperus erythrocarpa* Cory, *J. flaccida* Schltdl., *Garrya ovata* Benth., and *Prunus serotina* Ehrh.

Montane Conifer Forests: mesic montane forests in higher north-facing canyons and upper slopes of the highest sierras that include some or all of *Pseudotsuga menziesii* (Mirb.) Franco, *Abies durangensis* var. *coahuilensis* (I.M. Johnst.) Martínez, *Pinus strobiformis* Engelm., *P. arizonica* Engelm , *Cupressus arizonica* Greene in the canopy and *Quercus greggii* (DC.) Trel , *Arbutus texana*, *Acer grandidentatum* Nutt., and *Cornus sericea L.* (previously listed as *C. stolonifera* Michx.) in the understory.

FLORISTIC/VEGETATIONAL UPDATES

Numerous studies and publications since Pinkava's investigations on the vegetation and flora of the BCC permit some updating of his accounts. Brown (1982) and Brown et al. (1998) developed a continent-wide classification of biotic communities for North America and Central America. At least six of Pinkava's vegetation zones each correspond well to one of these biotic communities, as follows: Chihuahuan Interior Marshland (aquatic and semi-aquatic habitats), Chihuahuan (Semidesert) Grassland (basin sacaton grasslands),

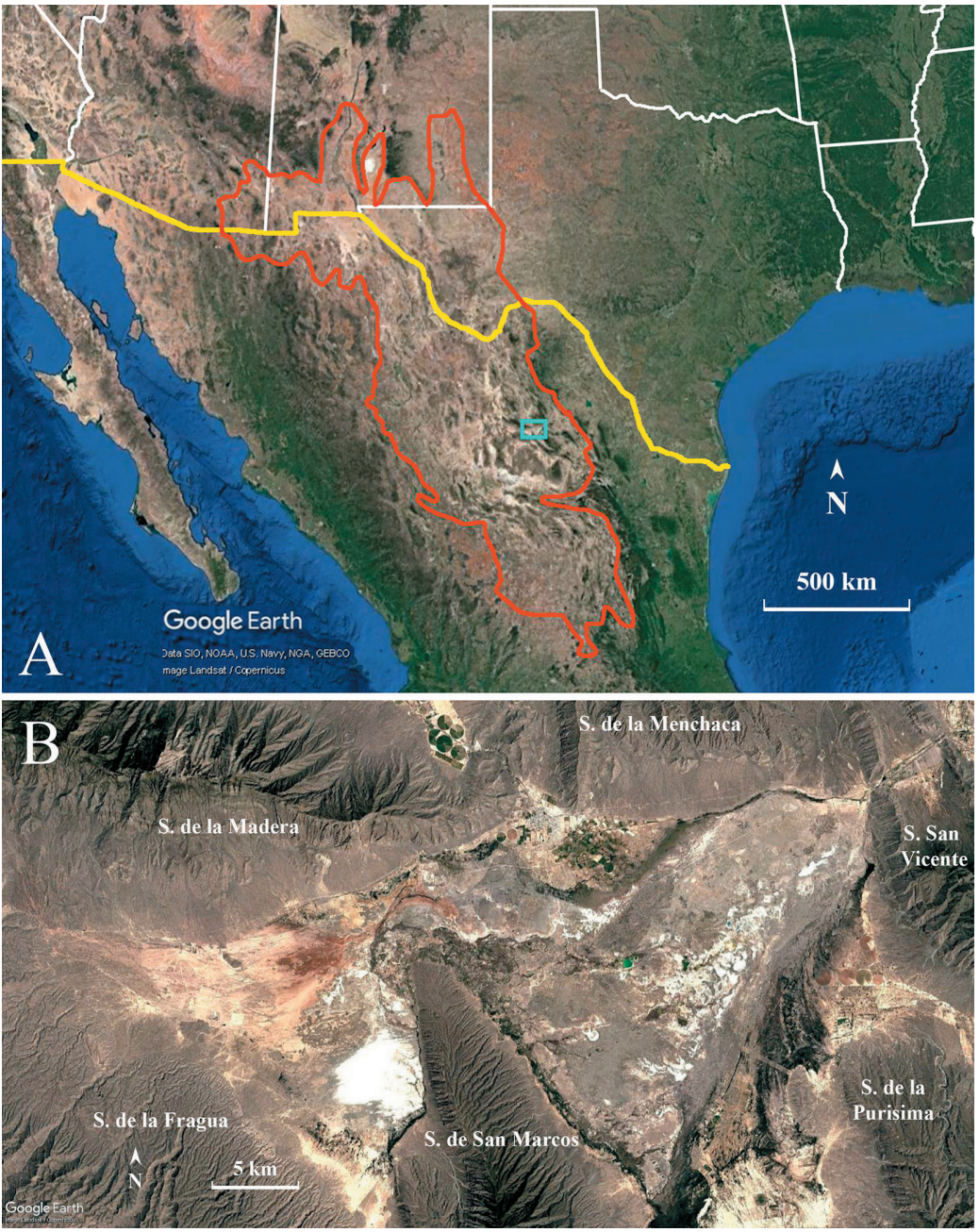

Fig. 2. **A.** Map of portions of the southern United States and northern Mexico (international border in yellow), the approximate boundaries of the Chihuahuan Desert region (red), and location of the Bolsón de Cuatro Cienégas (blue rectangle). **B.** Satellite image of the Bolsón de Cuatro Ciénegas in 2020, with the six surrounding sierras identified; the white area to the west of the S. de San Marcos is the Laguna Grande region (dry) surrounded by white gypsum sand that form dunes up to 10 m high; the town of Cuatro Ciénegas lies just inside the basin near top-center, to the south of the pass between the S. de Madera and the S. de la Menchaca. Both images from Google Earth Pro (US Dept. of State Geographer, © 2021 Google, Image Landsat/Copernicus, ©2021 INEGI).

Chihuahuan Desertscrub (desertscrub), Chihuahuan Interior (Coahuila) Chaparral (chaparral), Madrean Evergreen Forest and Woodland (oak-pine and oak woodlands), and Madrean Montane Conifer Forest (montane conifer forests).

While Brown et al.'s (1998) biotic communities are useful and readily mapped on a large-scale, Pinkava's classification of the vegetation in the BCC offers some advantages for understanding and distinguishing vegetation patterns in a smaller, but highly diverse, region. For example, Brown et al. (1998) included the "gypsum dunes" as a component of Chihuahuan Interior Strand, a wetland biotic community, because the dunes are formed by and associated with the water bodies of the basin floor. However, from a vegetation perspective, the species occurring on and those important in stabilizing the dunes are more typical of drier habitats than wetlands. Also, Pinkava's transition zone (between basin sacaton grasslands and bajadas) would be a transition zone between Chihuahuan (Semidesert) Grassland and Chihuahuan Desertscrub, characterized by mogotes. Brown (1982) and Brown et al. (1998) treated these "islands" as a series (a level of vegetation classification below biotic communities) within the Chihuahuan (Semidesert) Grassland.

Recently, Zavala-Hurtado and Jiménez (2020) offered a useful classification of plant communities, and threats to them, for the Chihuahuan Desert. Their communities "roughly correspond" to those of Pinkava, but are not "fully equivalent." For example, Zavala-Hurtado and Jiménez (2020:13) distinguish microphyllous from rosetophyllous desertscrub, and treat Pinkava's transition zone as "a kind of transition between rosetophyllous desert scrub and the herbaceous vegetation of the halophytic communities."

The floristic totals indicated for the BCC by Pinkava (1984, and noted above) continue to be cited (e.g., Pinkava & Villarreal-Quintanilla 1997; Ezcurra et al. 2020). However, since 1984, there have been numerous name changes, identification corrections, taxonomic realignments, and taxa newly recorded from the region. Building on Pinkava's final list, Vásquez-Aldape et al. (2001) provided an updated account of the flora of the BCC. Based on more recent field collections and literature, they listed 112 families, 466 genera, and 893 total taxa (888 species + five additional infraspecific taxa). Their additions included native, non-native, and cultivated species. Vásquez-Aldape et al. (2001) also provided a list of some name changes; and for each taxon they included: vegetation zone (Pinkava's categories), a common name, life-cycle duration, native vs. introduced, and information on uses by humans. Eight hundred-sixty species were reported as native and 28 as introduced. New totals for the four families with the most species remain in the same order but with new counts: Asteraceae (127), Poaceae (81), Cactaceae (47), and Fabaceae (47). Many of the totals for numbers of taxa reported by Vásquez-Aldape et al. (2001) are based on my recounts of their data rather than the totals stated in their publication. Additional species recorded from the BCC since 1987, but not cited by Vásquez-Aldape et al. (2001), include: *Baccharis crassicuneata* Nesom, *Gundlachia truncata* (Nesom) Urbatsch & R.P. Roberts, *Nama cuatrocienegensis* Nesom, and *Solidago gypsophila* Nesom, The latter two species are gypsophiles or gypsovags (Ochoterena et al. 2020), endemic to the BCC. It is noteworthy that the BCC is reported to have the highest number of CDR endemic (or nearly so) plant taxa (86) among various regions of the CDR (Villarreal-Quintanilla et al. 2017). Also, Ochoterena et al. (2020) reported occurrences for 297 species on gypsum soils in the Municipality of Cuatro Ciénegas, a much larger region that includes the BCC, with at least 31 of them gypsophiles.

CONSERVATION

Minckley, who had introduced Pinkava to the BCC, was a devoted and constant proponent for protection of that landscape and its biota; Pinkava soon came to share that sentiment. In his first publication on the BCC, Pinkava (1979:41) noted that because of the high percentage of endemic plants and animals, the unique aquatic habitats, and the region's scenic value, "there is an urgent need to continue efforts in preserving at least a portion of this ecosystem before an important part of man's heritage is lost." In his subsequent publications, Pinkava (1979, 1984) extolled the distinctive aquatic habitats, botanical richness/endemism, and scenic value of the BCC; listed apparent threats to the landscape; and urged preservation of the region's unique ecosystems. His final two publications on the BCC (Pinkava 1987; Pinkava & Villarreal-Quintanilla 1997) were focused

on the urgent need for conservation efforts to preserve the region's unique landscape. The threats noted to the basin's biota and ecosystems included: goat and cattle grazing, agriculture, periodic burning of the basin floor, canalization, contamination and depletion of water, extraction/mining of gypsum, and logging of conifers. Over time these threats have altered the basin in several ways, including: man-made canals that now ultimately drain eastward out of the naturally internally drained basin; several pozos and lagunas have become ephemeral or have dried-up in recent decades (Minckley 1969); and agriculture has altered the soil nutrient dynamics (Hernández-Becerra et al. 2016). Other more recently recognized threats include: the spread of exotic species, plant and animal poaching, unregulated tourism, and climate change. The effects of climate change on regions in the CDR during the current century, with rising temperatures resulting in increased evaporation, will likely have profound impacts, especially on the basin's aquatic ecosystems (Briggs et al. 2019).

Based on the accumulated inventories and other scientific data derived from, the ecological fragility of, and the known threats to the BCC, in 1994 the Mexican government designated an 84,347 hectare region there as the Área de Protección de Flora y Fauna Cuatrociénegas. A comprehensive management plan for the protected area was published in 1999 (Secretaria de Medio Ambiente, Recursos Naturales y Pesca 1999). This same region was subsequently designated as Ramsar Site no. 734 by the Ramsar Convention on Wetlands of International Importance, and in 2006 as the Cuatrocienegas Biosphere Reserve by UNESCO's Man and the Biosphere Programme in its World Network of Biosphere Reserves. In 2006, the Desert Fishes Council established the Centro de Investigación Científica de Cuatrociénegas, a research station to assist researchers, educators, and the local community in efforts to study and preserve the BCC.

Conservation efforts continue at several sites in the CDR and especially in the BCC. An international conservation planning effort singled out Cuatro Ciénegas and other isolated spring systems as one of four main areas of conservation priority in the Chihuahuan Desert Ecoregion (Bell et al. 2014). Indeed, the Complejo de Cuatro Ciénegas was rated as having the highest priority for conservation among both terrestrial and aquatic sites in the Mexican portion of the Chihuahuan Desert when prioritizing both degree of threat and degree of irreplaceability (Bell et al. 2014).

ACANTHACEAE IN AND AROUND THE BOLSÓN DE CUATRO CIÉNEGAS

With more than 400 species, Mexico has the fifth richest assemblage of Acanthaceae among the world's nations—after Madagascar, Brazil, Tanzania, and India (Daniel, unpublished). Because Acanthaceae occur widely in both wet and dry environments, one likely evolutionary driver accounting for the richness of species in Mexico is the occurrence of both types of biotic communities in various parts of the country. Within both large deserts and smaller, often isolated, arid and semi-arid regions, numerous and often endemic Acanthaceae occur. Of the two largest, creosotebush-dominated deserts of North America, the Sonoran Desert (as delimited by Brown et al. 1998) and Chihuahuan Desert region, the latter is richer in both occurrences and endemism of species of Acanthaceae (Appendix 1). At least 42 species of the family occur in the CDR with 21 (50%) of them restricted to it. Indeed, the family has the eighth highest number of endemic species (tied with Euphorbiaceae) among families of flowering plants in the CDR (Villarreal-Quintanilla et al. 2017). The higher number of endemic species in the Chihuahuan Desert suggests either greater speciation in that larger, higher, wetter, cooler, and more limestone-rich region, or longer survival for Acanthaceae there. Of the seven species common to the two deserts, five (*Carlowrightia arizonica* A. Gray, *Dicliptera resupinata* (Vahl) Juss., *Elytraria imbricata* (Vahl) Pers., *Ruellia ciliatiflora* Hook., and *Tetramerium nervosum* Nees) are widespread well beyond those regions.

Based on herbarium specimens of Acanthaceae emanating from CDR that I encountered during my graduate studies on the acanthaceous genera *Carlowrightia* A. Gray and *Holographis* Nees at the University of Michigan (Daniel 1983a, b), I was drawn numerous times to the CDR and especially the BCC during my fieldwork in Mexico. The BCC is likely the most species-rich portion of the CDR for Acanthaceae. Pinkava (1984) and Vásquez-Aldape et al. (2001) both listed 12 species in seven genera for this family in the flora area.

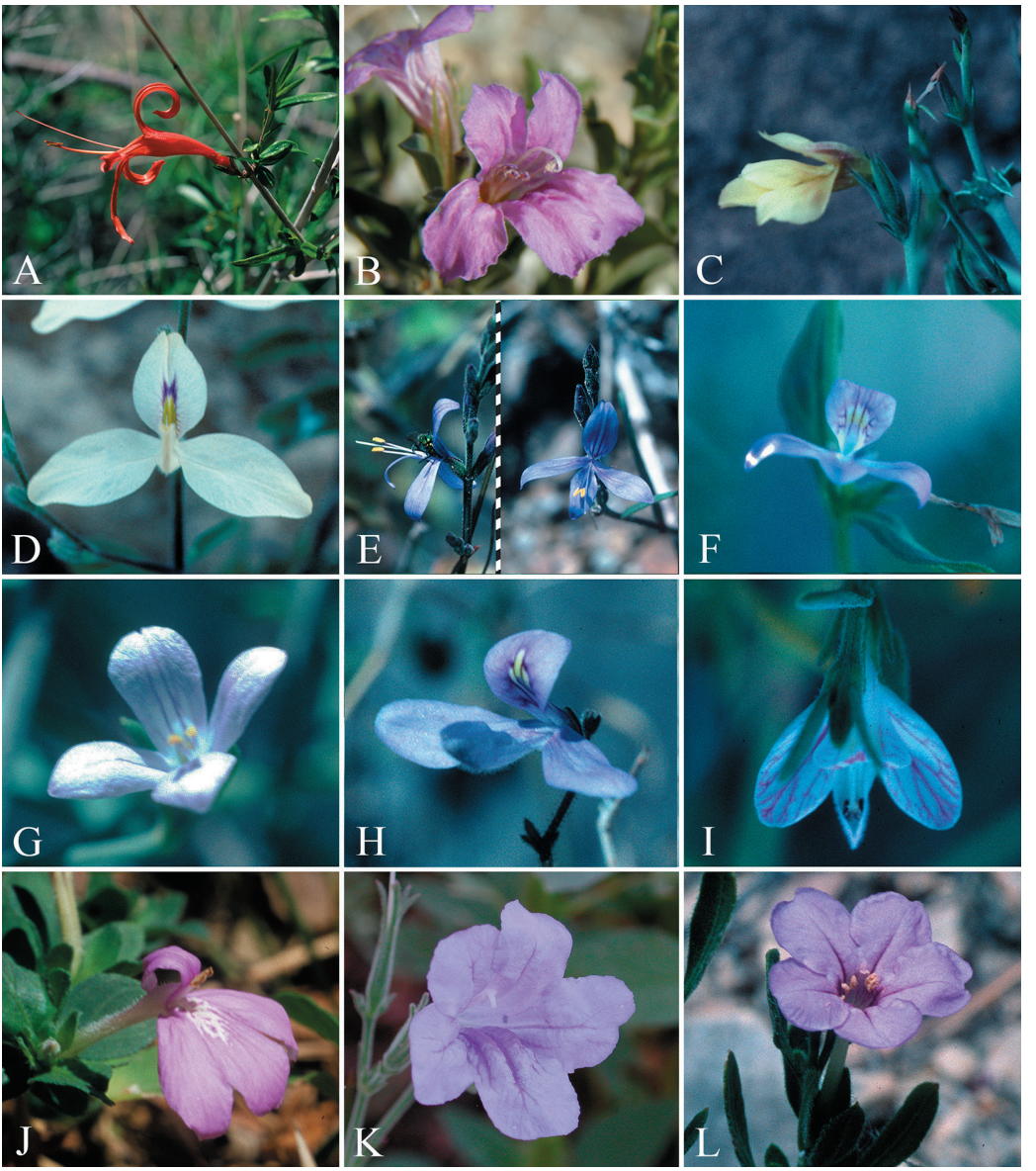

Fig. 3. **Flowers of Acanthaceae (except for *Justicia coahuilana*) occurring in the Bolsón de Cuatro Ciénegas and on surrounding mountains. A.** *Anisacanthus linearis*. **B.** *Dyschoriste cinerascens*. **C.** *Holographis ilicifolia*. **D.** *Carlowrightia arizonica*. **E.** *Carlowrightia parviflora* (lateral view, left and frontal view, right). **F.** *Carlowrightia mexicana*. **G.** *Carlowrightia parvifolia*. **H.** *Carlowrightia serpyllifolia*. **I.** *Carlowrightia texana*. **J.** *Justicia pilosella*. **K.** *Ruellia ciliatiflora*. **L.** *Ruellia parryi*. Photos by TFD, except B © 2014 Wynn Anderson (CC BY-NC-SA 3.0), cropped.

Thirteen species in six genera of Acanthaceae are now known from there (Fig. 3), constituting 31% of the species and half of the genera of that family known from the entire ca. 507,000 km^2 CDR. All 13 species of Acanthaceae in the BCC occur either exclusively or at least primarily in desertscrub. Three of them have been reported to occur, though not exclusively, on gypsum soils there (i.e., gypsovags; Ochoterena et al. 2020). One of these, *Justicia coahuilana* T.F. Daniel, is the only species of the family endemic to the BCC. Possessing six of

the 13 CDR-occurring species of the acanthaceous genus *Carlowrightia* (25 total species), the BCC likely boasts the highest concentration of species in that genus. Additional species that occur in close proximity to the BCC, but have yet to be documented therein, include: *Carlowrightia torreyana* Wassh., *Dyschoriste linearis* (Torr. & A. Gray) Kuntze, and *Stenandrium dulce* (Cav.) Nees.

The following account of Acanthaceae in the BCC updates taxonomic nomenclature, documents an additional species in the flora area, and provides a key to all Acanthaceae currently known from the basin and surrounding mountains. Pollen morphology often provides useful taxonomic characters for distinguishing genera (and sometimes species) in the family. Figure 4 shows the diverse types of pollen among Acanthaceae in the BCC, and illustrates palynological characteristics noted in the key.

KEY TO THE GENERA AND SPECIES OF ACANTHACEAE IN THE BOLSÓN DE CUATRO CIENÉGAS REGION

1. Cystoliths absent; leaves quaternate; corollas yellow; stamens 4, anthers 1-thecous; pollen 3-colpate _____ **Holographis ilicifolia**
1. Cystoliths present; leaves opposite; corollas white, blue, purple, pink, or red to red-orange; stamens 2 or 4, anthers 2-thecous; pollen not 3-colpate.
2. Stamens 4; corolla lobes contorted in bud.
3a. Corollas (12.5–)14–18(–20) mm long; regions of calyx tube proximal to sinuses ± translucent and often rupturing when capsule dehisces; thecae basally awned; pollen 3-colporate and with multiple pseudocolpi in mesocolpia _____ **Dyschoriste cinerascens**
3. Corollas 20–50 mm long; regions of calyx tube proximal to sinuses not differentiated from rest of tube; thecae lacking basal awns; pollen 3-porate and coarsely reticulate _____ **Ruellia**
4. Leaf surfaces lacking any branched or stellate trichomes; inflorescence of (1–)3–many-flowered dichasia in axils of proximal leaves (sometimes not evident) and expanded dichasia in axils of distal (usually reduced) leaves and bracts, the latter dichasia collectively forming a terminal leafy and sometimes basally branched paniclelike thyrse, dichasia borne on peduncles 4–45 mm long; bracteoles not subfoliose, 2–8 mm long, 0.6–2 mm wide, abaxial surface glabrous or with pubescence including glandular trichomes; calyces (9–)11–25 mm long, externally with pubescence including glandular trichomes, anterior lobes not fused for half or more of their length; capsules 12–29 mm long, glandular-pubescent (at least distally) _____ **R. ciliatiflora**
4. Leaf surfaces with at least some trichomes branched or stellate; inflorescence of 1(–3)-flowered dichasia in leaf axils, borne on peduncles 0.5–6 mm long; bracteoles subfoliose, 6.5–18 mm long, 2–6.5 mm wide, abaxial surface pubescent with eglandular trichomes only; calyces 5–11 mm long, externally pubescent with eglandular trichomes only, anterior lobes usually fused for half or more of their length; capsules 9–11(–13) mm long, glabrous or pubescent with eglandular trichomes only _____ **R. parryi**
2. Stamens 2; corolla lobes ascending cochlear in bud.
5. Upper lip of corolla rugulate (i.e., with an internal infolding, which often holds the style); stamens ± appressed to or positioned nearer to upper lip of corolla and anthers dehiscing toward lower lip (i.e., flower nototribic); thecae unequally inserted, lower theca of the pair bearing a basal appendage _____ **Justicia**
6. Young stems glabrous; leaves usually sessile to subsessile, linear to narrowly oblanceolate, 1–2.5 mm wide, 8–25 times longer than wide; dichasia pedunculate, peduncles 5–13 mm long; corollas externally glabrous, tube 4–7 mm long; capsules 9–10 mm long; seeds smooth and glabrous on one face, smooth to muricate and pubescent with eglandular trichomes on the other face, margin fringed with glandular trichomes 0.1 mm long _____ **J. coahuilana**
6. Young stems pubescent with eglandular trichomes; leaves petiolate, ovate-elliptic to elliptic to obovate-elliptic, 2.8–14 mm wide, 1.4–5.3 times longer than wide; dichasia sessile to subsessile (i.e., with peduncles up to 2 mm long); corollas externally pubescent with eglandular trichomes, tube 7–21 mm long; capsules 7–8.5 mm long; seed surfaces and margin bubbly tuberculate, lacking trichomes and glands _____ **J. pilosella**
5. Upper lip of corolla lacking a rugula; stamens positioned closer to lower lip of corolla and anthers dehiscing toward upper lip (i.e., flower stenotribic); thecae equally to subequally inserted, lacking basal appendages.
7. Erect shrubs to 2.5 m tall; corollas red or orange-red, 35–55 mm long, tube conspicuously expanded distally, 17–26 mm long, lips often conspicuously recoiled, lacking visible nectar guides; stamens 22–32 mm long; capsules 16–22 mm long _____ **Anisacanthus linearis**
7. Perennial herbs or shrubs usually less than 1 m tall; corollas white, blue, purple, or pinkish, 5.5–19 (–26) mm long, tube subcylindric, scarcely expanded distally, 1.5–8 (–10) mm long, lips not conspicuously recoiled, at least upper lip with colored nectar guides; stamens 3.3–9 (–10.5) mm long; capsules 7–14 mm long _____ **Carlowrightia**
8. Leaves sessile, linear to narrowly lanceolate; seeds usually 2, these concavo-convex, tuberculate on concave (inward-facing in capsule) side and papillose on convex side, 3rd or 4th seeds (if present) usually with poorly developed ornamentation and exaggerated marginal teeth _____ **C. parvifolia**
8. Leaves subsessile to petiolate, very rarely linear to narrowly lanceolate, mostly lanceolate to ovate to elliptic to circular to obovate; seeds 4 (or fewer), all similar, flat, variously ornamented, sometimes marginally dentate, but never with exaggerated teeth.
9. Corollas white to cream with colored nectar guides.

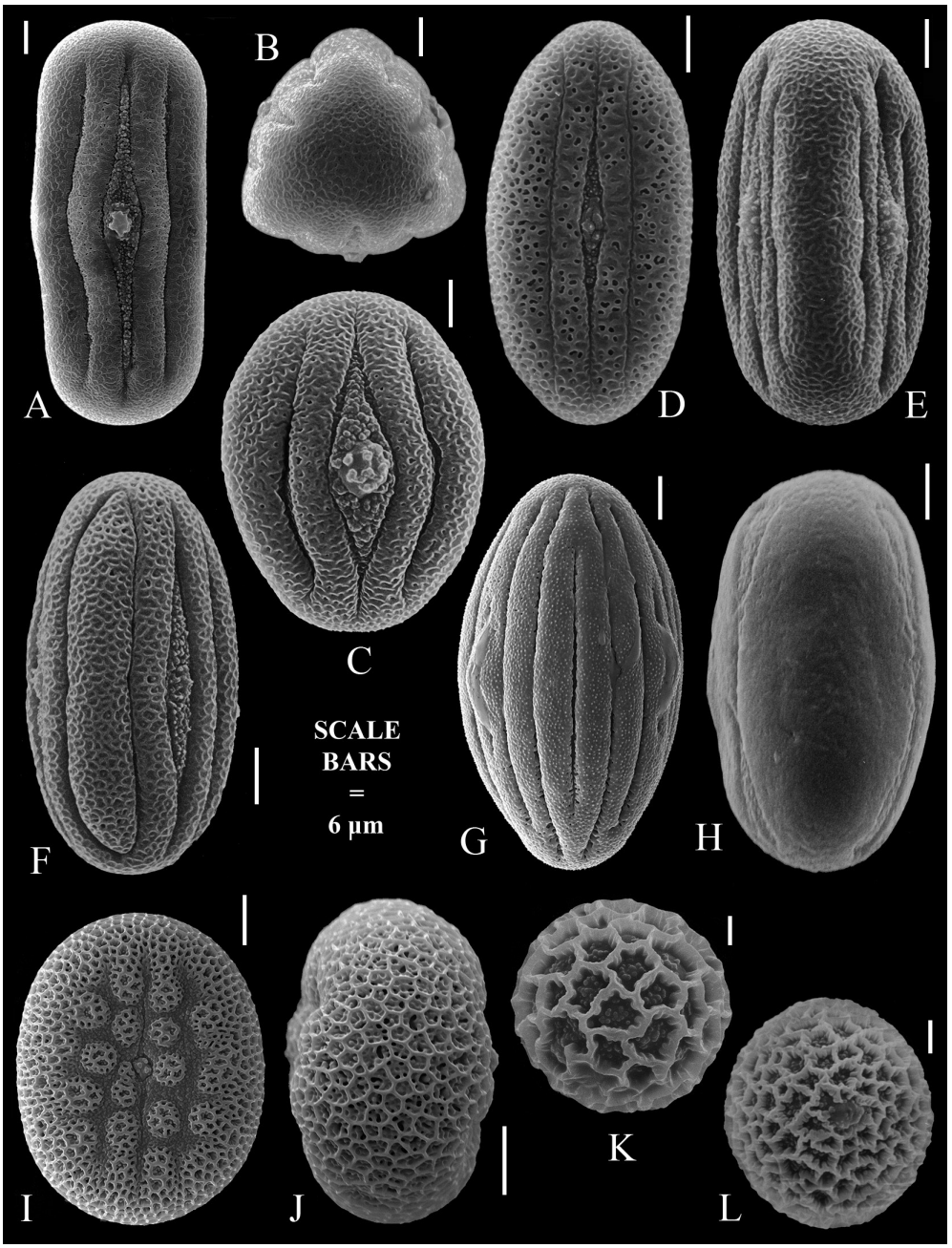

Fig. 4. Pollen of some Acanthaceae that occur in the Bolsón de Cuatro Ciénegas region. **A–F.** Pollen 3-colporate, 6-pseudocolpate, sometimes with pseudocolpi fused toward poles in mesocolpia: A–B. *Anisacanthus linearis* (*Daniel 538*), apertural view (A), polar view (B); C. *Carlowrightia mexicana* (*Henrickson & Lee 16013*)), apertural view; D. *Carlowrightia arizonica* (*Daniel et al. 6845*), apertural view; E. *Carlowrightia parviflora* (*Daniel 899*), interapertural view; F. *Carlowrightia serpyllifolia* (*Daniel 653*), interapertural view. **G.** Pollen 3-brevicolporate, polypseudocolpate, ora flanked by "sexine lips:" *Dyschoriste cinerascens* (*Daniel 175*), interapertural view. **H.** Pollen 3-colpate, colpi expanded toward poles: *Holographis ilicifolia* (*Daniel 659*), interapertural view. **I–J.** Pollen 2-colporate, colpori flanked on each side by 1–2 rows of insulae and additional peninsulae in a "trema region:" *Justicia pilosella* (*Ertter 5230a*), apertural view (I), polar view (J). **K–L.** Pollen spheric, 3-porate, exine coarsely reticulate: K. *Ruellia ciliatiflora* (*Wiggins & Rollins 136*), interapertural view; L. *Ruellia parryi* (*Daniel 247*), apertural view.

10. Corollas 9–19 (–26) mm long, upper lip with a yellow "eye" fringed with maroon markings, lower-central lobe 6–11 (–14) mm long, forming a V-shaped keel enclosing stamens and style; bracteoles not foliaceous; seed margin dentate ____ **C. arizonica**
10. Corollas 5.5–7 mm long, lacking an "eye" on upper lip, but both lips with maroon veins, lower-central lobe 4–4.5 mm long, forming a shallow, U-shaped keel often holding stamens and style; bracteoles foliaceous; seed margin entire ____ **C. texana**

9. Corollas blue to pink-purple to pink.
11. Young stems bisulcate with 4 prominent ridges; corollas subactinomorphic, lobes of the lower lip homomorphic (the lower-central lobe not conduplicate or forming a keel); anthers golden yellow; head of capsule spherical to partially flattened ____ **C. parviflora**
11. Young stems quadrate to terete; corollas bilabiate to pseudopapilionaceous, lobes of the lower lip heteromorphic (the lower-central lobe partially conduplicate, forming a keel in which stamens and style are often held); anthers maroon turning black; head of capsule conspicuously flattened.
12. Pubescence of young stems, leaves, bracts, bracteoles, and calyces eglandular; corollas 6.5–9 mm long, lower-central lobe (keel) 4.5–5.5 mm long; seed margin entire to crenulate ____ **C. mexicana**
12. Pubescence of young stems, leaves, bracts, bracteoles, and calyces including (on some or all of these structures) conspicuous glandular trichomes; corollas 9–15 mm long, lower-central lobe (keel) (5.5–) 7–10 (–13) mm long; seed margin dentate ____ **C. serpyllifolia**

Notes on species

For the 13 species in six genera of Acanthaceae occurring in the BCC and surrounding sierras, their overall geographic distributions, the various biotic communities in and elevational ranges at which they occur (within and external to the BCC), and miscellaneous taxonomic and/or nomenclatural notes are noted below.

Anisacanthus linearis (S.H. Hagen) Henrickson & E.J. Lott. This species is endemic to, and one of five congeners found in, the CDR, where it occurs from the Trans-Pecos region of western Texas to Chihuahua, Coahuila, and Nuevo León in north-central Mexico. Plants inhabit Chihuahuan Desertscrub at elevations from 600 to 1600 meters.

Carlowrightia arizonica A. Gray. This morphologically variable and widespread species occurs in the Sonoran and Chihuahuan deserts of the southwestern United States (Arizona, California, Texas) and Mexico, other arid and semi-arid regions throughout most of Mexico, and northern Central America to Costa Rica. Plants occur primarily in desertscrub, thornscrub, and tropical dry forests from sea level to 1400 meters elevation.

Carlowrightia mexicana Henrickson & T.F. Daniel. This CDR endemic is known from Trans-Pecos Texas and Coahuila, Mexico. Plants occur in Chihuahuan Desertscrub and oak chaparral at elevations from 1050 to 1410 meters.

Carlowrightia parviflora (Buckley) Wassh. This widespread species occurs from southern Texas and northeastern Mexico (Coahuila, Nuevo León, Tamaulipas) southward to Aguascalientes, Durango, Guanajuato, Hidalgo, Querétaro, and San Luis Potosí. Plants occur in desertscrub, thornscrub, and tropical deciduous forests at elevations from 10 to 2800 meters. Some populations in the southern portion of the range (e.g., Hidalgo and Querétaro) generally have linear leaves (0.8–2.5 mm wide) whereas those in the northerly populations are lanceolate to ovate and mostly wider (4–23 mm wide). This species was not included in the flora area by Pinkava (1984), but its occurrence in the BCC is herewith documented based on *I. Johnston 8958* (GH) from the Sierra de la Madera and *M. Johnston et al. 10296* (LL) from the Sierra de la Purisima. It was included in the updated listing of the flora by Vásquez-Aldape et al. (2001), but likely in place of *C. parvifolia*, which is well-known from the BCC, but was not listed in their account.

Carlowrightia parvifolia Brandegee. This CDR endemic is known from Trans-Pecos Texas and Coahuila. Plants occur on limestone in Chihuahuan Desertscrub at elevations from 1200 to 1500 meters.

Carlowrightia serpyllifolia A. Gray. This CDR endemic is known from Trans-Pecos Texas and north-central Mexico (Chihuahua, Coahuila, Durango, Zacatecas). Plants occur in Chihuahuan Desertscrub at elevations from 750 to 1900 meters. The species was reported as a gypsovag by Ochoterena et al. (2020).

Carlowrightia texana Henrickson & T.F. Daniel. This species occurs in the southwestern United States (Arizona, New Mexico, Texas) and northern Mexico (Chihuahua, Coahuila, Nuevo León, San Luis Potosí, Sonora). Plants occur in Chihuahuan Desertscrub, mesquite woodlands, and oak-juniper woodlands at elevations from 25 to 1700 meters.

Dyschoriste cinerascens (Henrickson & Hilsenb.) T.F. Daniel. This species is endemic (or very nearly so) to the CDR, occurring in the southwestern United States (southeastern New Mexico, Trans-Pecos Texas) and northern Mexico (Chihuahua, Coahuila, Durango). Plants inhabit Chihuahuan Desertscrub, desert grassland, thornscrub, and pine-juniper communities at elevations from 650 to 2000 meters. The

infrageneric taxonomy of *Dyschoriste* in the southwestern United States and northern/central Mexico requires additional studies to better understand the number and circumscriptions of taxa in those regions. Previous accounts involving some or all of these taxa have been proposed by Henrickson (1999), Turner (2003), and Daniel (2013). *Wendt et al. 1732* (ASU, TEX), collected from an arroyo in a region of Chihuahuan Desertscrub on the northern bajada of the Sierra de la Madera, was originally identified as *D. linearis*, and was included under that name by Pinkava (1984) and Vásquez-Aldape et al. (2001). The specimen at TEX was subsequently annotated by Henrickson in 1994 as *D. schiedeana* var. *cinerascens* Henrickson & Hilsenb (= *D. linearis* subsp. *cinerascens* (Henrickson & Hilsenb.) Turner). This infraspecific taxon was elevated to specific rank by Daniel (2013). Other collections from higher on the northern slopes of the Sierra de la Madera (e.g., *Henrickson & Lee 15969*, TEX) and at Rancho San Pedro, just northwest of that sierra (e.g., *Henrickson & Bekey 18715-5*, TEX), also pertain to *D. cinerascens*. Henrickson annotated some collections of *Dyschoriste* from nearby sites to the south and east of the Bolsón de Cuatro Ciénegas as *D. schiedeana* var. *schiedeana* (e.g., *Daniel 750*, ASU, CAS, MICH; *Daniel 902*, CAS, MICH) and others as var. *cinerascens* (e.g., *Henrickson 23456*, TEX; *Henrickson et al. 16067*, TEX). There is variation among these plants in size of the corolla and in the disposition, quantity, and length of trichomes on the stems and calyces. It is possible that more than one taxon of *Dyschoriste* may be present in the Bolsón de Cuatro Ciénegas region, but intergradations among the diagnostic characters used to distinguish taxa appear to be prevalent. Some of these intergradations were discussed by Henrickson (1999) and Daniel (2013).

Holographis ilicifolia Brandegee. This CDR endemic occurs in Coahuila and Durango, where plants occur in Chihuahuan Desertscrub at elevations from 850–1600 meters.

Justicia coahuilana T.F. Daniel. This CDR endemic is known only from one or more canyons/bajadas in the eastern slopes of the Sierra de la Madera in the BCC. It occurs in Chihuahuan Desertscrub at elevations of ca. 700 to 850 meters. Only three collections of *J. coahuilana* are known, the most recent having been collected during the explorations by Pinkava et al. in 1968 (i.e., *Lehto et al. 5485*, ASU). The species was reported as a gypsovag by Ochoterena et al. (2020).

Justicia pilosella (Nees) Hilsenb. This widespread species occurs from the southwestern United States (New Mexico, Texas) southward throughout much of northern Mexico to the Tehuacán Valley in the state of Puebla. Plants occur primarily in Chihuahuan Desertscrub, thornscrub, desert grassland, tropical deciduous forests, and oak forest at elevations from 6 to 2100 meters. This species was treated as *Siphonoglossa pilosella* (Nees) Torr. by Pinkava (1984) and Vásquez-Aldape et al. (2001).

Ruellia ciliatiflora Hook. This species (including *R. nudiflora* (Engelm. & A. Gray) Urb., as treated by Pinkava (1984) and Vásquez-Aldape et al. (2001)) is a widespread and morphologically variable species occurring from the southwestern United States (Arizona, Texas) southward throughout most of Mexico and Central America to subtropical South America (northern Argentina). In North America, plants occur primarily in desertscrub, thornscrub, desert grassland, tropical deciduous and subdeciduous forest, oak forest, evergreen seasonal forest, and pine-oak forest at elevations from 5 to 1800 meters. As noted by Pinkava (1984) for plants in the basin, this species occurs in both desertscrub and in aquatic habitats (e.g., riparian zones).

Ruellia parryi A. Gray. This CDR endemic is known from the southwestern United States (Arizona, New Mexico, Texas) and northern Mexico (Chihuahua, Coahuila, Durango, Nuevo León, Sonora and Zacatecas). Plants occur in Chihuahuan Desertscrub and juniper chaparral at elevations from 500 to 1950 meters. The species was reported as a gypsovag by Ochoterrna et al. (2020).

SUMMARY AND CONCLUSIONS

The BCC has been characterized as "one of the outstanding natural resources of the Western Hemisphere" (Wauer & Riskind 1974:iv). Indeed, a recent book (Mandujano et al. 2020) is largely devoted to describing and interpreting the uniqueness of the BCC. Donald Pinkava was the first botanist to assemble a comprehensive floristic inventory of this region, one of the biologically richest, scenically most impressive, and highly threatened areas of the Chihuahuan Desert. The floristic richness of the BCC is reflected in the numbers and diversity of Acanthaceae occurring in the region. The work of Pinkava and his co-collectors, botanists from the University of Texas (e.g., Fernando Chiang, Jim Henrickson, Marshall Johnston, Emily Lott, Guy Nesom, Billie Turner, and Tom Wendt), and many others, helped to reveal the high degree of endemism among plants in the BCC. These efforts, and those of many others working on various faunal taxa, provided data that resulted in much-needed protected status for major portions of the BCC. Building on the efforts of Pinkava

and Vásquez-Aldape et al. (2001), an updated, comprehensive floristic account of the plants of the BCC is much to be desired.

APPENDIX 1

Acanthaceae of Chihuahuan and Sonoran deserts.

Comparison of Acanthaceae in the Sonoran Desert (based on Daniel 1997, 2004, 2016), and Chihuahuan Desert region (Daniel, unpublished) with: areas of regions, numbers and names of genera and species, and numbers and (percentages) of species endemic to each region. An * indicates species endemic to the region. Species listed for each region are those occurring in desertscrub (exclusively or at least partially). Occurrences of additional taxa of *Dyschoriste* from the CDR were recognized by Henrickson (1999), but due to the complex state of the taxonomy of that genus, only three are listed here.

Chihuahuan Desert region: ca. 507,000 km^2, genera = 12, species = 42, endemics = 21 (50%)

**Anisacanthus junceus* (Torr.) Hemsl.
**Anisacanthus linearis* (S.H. Hagen) Henrickson & E.J. Lott
Anisacanthus puberulus (Torr.) Henrickson & E.J. Lott
Anisacanthus pumilus (Dietr.) Nees
Anisacanthus quadrifidus (Vahl) Nees
Anisacanthus thurberi (Torr.) A. Gray
Carlowrightia arizonica A. Gray
Carlowrightia hapalocarpa B.L. Rob. & Greenm.
**Carlowrightia leseurii* Henrickson & T.F. Daniel
**Carlowrightia linearifolia* (Torr.) A. Gray
**Carlowrightia mexicana* Henrickson & T.F. Daniel
Carlowrightia neesiana (Schauer ex Nees) T.F. Daniel
**Carlowrightia ovata* A. Gray
Carlowrightia parviflora (Buckley) Wassh.
**Carlowrightia parvifolia* Brandegee
**Carlowrightia purpurea* T.F. Daniel
**Carlowrightia serpyllifolia* A. Gray
Carlowrightia texana Henrickson & T.F Daniel
Carlowrightia torreyana Wassh.
Dicliptera resupinata (Vahl) Juss.
**Dyschoriste cinerascens* (Henrickson & Hilsenb.) T.F. Daniel
Dyschoriste decumbens (A. Gray) Kuntze
Dyschoriste linearis (Torr. & A. Gray) Kuntze
Elytraria imbricata (Vahl) Pers.
**Holographis ilicifolia* Brandegee
**Justicia coahuilana* T.F. Daniel
**Justicia decurvata* Hilsenb.
**Justicia durangensis* (Henrickson & Hilsenb.) T.F. Daniel
**Justicia henricksonii* T.F. Daniel
**Justicia linearis* B.L. Rob. & Greenm.
Justicia longii Hilsenb.
Justicia pilosella (Nees) Hilsenb.
**Justicia warnockii* B.L. Turner
**Justicia wrightii* A. Gray
**Mirandea grisea* Rzed.
Ruellia ciliatiflora Hook.
Ruellia metzae Tharp
**Ruellia parryi* A. Gray
**Stenandrium barbatum* Torr. & A. Gray
Stenandrium dulce (Cav.) Nees
Tetramerium nervosum Nees
Yeatesia platystegia (Torr.) Hilsenb.

Sonoran Desert: ca. 306,000 km^2, genera = 9, species = 20, endemics = 0 (0%).

Anisacanthus thurberi (Torr.) A. Gray
Aphanosperma sinaloense (Leonard & Gentry) T.F. Daniel
Carlowrightia arizonica A. Gray
Carlowrightia pectinata Brandegee
Dicliptera resupinata (Vahl) Juss.
Elytraria imbricata (Vahl) Pers.
Holographis virgata (Harv. ex Benth. & Hook.f.) T.F. Daniel
Justicia californica (Benth.) D.N. Gibson
Justicia candicans (Nees) L.D. Benson
Justicia hians (Brandegee) Brandegee
Justicia insolita Brandegee
Justicia longii Hilsenb.
Justicia palmeri Rose
Justicia sonorae Wassh.
Ruellia californica (Rose) I.M. Johnst.
Ruellia ciliatiflora Hook.
Ruellia intermedia Leonard
Ruellia leucantha Brandegee
Tetramerium fruticosum Brandegee
Tetramerium nervosum Nees

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