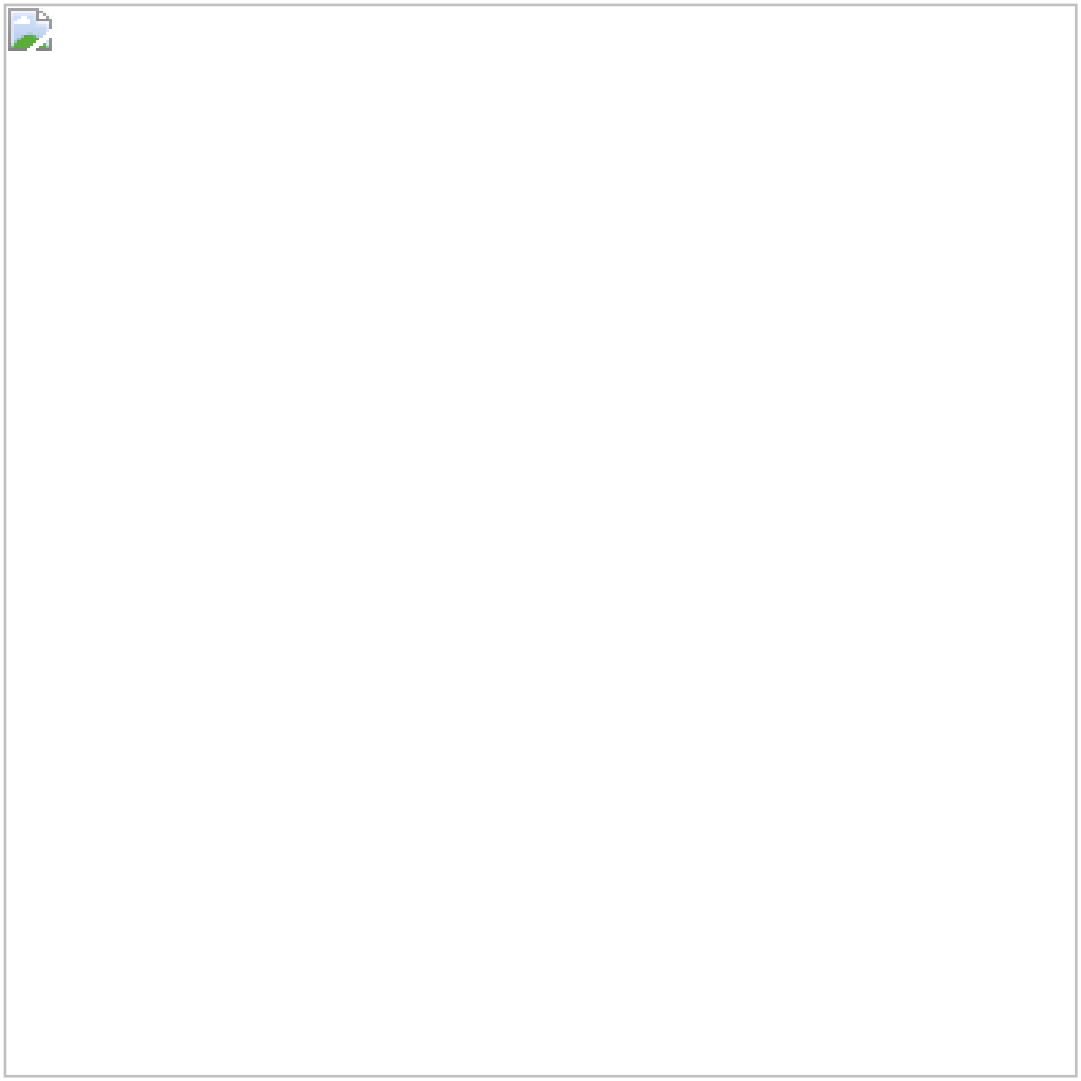

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Two New Species of *Aphyllon* from Northeastern Mexico

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Abstract—Plants originally identified as *Aphyllon ludovicianum* that occur near Monterrey, Nuevo Leon, and Cuatro Ciénegas Bolson, Coahuila, Mexico, were found to not align with the protologue of that species, the close relative *A. multiflorum*, or any other species of *Aphyllon*. Following a detailed study of floral morphology, geographic range, host species, and phylogenetic position using dry herbarium specimens, field study, and georeferenced color photographs, we propose the new binomials ***Aphyllon spectabile*** for the plants from Nuevo Leon and ***Aphyllon gypsophilum*** for the plants from Coahuila, Mexico. These additions increase the taxonomic diversity of *Aphyllon* to 27 species plus ten additional subspecies. *Gymnosperma glutinosum* and two species of *Xanthisma* were reported for the first time as a host species for the genus *Aphyllon*. We also provide an updated key to *Aphyllon* in Mexico.

Resumen—Las plantas identificadas como *Aphyllon ludovicianum* y que ocurren cerca de Monterrey, Nuevo León y Cuatro Ciénegas Bolsón, Coahuila, México no se alineaban con el protólogo de *A. ludovicianum*, de *A. multiflorum* o de alguna otra especie de *Aphyllon.* La morfología floral, rango geográfico y la especie de planta hospedera fueron incluidas en esta comparación utilizando ejemplares de herbario y múltiples fotografías a color. Proponemos el nuevo binomio ***Aphyllon spectabile*** para las plantas de Nuevo León y ***Aphyllon gypsophilum*** para las plantas de Coahuila, llevando la total diversidad taxonómica a 27 especies de *Aphyllon* y 10 subespecies adicionales. *Gymnosperma glutinosum* y dos especies de *Xanthisma* son reportadas por primera vez como planta hospedera para el género *Aphyllon*. Se presenta una clave actualizada de *Aphyllon* en México.

Keywords—Endemic, key, iNaturalist, phylogeny.

The genus *Aphyllon* A.Gray (Orobanchaceae) is distributed throughout the western hemisphere, but is most species-rich in western North America. During the examination of herbarium exsiccatae for the Flora of North America (Collins et al. 2018), several accessions of the genus *Aphyllon* could not be assigned an available binomial. Two such groups of these specimens originated from northeastern Mexico; one set from the area surrounding Monterrey, Nuevo León, and the other from the Cuatro Ciénegas Bolson in Coahuila. Meanwhile, observations of the plants near Monterrey began to appear on the iNaturalist.org website (Ernesto 2015). Compared with known species of *Aphyllon* from northeastern Mexico and southern Texas, these plants were striking because of the large colorful flowers (Fig. 1). The second set of specimens, around Cuatro Ciénegas Bolson and apparently confined to gypsum dune habitat, stood out by their rather small corollas with extremely short corolla lobes (Fig. 2).

Many of these plants had previously been identified as *A. ludovicianum* (Nutt.) A.Gray or *A. multiflorum* (Nutt.) A.Gray, two closely related species within *Aphyllon* sect. *Nothaphyllon* A.Gray. Within the section, both species are part of a complex with racemose inflorescences, informally called the *A. ludovicianum* complex (Collins 1973; Collins et al. 2009; Schneider et al. 2016), in contrast to species with corymbose inflorescences (*A. californicum* complex) or those that have a small number of clustered flowers with long pedicels (*A.* sect. *Aphyllon*).

As Collins (1973; Collins et al. 2009) pointed out, the binomial *Aphyllon ludovicianum* (as *Orobanche*) has been historically applied to plants now representing at least four different species, including *A. cooperi* A.Gray, *A. validum* (Jeps.) A.C.Schneid, and the more recently described *A. arizonicum* (L.T.Collins) A.C.Schneid. and *A. riparium* (L.T.Collins) A.C.Schneid. Since all these species have racemose (spike-like) inflorescences among other shared morphological features, it is understandable that earlier researchers did not distinguish them. Especially so, given that few specimens, sometimes fragmentary, were available for examination at the time of the descriptions.

Likewise, the taxon *Aphyllon multiflorum* (Nutt.) A.Gray has been treated in a variety of ways, from Munz's (1930) recognition of four varieties of this species (classified in *Orobanche*) to Holmes and White's (2001) demotion of rank to a subspecies of *Orobanche ludoviciana*. While *A. multiflorum* has been reported in Mexico, we suspect the name has been misapplied. No vouchered specimens from Mexico were observed in this study that could be correctly identified to this taxon.

Finding distinguishing characters in the genus *Aphyllon* is a difficult task due to the many shared morphological characters and the absence of true leaves and roots. As a result, almost all useful taxonomic characters in the genus are found in the inflorescence and flowers. Several species of *Aphyllon* in Mexico are similar in overall appearance and share several morphological characters in common, including *A. cooperi* subsp. *Palmeri* (Munz) A.C.Schneid., *A. ludovicianum*, and *A. castilloi* Franc.Gut., Cházaro, & Espejo. Hence, it was necessary to assess their phylogenetic relationships and to find morphological characters that could easily separate the species.

Materials and Methods

Species Characterization—Data were obtained from two sources, herbarium exsiccatae and geolocated color photographs. Morphological data were obtained from herbarium specimens from the following collections; ANSM, ASU, F, ILL, MO, NY, TEX-LL, and US. Online records and scans of *Aphyllon* specimens from several Mexican herbaria (ANSM, UNAM, CFNL) were also observed. Data for Coahuila plants were obtained entirely from dried herbarium specimens from two herbaria, TEX-LL and ASU. SEINnet (https://swbiodiversity.org/seinet/index.php) records of *Aphyllon* from Mexico were also searched, but no additional matching

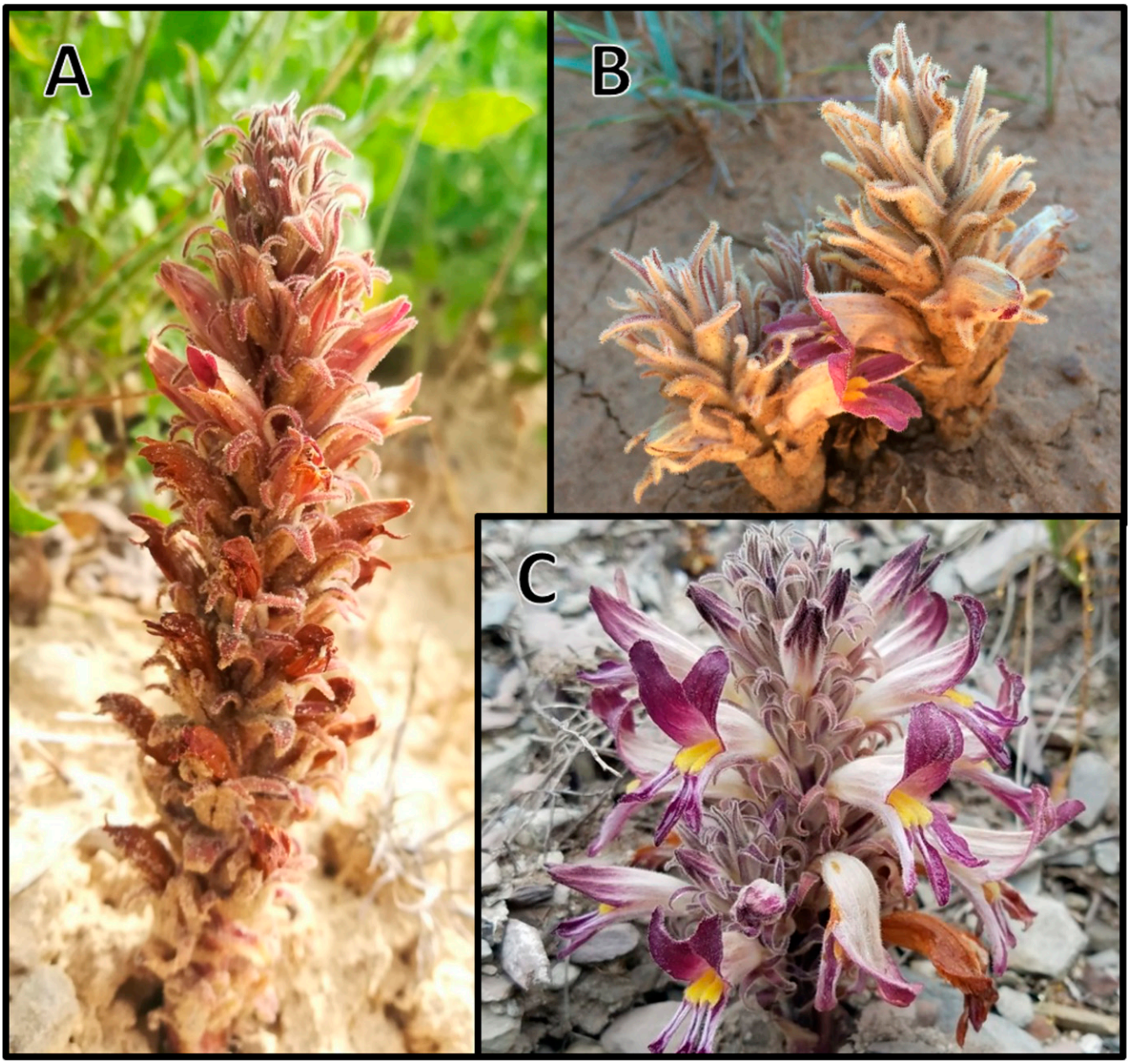

FIG. 1. Photographs comparing (A) *Aphyllon ludovicianum*, (B) *Aphyllon multiflorum,* and (C) *Aphyllon spectabile.*

images were found. Finally, measurements and morphological structures were compared with several closely related species (Table 1). *Aphyllon dugesii* S.Watson was not included in the comparative study due to uncertain taxonomic status but is quite distinct from *A. ludovicianum* and its segregates.

Further assessment of qualitative characters of plants from Nuevo León such as color, shape of floral parts, and inflorescence type, was based on 54 photographs from 50 iNaturalist records of plants in situ (iNaturalist 2023). Unfortunately, such records of the Coahuila plants were not available for examination, nor was fresh material.

Phylogenetic Analysis—DNA from three specimens of *A. spectabile,* including the holotype, and as well as one specimen of *A. gypsophilum* were extracted from dried floral tissue using a Qiagen DNeasy Plant Pro Kit. The five nuclear ribosomal (ITS and ETS) and plastome (*matK*, *rps2*, and *trnL-trnF*) regions used by Schneider et al. (2016) were amplified and Sanger sequenced following their methodology. Sequence chromatograms were inspected for quality and trimmed, then aligned with existing nuclear ribosomal and concatenated plastid sequence alignments from Schneider et al. (2016) using the MUSCLE plugin for Geneious 9.1.8. To expand geographic sampling of closely related species, we also extracted and sequenced DNA from one specimen of *A. ludovicianum* from Florida (Schneider et al. 2021), and one specimen of *A. riparium* from Arizona. Newly generated sequences were deposited to GenBank (Appendix 1), and sequence alignments have been deposited in the Dryad Digital Repository (Collins et al. 2023).

Maximum likelihood phylograms were inferred by RAxML-NG (Kozlov et al. 2019) using the CIPRES Science Gateway (Miller et al. 2010). We applied a GTR + G nucleotide substitution model, partitioned by each cpDNA gene, 500 rapid bootstrap replicates, and used one or two specimens of *A. pinorum* (Hook.) A.Gray (*Colwell 96-WA-LC1* and *Egger 804*, vouchers at WTU) as an outgroup.

TAXONOMIC TREATMENT

Aphyllon spectabile L.T.Collins, Velazco, & A.C.Schneid., sp. nov. TYPE: MEXICO. Nuevo León: Santa Catarina, La Huasteca Park entrance, 21 Aug 2021, *Carlos Velazco s.n.* (holotype: MO).

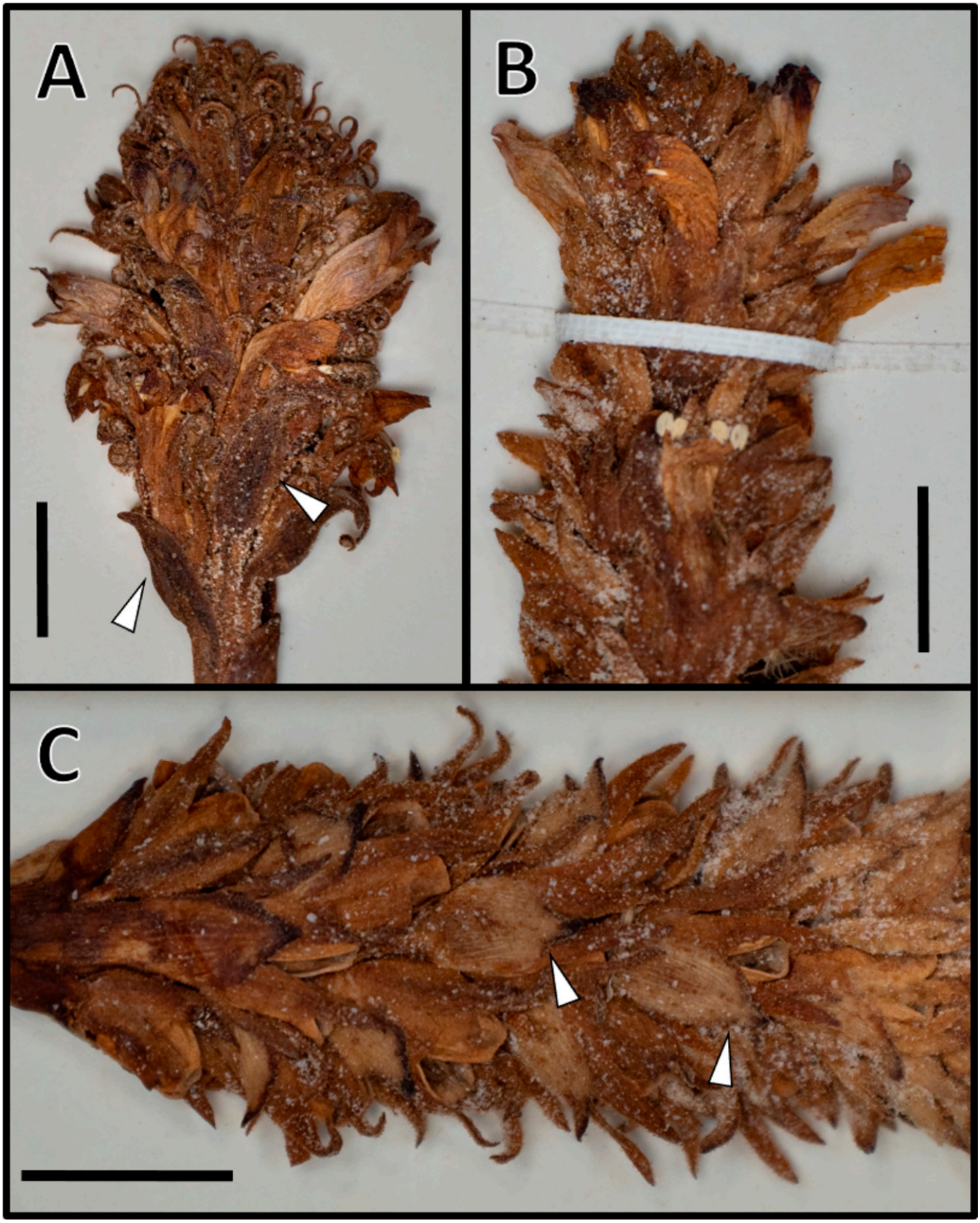

FIG. 2. Photographs of herbarium specimens comparing *Aphyllon ludovicianum* with *Aphyllon gypsophilum*. A. *Aphyllon ludovicianum* with lanceolate bracts (at white wedges). B–C. *Aphyllon gypsophilum.* B. Inflorescence at anthesis showing glabrous anthers. C. Infructescence with unique deltoid bracts and apiculate apices. Voucher specimens: (A) *Collins 2024* (MO); (B–C) *Lewis s.n.* (ASU). Scale bars = 1.00 cm.

TABLE 1. Morphological comparison of *A. spectabile* and *A. gypsophilum* with six other species of *Aphyllon*. Diagnostic characters for each species indicated in bold font. Data for *A. castilloi* and *A. chiapense* taken from the protologues of these taxa (Francisco-Gutiérrez et al. 2019; Francisco-Gutierrez and Alvarado-Cárdenas 2023).

Species	Calyx length	Corolla length	Corolla lobe length and apex shape	Anther vestiture	Filament vestiture
A. spectabile	**16–20 mm**	**35–45 mm**	**10–15 mm**, rounded	**± Villous**	**Glabrous**
A. gypsophilum	**7–10 mm**	**8–15 mm**	**2 mm**, rounded	**Glabrous**	**Pubescent at base**
A. ludovicianum	**8–14 mm**	**14–20 mm**	**4–6 mm**, rounded	**Pubescent or glabrous**	Glabrous
A. multiflorum	**15–21 mm**	**22–36 mm**	6–12 mm, rounded	**Wooly**	**Pubescent at base**
A. cooperi (all subspp.)	**8–12 mm**	**15–32 mm**	**6–10 mm, pointed w/ appendage**	**Glabrous or ± pubescent**	Glabrous
A. castilloi	6–10 mm	**10–19 mm**	**3–5 mm**, rounded	**Glabrous**	Glabrous
A. chiapense	7–12 mm	18–21 mm	4–5 mm	Glabrous ± pubescent	Glabrous
A. californicum subsp. *feudgei*	8–20 mm	**25–35 mm**	10–14 mm, rounded or pointed	**Villous**	Glabrous

Plants unbranched (excluding inflorescence), 7–27 cm. Stem base not or only slightly enlarged. **Roots** few to many, short, fragile, root mass poorly developed and less than 10 mm in diameter. **Leaves** several to numerous, lanceolate or broadly triangular, 3–10 mm, glabrous, margins entire, or sometimes ciliate. **Inflorescences** compact racemes, short or elongate, glandular-puberulent, rarely branched, pallid (sometimes entirely creamy-white) or purple tinged, bracts narrowly lanceolate to lanceolate, 11–20 mm, apex acute or acuminate, densely glandular-pubescent. **Pedicels** 0–5(10) mm, only proximal flowers pedicellate; bracteoles 2. **Flowers:** calyx (15)19–23 mm, slightly asymmetric, cup 4–5 mm, lobes 15–16 mm, reflexed, narrowly lanceolate-attenuate, pallid externally or purple tinged, purple internally, densely glandular pubescent; corolla 35–40 mm, tube white, pubescent externally, only slightly bent, mouth flared, abruptly constricted above ovary, purple veins in the lobes but not in the tube; palatal folds prominent, yellow, pubescent; abaxial (lower) lip 12–15 mm, lobes dark purple, lavender or white, rarely pale blue, apex obtuse or rounded, margins incurved or involute; adaxial(upper) lip 12–15 mm, erect or reflexed, dark purple, lavender, or rarely white, or pale blue, lobes erect or reflexed, sometimes torqued (bent) centripetally, rounded, margins entire, undulate or erose, pubescent or glabrous; filaments pilose, glabrous at insertion, anthers included, pilose; stigma peltate, discoid-crateriform or 2-lobed, sometimes with a descending narrow appendage. **Fruit:** Capsule. Flowering from Nov–May, most frequently in Feb and Mar. Figure 1C.

Diagnosis—*Aphyllon spectabile* can be distinguished from *A. ludovicianum* by its much larger flowers, narrow distribution range around Monterrey, Mexico, and the unique host species *Gymnosperma glutinosum*.

Distribution—*Aphyllon spectabile* is restricted to a small area in the Sierra Madre Oriental in northeastern Mexico, in the vicinity of Monterrey, Nuevo Leon, including Sierra de las Mitras, Sierra de la Sillas, and Sierra de la Loma Largo. A single specimen is reported from the adjacent state of Coahuila, with the location given only as "Saltillo." Since the authors were not able to access other collections from the Sierra Madre Oriental, it is possible that the species is more widely distributed than indicated in this treatment.

Habitat—The species occurs in the zone of xeric vegetation (mattoral xerofila) primarily on arid and semiarid mountain slopes of the Sierra Madre elevations between 500 and 1500 m. This species is found in several different vegetation assemblages within this zone, whereas *A. ludovicianum* is primarily found in prairies.

Host—The only reported host species is *Gymnosperma glutinosum* Less. (Asteraceae), although the authors were not able to confirm this association by direct observation. *Aphyllon* was not previously known to parasitize *Gymnosperma* Less., but other members of the subtribe Gutierreziinae do serve as host species, including *Gutierrezia* Lag. (*A. arizonicum*, *A. multiflorum*), and *Euthamia* (Nutt.) Cass. (*A. californicum* subsp. *grayanum* (Beck) A.C.Schneid.; herbarium vouchers *Colwell 14–25* at YM; *Mason 12127,* JEPS 20913).

Etymology—The epithet *spectabile* refers to the distinctively large and brightly colored flowers.

Phylogenetic Affinities—Phylogenetic evidence strongly supports the placement of *A. spectabile* within the *A. ludovicianum* complex, although existing markers are not sufficient to further resolve most species within this clade, nor provide support for or against species monophyly (Fig. 3).

Notes—Morphologically, several floral characters clearly differentiate *Aphyllon spectabile from A. ludovicianum* and other close relatives or co-occurring species (Table 1). The corollas of *A. spectabile* are 35–45 mm long, which is approximately double the size of the 14–20 mm long corollas of *A. ludovicianum*. Likewise, the corolla lobe lengths of *A. spectabile* (13–15 mm) are about twice as long as those of *A. ludovicianum* (5–8 mm long). Only the highly disjunct *A. californicum* has flowers this large, but the two species differ in floral architecture, biogeographic distribution, and host affinity (Tables 1, 2).

The corolla tube of *A. spectabile* is white with large purple lobes, purple veins, and measuring about 10 mm at the opening. This is noticeably different from *A. ludovicianum*, in which the tube is lavender, pinkish, or yellow, rarely pure white, with lobes similarly colored, without purple veins and measuring only about 5 mm at the opening. Additionally, the margins of lower corollas lobes are involute in *A. spectabile*, while the margins in *A. ludovicianum* are only slightly incurved.

Ecologically and biogeographically, *Aphyllon spectabile* and *A. ludovicianum* are also distinct. *A. ludovicianum* is a prairie species distributed throughout the North American Prairies to the eastern slopes of the Rocky Mountains. It utilizes a variety of host species, but is found primarily on *Artemisia* L. spp., *Heterotheca* Cass. sp., and *Grindelia squarrosa* (Pursh) Dunal, but never *Gymnosperma*.

Contrasted with the two previously mentioned species, *A. multiflorum* has intermediately sized corollas that are 22–36 mm long with lobes 5–9 mm long (Table 1). The distribution of *A. multiflorum* is in the arid grasslands and semidesert of the southern plains in Colorado, New Mexico, and

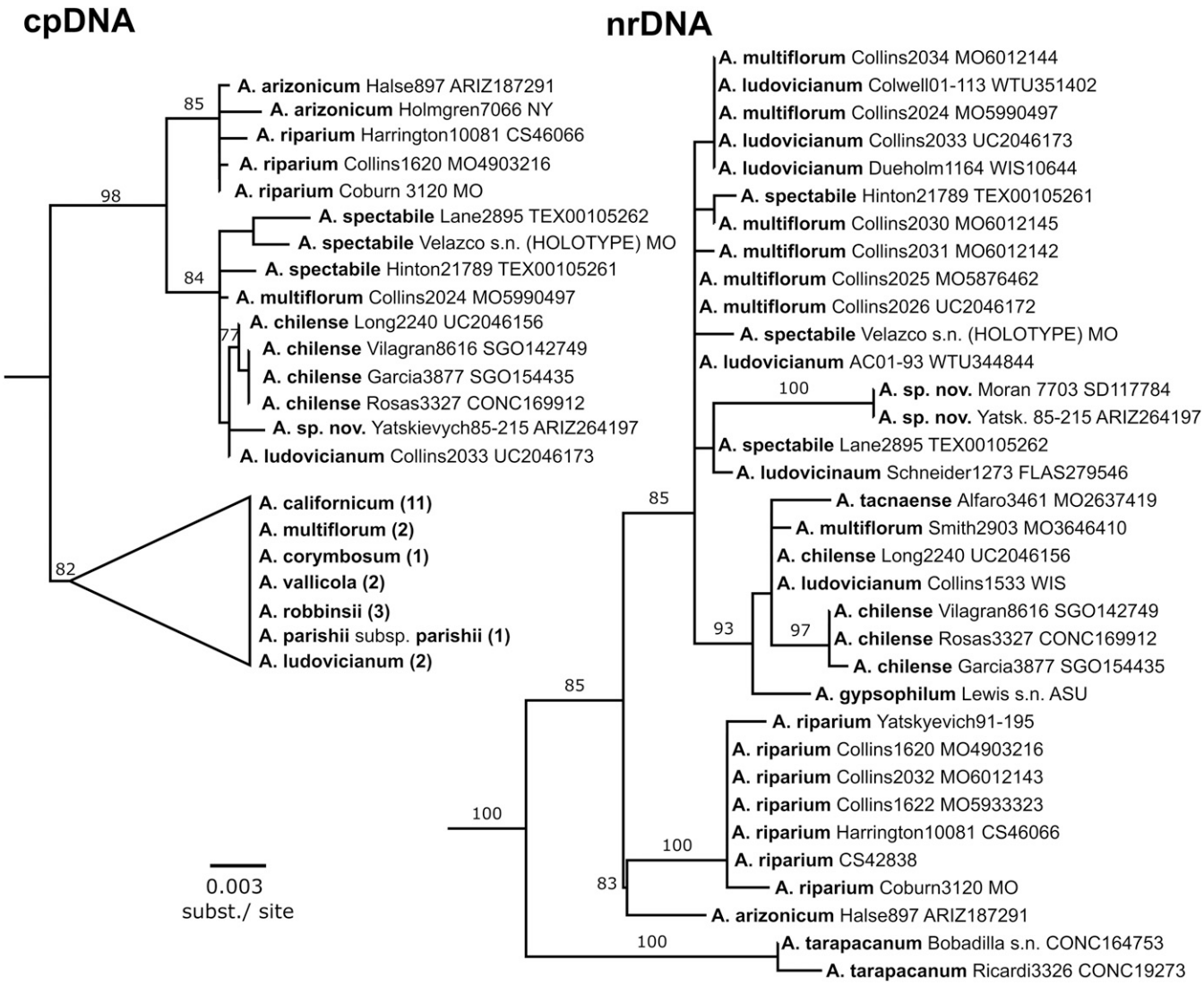

FIG. 3. Relationship of *Aphyllon spectabile* to close relatives in *A.* sect. *Nothaphyllon* based on plastid (cpDNA) and nuclear ribosomal (nrDNA) evidence. Bootstrap support > 75% shown. Clade of 22 specimens representing seven species collapsed for concision. Collector, collection number, herbarium, and herbarium accession number shown at tips.

western Texas. The primary host is *Gutierrezia sarothroe* (Pursh) Britton & Rusby, but occasionally is found on *Heterotheca* spp.

The only other species that occurs with *A. spectabile* in the Sierra Madre in the vicinity of Monterrey, Mexico is *Aphyllon cooperi* A.Gray. However, several morphological characters distinguish these two taxa, most notably corolla and calyx measurements and corolla lobe differences (Table 2). Host and phylogenetic position are also highly distinct from *A. spectabile* (Fig. 3).

***Additional Specimens Examined*—Mexico.** —COAHUILA: Saltillo [no location or habitat data], 1–15 Apr 1880, *E. Palmer s.n.* (NY). NUEVA LEON: near Monterrey, 20 May 1900, *Wm. Canby 183* (TEX). Monterrey, 3 Mar 1900, *Trelease 183* (MO, GH). 5 miles SE of Monterrey, *J.T.Bucholz s.n.* (ILL). Corrizalejo, 3 miles out [from Monterrey?], 23 Mar 1946, *Jose Roybal 48* (US). Monterrey, 20 Apr 1947, *M.M. Lacas 266* (F). Monterrey, Obispado, 1 May 1947, *M.M. Lucas 338* (F). Hillside, thorny vegetation, Monterrey, San Augustino, 22 Apr 1960, *Robert F. Smith M125* (TEX). Loma larga, frente Monterrey, 15 Nov 1966, *Jose Luis Gutierrez 220* (TEX). Estación Mariposa between Monterrey and Saltillo, 30 May 1981, *M. Lane & M. Leidig 2895* (TEX). Gypsum hills, Santa Rosa, Reyones, *n.d., G.B. Hinton 21789* (TEX).

Aphyllon gypsophilum L.T.Collins sp. nov. TYPE: MEXICO: Coahuila: Along road to gypsum dunes 4 miles w of Cuatro Ciénegas hwy [30], 10 Jun 1968, *Donald Pinkava 5271* (Holotype: LL, Isotype ASU).

Plants annual, stems slender, 15–21 cm long, 2–3(5) mm diam, unbranched, stem base not enlarged. **Roots** few simple, mass poorly developed less than 10 mm in diameter. **Leaves** few, lanceolate, 6–10 mm long, glabrous, margins entire, sometimes minutely ciliate. **Inflorescence** dense raceme, 3–9 cm long, rarely branched; glandular pubescent, floral bracts 9–10 mm, proximal narrow lanceolate, distal deltoid with apiculate apex, purple tinged, glandular pubescent, apex pubescent. **Pedicels** 0–3 mm (10 mm proximally), bracteoles 2; **Flowers**: calyx 7–10 mm, ± symmetric; purple tinged, lobes 4–6 mm, narrowly lanceolate-attenuate; corolla 8–15 (17) mm, tube almost straight, pale, slightly constricted above ovary, glandular pubescent becoming glabrate, lobes purple, 2 mm long, 1–2 mm wide, apex rounded; palatal folds not prominent, pubescent; anthers 1–1.5 mm, glabrous,

TABLE 2. Biogeographical and ecological comparison of *A. spectabile* and *A. gypsophilum* with six other species of *Aphyllon* sect. *Nothaphyllon*. Asterisk denotes multiple subspecies included.

Species	Ecology and Biogeography	Hosts
A. spectabile	Xeric vegetation, northeastern Sierra Madre mountains. Vicinity of Monterrey, Mexico	*Gymnosperma glutinosum* (probable)
A. gypsophilum	Gypsum sand dunes, Cuatro Ciénegas, Coahuila	*Xanthisma restiforme, Xanthisma gypsophilum*
A. ludovicianum	Prairie, desert grassland, widely distributed in central North America	*Artemisia* spp., *Grindelia squarrosa*, *Heterotheca* spp.
A. multiflorum	Prairie, desert grassland, arid woodland, Colorado, New Mexico, Texas, but not Mexico	*Gutierrezia sarothrae*, occasionally *Heterotheca*
*A. cooperi**	Desert shrubland, Sonoran Desert, California Desert, Chihuahuan Desert	*Ambrosia dumosa, Hymenoclea salsola, Encelia farinosa, Vigueria stenoloba*
A. castilloi	Tropical semideciduous forest, known only from Veracruz, Mexico	*Simsia foetida*
A. chiapense	Tropical Forest, known only from Chiapas, Mexico	Unknown
*A. californicum**	Coastal mountains, arid lands, coastal wetlands, Baja California Norte	Numerous Asteraceae including *Artemisia, Aster, Baccharis, Grindelia,* and *Corethrogyne* spp.

filament glabrous, pubescent at insertion; **Fruit**: Capsule oval to ovate, 6–7 mm long. Flowering Apr–Oct. Figure 2.

Diagnosis—Superficially, *A. gypsophilum* and *A. ludovicianum* seem almost identical, however, the fine details of the flower and the ecological data clearly separate the two species. *Aphyllon gypsophilum* can be distinguished from *A. ludovicianum* by its smaller flowers, extremely short corolla lobes, and deltoid bracts in the inflorescence, and the unique host species *Xanthisma gypsophilum* (B.L.Turner) D.R.Morgan & R.L.Hartm. and *X. restiforme* (B.L.Turner) D.R.Morgan & R.L.Hartm. In fact, the host affinity and presence of dimorphic floral bracts sets *A. gypsophilum* apart from all other species. *Aphyllon gypsophilum* occurs exclusively in gypsum sand dunes whereas *A. ludovicianum* is a prairie species primarily parasitizing *Artemisia* L. spp., *Heterotheca* spp., and *Grindelia squarrosa* (Pursh) Dunal.

Distribution and Habitat—*Aphyllon gypsophilum* appears to be endemic to the Cuatro Ciénegas Bolson which is part the Chihuahuan Desert in the state of Coahuila, Mexico. Within the bolson, the plants only occur in the gypsum sand dunes.

Host—This species parasitizes at least two gypsophilic species of *Xanthisma* (*Machaeranthera*). *Xanthisma restiforme* is endemic to the Cuatro Ciénegas gypsum dunes (Turner 1973). The second host, *X. gypsophilum*, is another gypsophile widely distributed in the Chihuahuan Desert. This is the first report of a gypsophilic host for the genus *Aphyllon* and the first report of *Xanthisma* as host for a species of *Aphyllon*, though several other species do parasitize its close relative *Grindelia*.

Etymology—The epithet 'gypsophilum' refers to the distinctive gypsum sand dune habitat and the host *Xanthisma gypsophilum*.

Phylogenetic Affinities—Phylogenetic evidence using nuclear ribosomal genes strongly supports the placement of *A. gypsophilum* within the *A. ludovicianum* complex and a subclade (BS = 93) composed in part of the South American taxa *A. chilense* and *A. tacnense* (Fig. 3; Schneider et al. 2016). All known hosts parasitized by members of this clade are in the subtribe Machaerantherinae of the Astereae. The single sample of *A. gypsophilum* resolved sister to the rest of the clade with very weak support (BS = 66).

Notes—Morphologically, *A. gypsophilum* resembles *A. ludovicianum*, but is noticeably smaller in all aspects with slender delicate stems. The flowers are much smaller with rather short narrow corolla lobes (2 mm long by 1 mm wide when dried). The corolla tube is only slightly bent, sometimes essentially straight, and has reduced pubescence, becoming glabrate with age. Inside the corolla tube there is pubescence around the base of the filaments at the insertion, but otherwise the inner tube is glabrous. Although this character occurs in a few other species of *Aphyllon*, it is not known in *Aphyllon ludovicianum* which does not have pubescence in the corolla tube. Other taxa known in Mexico also have glabrous filaments.

Most individuals of *Aphyllon gypsophilum* have two distinctly differently shaped floral bracts (Fig. 2). The lower portion of the inflorescence has lanceolate bracts with acute apices which is typical for the genus. However, in the upper portion of the inflorescence the bracts are oval or deltoid with a distinct apiculate apex (Fig. 2C). These deltoid bracts with apiculate apex have not been reported before in *Aphyllon*. This is unusual as floral bracts in *Aphyllon* are generally rather uniform throughout the plant, mostly lanceolate or triangular, varying only slightly in shape, length and width, with an occasional variation of the apex. Hence, they are usually of minimal value taxonomically. This is the first report of dimorphic floral bracts in a species of *Aphyllon*, though a single specimen was observed with only lanceolate bracts.

Additional Specimens Examined—**Mexico.** —COAHUILA: 1.8 miles sw of Posa de la Becarra opposite Laguna Grande, 9 Jun 1968, *Donald Pinkava et al. 5178*, (ASU). Along road to gypsum sand dunes 4 miles west of Cuatro Ciénegas hwy, 10 Jul 1968, *Donald Pinkava et al. 5276* (ASU). 1.1 mi s of Puerto Salada along road & canal to Santa Tecla, 13 Jun 1968, *Donald Pinkava et al. 5564* (ASU). Mt. Anteojo, 17 Jun 1968, *Donald Pinkava et al. 5764* (ASU). Tip of Sierra de San Marcos, 10–15 Aug 1968, *Janice Lewis s.n.* (ASU; Fig. 2B, C). Gypsum dunes 12 mi southwest of Cuatro Ciénegas on Hwy 30, 16 Oct 1971, *J. Bacon & W.R. Leverich 1146* (TEX). Gypsum dunes 22 mi southwest of Cuatro Ciénegas, 3 Apr 1972, *A.M. Powell & B.L. Turner 2241* (TEX). Gypsum dunes 12 miles southwest of Cuatro Ciénegas, 18 Aug 1973, *James Hendrickson 12537* (TEX). Poza El Bonito, Cuatro Ciénegas, Coahuila, 16 Jun 1977, *J. Marroquín s.n.* (ANSM).

DISCUSSION

Aphyllon Diversity in Mexico—In the first two decades of the 21st century, seven new species of *Aphyllon* were added to the flora of North America, including Mexico. Along with *A. spectabile, A. gypsophilum,* and the recently described

Aphyllon chiapense Francisco-Gutierrez, this is a total of ten new species added to the genus, all but three of which are in *A.* section *Nothaphyllon*, which comprises over eighty percent of the species in the genus. Numerous specimens currently in herbaria cannot be identified with confidence because they do not fit the protologue of known species and at least two published names remain poorly defined, *Aphyllon dugesii* Wats. and a variety of *A. multiflorum* that lacks an available name in the genus (basionym *Orobanche multiflora* var. *pringlei* Munz).

The concept of *A. dugesii* is presented quite differently by Collins and Yatskievych (2015) and de Rzedowski (1998), and host affinities remain incomplete. On the other hand, documentation of *Orobanche multiflora* var. *pringlei* is almost nonexistent. Beyond the protologue (Munz 1930) and the two specimens from Chihuahua cited therein, not a single research paper discusses this variety. While the binomial *A. multiflorum* has been regularly applied to herbarium specimens for plants in western US and Mexico, the first author has searched diligently for other specimens to refer to this varietal name but has found none.

Despite the recent progress, undescribed species of *Aphyllon* still exist. Some of these new forms parasitize unique hosts (e.g. *Zaluzania* Pers.) and clearly represent separate lineages (*A.* sp. nov. in Fig. 3; Schneider et al. 2016). In other cases, certain specimens simply do not seem to match any of the known species of *Aphyllon* in North America. Despite the recent addition of species to the genus, especially in Mexico, the rate of increase should alert the botanical community that additional explorations will almost certainly yield further discoveries.

Further Evidence for Madrean Diversification of Aphyllon—The expanded recognition of taxonomic diversity of *Aphyllon* in Mexico further refines understanding of the diversification and biogeography of the genus as a whole. Four new species have been split from *A. ludovicianum* in the last four years, and at least one more awaits a formal description. DNA sequence data from three of these (*A. spectabile, A. gypsophilum,* and the undescribed species parasitizing *Zaluzania*) show very little differentiation from other *A. ludovicianum* complex taxa (Fig. 3). Taken together, along with the edaphic-endemic host in the case of *A. gypsophilum*, we suggest these newly described Mexican species of *Aphyllon* speciated in situ, in parallel with the diversification of *Aphyllon californicum* into a host-specific subspecies within the California Floristic Province over the last several hundred thousand years (Schneider and Moore 2017).

More specifically, *A. spectabile* and *A. gypsophilum* both have narrow geographical distributions in the Sierra Madre Oriental and Chihuahuan Desert Region, and likely evolved there. The Chihuahuan Desert is the largest desert in North America and arguably the most biologically diverse desert in the Western Hemisphere, with some 3382 plant species, of which at least 826 taxa are endemic or nearly endemic (Daniel 2022). Pinkava (1984) reported 23 species as endemic to the Cuatro Ciénegas Bolson, including several endemic gypsophiles or halophiles. The two gypsophile species of *Xanthisma* cited earlier are a part of this specialized assemblage, and by way of association, *A. gypsophilum* must be added to this list as well. Although the area around Monterrey where *A. spectabile* occurs is not technically part of the Chihuahuan Desert, the vegetation is significantly influenced by the adjacent desert biota.

Phylogenetic data is not yet available for two of the southernmost Mexican species of *Aphyllon*, *A chipanese* and *A. castilloi*, however, the protologues hypothesize an affinity to *A. dugesii* and *A. cooperi* subsp. *palmeri*. If this is correct, these species would represent a separate burst of diversification onto unique hosts in tropical forests within a separate clade that is about twice as old as the *A. ludovicianum* complex (Schneider et al. 2016; Schneider and Moore 2017; Francisco-Gutierrez et al. 2019; Francisco-Gutierrez and Alvarado-Cárdenas 2023). Further clarification of taxonomic limits (*A. dugesii,* species novae, etc.), and improved phylogenetic resolution towards the tips of the phylogeny will continue to refine relationships among individual taxa, the extent and significance of Mexican centers of diversity, and precision in reconstructing the geographic origin of key clades, including *Aphyllon* itself.

Key to *Aphyllon* in Mexico

1. Pedicels 10–110 mm, equal to or longer than plant axis; bracteoles subtending calyx absent (but floral bract subtending each pedicel present) 2 [*A.* sect. *Aphyllon*]
   2. Corollas yellow, flowers in fascicles, of 6–15(–20) flowers, forming an irregular corymb, nw Mexico, especially n Baja, host not Asteraceae. . . . *A. franciscanum*
   2. Corollas white or tinged lavender, flowers 1–3 per inflorescence, host Asteraceae: Astereae. (widespread in USA and Canada but known in Mexico only from a single disjunct collection from Oaxaca: *Camp 2451*, NY). . . . *A. uniflorum*
1. Pedicels 0–30 mm, shorter than plant axis; bracteoles 2; inflorescences racemes, sometimes spikelike, corymbs, or panicles, corollas purple, lavender, pink, maroon or white, flowers numerous, . . . 3 [*A.* sect. *Nothaphyllon*]
   3. Corolla lobe apices rounded or obtuse; plants lavender, pinkish, yellow, or sometimes purple. . . . 4
      4. Corolla lobes ovate, 3–5 mm long, 1–3 mm wide; tropical forests in s Mexico . . . 5
         5. Corolla mouth open, lower lobes slightly reflexed, apex rounded, host *Simsia foetida*; known only from tropical semideciduous forest in Veracruz . . . *A. castilloi*
         5. Corolla mouth closed, lower lobes not spreading or reflexed, apex bifid; known only from tropical forest in Chiapas . . . *A. chiapense*
      4. Corolla lobes oblong, 4–15 mm long, 3–9 mm wide; hosts Asteraceae other than *Simsia foetida*; known mostly from arid or semiarid prairies, desert, or mountains . . . 6
         6. Corolla lips internally maroon or reddish purple, sometimes with maroon or reddish-purple stripes, veins, or blotches; palatal folds glabrous; Baja California . . . *A. parishii*
         6. Corolla lips internally purple or pink, sometimes white with purple veins, rarely light yellow; palatal folds pubescent. . . . 7
            7. Inflorescence corymbose; n Baja California . . . *A. californicum* subsp. *feudgei*
            7. Inflorescence racemose or spike-like. . . . 8
               8. Corollas 8–20 mm, lips 2–6 mm; anthers glabrous or with a few hairs. . . . 9
                  9. Corollas 14–20 mm, lips 3–6 mm; filament glabrous at insertion; prairies and arid grasslands, known along the Rio Grande in Coahuila. . . . *A. ludovicianum*
                  9. Corollas 8–15 mm, lips 2 mm; filament pubescent at insertion; gypsum dunes in Cuatro Ciénegas, Coahuila. . . . *A. gypsophilum*
               8. Corollas 22–45 mm, anthers wooly or lanate . . . 10

10. Corollas 22–36 mm, upper lobes 5–12 mm; anthers woolly; ring of hairs at base of filaments; not documented in Mexico; only southern USA . . . . . *A. multiflorum*
10. Corollas 35–45 mm, upper lobes 10–15; anthers lanate; filaments glabrous at base; Nuevo Leon, Monterrey and vicinity. . . . . *A. spectabile*

3. Corolla lobe apices acute, pointed, or with an apiculate tooth; plants mostly dark purple 11
11. Inflorescence a raceme; corolla 15–32 mm, tube lavender, or white, tinged with purple, lips dark purple to lavender, with darker purple veins, lobes often with apiculate teeth; anthers mostly pubescent and usually with inconspicuous stalked glands . . . . . *A. cooperi*
    a. *A. cooperi* subsp. *cooperi* – Sonoran Desert
    b. *A. cooperi* subsp. *latiloba* – Sonoran Desert
    c. *A. cooperi* subsp. *palmeri* – Chihuahuan Desert
11. Inflorescence a pyramidal panicle; corollas 13–19 mm, dark purple throughout, lobes sometimes with white margins; anthers glabrous or sparsely pubescent; palatal folds not prominent, pale or light yellow; host *Adenostema fasciculatum*; chaparral, n Baja California . *A. tuberosum*

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Author Contributions

LTC conducted the morphological comparisons, was the primary author of both species descriptions, and co-wrote the Discussion. CV collected the holotype of *A. spectabile*, and provided photographs, field notes, and ecological data for this species. ACS contributed the molecular phylogenetic analysis for both species, co-wrote the Discussion, and edited the content and organization elsewhere. The final manuscript was read, edited, and revised by all authors.

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Appendix 1. Voucher information for specimens newly sequenced in this study. Presented in the following format: ***Species***—*Collector*, Herbarium: GenBank accession codes for ITS, ETS, *matK*, *rps2*, *trnL–trnF* spacer, with missing data indicated by —. All other GenBank and herbarium voucher information available in Supplementary Information of Schneider et al. (2016).

Aphyllon gypsophilum—*Lewis s.n.* ASU: OR478190, OR479190, —, —, —. ***A. ludovicianum***—*Schneider 1273* FLAS279546: OQ645744, OQ674032, —, —, —. ***A. riparium***— *Coburn 3120 MO*: OR478189, OR479189, —, —, OR479191. ***A. spectabile***—*Lane 2895* TEX00105262: OQ645746, OQ674034, OQ675261, OQ674037, —; *Hinton 21789* TEX00105269: OQ645745, OQ674033, —, OQ674036, OQ674038; *Velazco s.n. (holotype)* MO: OQ645747, OQ674035, OQ675262, —, OQ674039. ***A. sp.***— *Moran 7703* SD117784: OQ645743, —, —, —, —.