EXPLORATIONS INTO *EUPHORBIA* SECT. *ANISOPHYLLUM* (EUPHORBIACEAE) IN THE TRANS-PECOS REGION OF TEXAS WITH A FOCUS ON THE FENDLERI CLADE

A Thesis

Presented to the

College of Arts and Sciences

Sul Ross State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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by

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December 2016

EXPLORATIONS INTO *EUPHORBIA* SECT. *ANISOPHYLLUM* (EUPHORBIACEAE) IN THE TRANS-PECOS REGION OF TEXAS WITH A FOCUS ON THE FENDLERI CLADE

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ABSTRACT

Several new discoveries in *Euphorbia* L. subg. *Chamaesyce* Raf. sect. *Anisophyllum* Roeper for the Trans-Pecos region of Texas are documented. These include *E. ophthalmica* Pers., a species new to the Trans-Pecos from Marfa, Presidio County; *E. abramsiana* L.C. Wheeler new to Texas from Brewster and Presidio Counties; *E. vermiculata* Raf., new to Texas from Alpine, Brewster County; *E. cryptorubra* N.C. Taylor & M. Terry, a newly described species from southern Hudspeth County and northern Chihuahua, Mexico; notes on *E. golondrina* L.C. Wheeler including two potential novelties; and notes on *E. fendleri* Torr. & A. Gray, a problematic species complex. The sections concerning *E. abramsiana* and *E. cryptorubra* have been published by Taylor and Terry (2016) in *Phytoneuron* and the *Journal of the Botanical Institute of Texas* respectively. Within *E. golondrina* and *E. fendleri*, there is much room for study, and directions for future investigations are indicated. Provided at the end is a key to all species now known for the Trans-Pecos region of Texas.

ACKNOWLEDGMENTS

I would like to thank my advisor Dr. Martin Terry, who has helped in getting to remote places, provided numerous revisions to the two publications presented here, and given financial support in publishing costs. I thank Dr. Ritzi and Dr. Warnock for their support, their time, and suggesting improvements on this thesis. I would especially like to thank Dr. Powell who has helped me in many different ways: from helping me understand concepts that directly relate to this work to allowing considerable access to the Sul Ross Herbarium, upon which this work relies heavily. In addition to the Sul Ross State University Herbarium (SRSC), I also thank the curators and staff of the following herbaria: University of Texas at Austin Herbarium (TEX-LL), University of Texas at El Paso Herbarium (UTEP), S. L. Welsh Herbarium (BRY), Colorado State University Herbarium (CS), and other herbaria that have put specimen images on websites like *Symbiota* and *Global Biodiversity Information Facility* (GBIF). Lastly, I would like to thank my parents Philip and Susan Taylor for considerable financial and emotional support.

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CHAPTER I

INTRODUCTION

The worldwide genus *Euphorbia* L. (Euphorbiaceae) is a large genus of flowering plants with about 2000 species (Horn et al., 2012 and 2014). Members of *Euphorbia* range in form from trees, shrubs and succulents, to prostrate mats. When encountered by humans, they range from popular ornamentals such as poinsettia (*E. pulcherrima* L.) to common garden weeds like spotted spurge (*E. maculata* L.). The genus is united by its inflorescences, called cyathia (singular, cyathium). A cyathium closely resembles a single flower (much like that of the family Asteraceae) but in actuality is made up of an involucre of fused bracts, glands and glandular appendages, many staminate flowers with each bearing a single stamen, and a single pistillate flower made up of one pistil (Brown, 1818). When compared to a "typical" flower, the involucre superficially resembles sepals and the glands and glandular appendages superficially resemble petals. *Euphorbia* is divided up into four subgenera with subgenus *Chamaesyce* Raf. being divided up into several groups with two recognizable sections (Horn et al., 2012). One of these sections is section *Anisophyllum* Roeper.

Euphorbia sect. *Anisophyllum* occurs worldwide in temperate and tropical regions, and includes about 365 species (Horn et al., 2014). Section *Anisophyllum* has been classified variously as different genera (primarily as *Chamaesyce* Gray), and subgenera (primarily as *E.* subg. *Chamaesyce* Raf.). The history of *Chamaesyce* prior to 1965 is explained in detail by Burch (1965), and is briefly explained here with the addition of later publications. Linnaeus (1753 and 1754) initially described the group as *Euphorbia* and interpreted the cyathium as an individual flower. It was not until 1818 that Robert Brown determined that the flower was not a flower but an inflorescence, what would later be called a cyathium. This realization greatly

aided the understanding of *Euphorbia*. The dissection of *Euphorbia* into subgroups started as early as 1806 with Persoon. Subsequent proposed subgroups of *Euphorbia* leading up to the formal recognition of *Chamaesyce* and sect. *Anisophyllum* were made by Rafinesque (1817), Roeper (1828), and Reichenbach (1841). *Chamaesyce* was formally described as a genus by S.F. Gray (1821) with *E. peplis* L., as *C. meritima* Gray, as its type. In 1862, Boissier published all the *Euphorbia* species known at the time in de Candolle's Prodromus. It is in de Candolle's Prodromus that Boissier (1862) introduces *Euphorbia* sect. *Anisophyllum*. Ever since the publication of *Chamaesyce* by Gray (1821), recognition at the generic or subgeneric level has alternated, even by the same authors. *Chamaesyce* as a genus has been recognized by Millspaugh (1889, 1890, 1898a, 1898b, 1914 and 1916), McVaugh (1961), Burch (1965), Mayfield (1993), Webster (1967 and 1994), Jercinovic (2007), and others. *Chamaesyce* has been recognized as a subgroup of *Euphorbia* or simply as *Euphorbia* by Boissier (1862), Wheeler (1934, 1936a, and 1941), Mayfield (1991), Correll and Johnston (1970), Johnston (1975), McVaugh (1993), Steinmann (1997), and others. After the year 2000, molecular techniques began to be applied to the question of whether *Chamaesyce* should be a genus or a subgeneric group. There is now considerable evidence suggesting that the group is nested within *Euphorbia* and should be treated as a subgroup of *Euphorbia* (Steinmann and Porter, 2002; Bruyns, et al. 2006; Park and Jansen, 2007; Zimmermann et al., 2010; Horn et al., 2012; Yang et al., 2012). The *Chamaesyce* group is currently treated as section *Anisophyllum* by many *Euphorbia* experts (Horn et al., 2012; Yang and Berry, 2011; Yang et al., 2012; Berry et al., 2016).

Members of sect. *Anisophyllum* are generally small herbaceous plants with cyathia commonly less than a millimeter wide. There are exceptions, as some species in Mexico and the tropics are shrubs and a few species in Hawaii can become trees. Section *Anisophyllum* is

delineated primarily by the following characters: sympodial branching which is the termination of the apical meristem followed by lateral branching at the nodes (Burch, 1965; Croizat, 1936b in Burch, 1965), stems with distinct dorsal (upper) and ventral (lower) sides (even when nearly erect), leaves that are opposite and asymmetric, non-glandular stipules, and C_4 photosynthesis (Mayfield, 1991; McVaugh, 1993; Felger et al., 2015). Corresponding with the C_4 photosynthesis in this section is the presence of Kranz anatomy, identified by a layer of bundlesheath cells surrounding the veins as a way of capturing CO_2 from mesophyll cells and using it in the bundlesheath cells. Kranz anatomy can be observed macroscopically in etiolated leaves as an intricate pattern of darker veins and lighter mesophyll. With the exception of opposite leaves, the aforementioned characters (viz., sympodial branching, dorsi-ventral stems, asymmetric leaves, non-glandular stipules and C_4 photosynthesis) are not universal in sect. *Anisophyllum* (particularly in subsect. *Acutae*, considered an ancestral group) but together give a good understanding of the commonalities. Though sect. *Anisophyllum* is distributed worldwide, there are certain areas that contain more species than others. One particularly convenient and diverse geographic region with many species within sect. *Anisophyllum* is the Trans-Pecos region of Texas.

The Trans-Pecos is a botanically diverse region between the Pecos River and the Rio Grande. It includes El Paso, Hudspeth, Culberson, Reeves, Jeff Davis, Presidio, Brewster, Pecos, Terrell, and part of Val Verde Counties. To clarify, the Pecos River runs through Val Verde County making the western part of the county also a part of the Trans-Pecos region and the eastern part "cis-Pecos." The adjacent "cis-Pecos" counties, namely Loving, Winkler, Ward, and Crane Counties, with deep sand dunes to the north and/or east of the Pecos River (known as "the sand counties") are often treated with the Trans-Pecos flora (Powell, 1994; Powell, 1998;

Yarborough and Powell, 2002; Powell and Weedin, 2004) and will be included here. Including the sand counties, approximately 37 species (not including *E. ophthalmica* Pers. for reasons discussed in chapter V) and three varieties (two of which have been treated as species primarily by Turner et al., 2003) of *Euphorbia* sect. *Anisophyllum* occur in the Trans-Pecos — more species than in any single state in the United States (compared to about 30 species in Arizona and 23 species in Florida). Accordingly, the number of species in *E.* sect. *Anisophyllum* only decreases in the surrounding areas, so complete treatments of this group covering the Trans-Pecos region of Texas may be applicable to most surrounding regions without gaining new species. Those surrounding regions include the Trans-Pecos region of New Mexico, the High Plains of Texas, the Rolling Plains of Texas, the Edwards Plateau of Texas, and the northern edge of Mexico (Chihuahua and Coahuila) where it borders the Rio Grande. Treatments covering *E.* sect. *Anisophyllum* in the Trans-Pecos region of Texas are less applicable to South Texas, areas east of the Edwards Plateau, and areas west of the Rio Grande where Sonoran species start to occur.

The taxa within sect. *Anisophyllum* that have been found in the Trans-Pecos as described above, are: *E. abramsiana* L.C. Wheeler, *E. acuta* Engelm., *E. albomarginata* Torr. & A. Gray, *E. angusta* Engelm., *E. arizonica* Engelm., *E. astyla* Engelm. ex Boiss., *E. chaetocalyx* var. *chaetocalyx* (Boiss.) Tidestr., *E. chaetocalyx* var. *triligulata* (L.C. Wheeler) M.C. Johnst., *E. capitellata* Engelm., *E. carunculata* Waterf., *E. cinerascens* Engelm., *E. cryptorubra* Taylor & Terry, *E. fendleri* Torr. & A. Gray, *E. geyeri* var. *geyeri* Engelm., *E. geyeri* var. *wheeleriana* Warnock & M.C. Johnst., *E. glyptosperma* Engelm., *E. golondrina* L.C. Wheeler, *E. hyssopifolia* L., *E. indivisa* (Engelm.) Tidestr., *E. jejuna* M.C. Johnst. & Warnock, *E. lata* Engelm., *E. maculata* L., *E. micromera* Boiss., *E. missurica* Raf., *E. nutans* Lag., *E. ophthalmica*, *E. parryi*

Engelm., *E. perennans* (Shinners) Warnock & M.C. Johnst., *E. prostrata* Aiton, *E. revoluta* Engelm., *E. serpens* Kunth, *E. serpillifolia* Pers., *E. serrula* Engelm., *E. setiloba* Engelm., *E. simulans* (L.C. Wheeler) Warnock & M.C. Johnst., *E. stictospora* Engelm., *E. theriaca* var. *theriaca* L.C. Wheeler, *E. theriaca* var. *spurca* M.C. Johnst., *E. vermiculata* Raf., and *E. villifera* Scheele.

The species of sect. *Anisophyllum* in the Trans-Pecos region of Texas are not only numerous but also represent many major groups. It is therefore useful to further subdivide sect. *Anisophyllum*. The following divisions follow the phylogeny presented in Yang and Berry (2011). According to Yang and Berry (2011), there are three primary clades that are broken into two subsections. The most basal clade is the Acuta Clade. This clade is equal to subsect. *Acutae* as modified by Mayfield (1991). Subsection *Acutae* was first described by Boissier (1862) as including *E. acuta*, *E. angusta*, and *E. lata*. Mayfield (1991) later modified this to exclude *E. lata* and include the then newly described *E. johnstonii* Mayfield. The reasoning Mayfield (1991) gives is that *E. acuta*, *E. angusta*, and *E. johnstonii* lack organized bundle sheath cells (i.e., they lack Kranz anatomy). Kranz anatomy is the presence of chlorenchymatous bundle sheath cells around the vascular bundles of leaves such that the leaves appear to have dark green veins but lighter areas in between (Webster et al., 1975; Sage et al., 2011). Kranz anatomy is also an indicator of C_4 photosynthesis (Webster et al., 1975; Sage et al., 2011). *Euphorbia acuta* was later determined to have a Kranz-like arrangement of cells and an intermediate photosynthetic pathway between C_3 and C_4 called C_2 photosynthesis (Sage et al., 2011). Sage et al. (2011) also say that *E. johnstonii* has Kranz-like anatomy and likely has the intermediate C_2 photosynthesis. *Euphorbia angusta* is unique in being the only species in sect. *Anisophyllum* to have C_3 photosynthesis (Sage et al., 2011). *Euphorbia angusta* and *E. acuta* both occur in the

Trans-Pecos region of Texas. All other species within sect. *Anisophyllum* have C_4 photosynthesis.

The other two clades that are described as being in the "Core Chamaesyce" make up subsect. *Hypericifoliae*, which is split into two clades: the Hypericifolia Clade and the Peplis Clade (Yang and Berry, 2011). The Hypericifolia Clade includes species from all over the world while those in the Peplis Clade are primarily restricted to North America, despite *E. peplis* itself being native to Europe, Africa, and western Asia. Two notable species within the Hypericifolia Clade are *E. astyla* and *E. jejuna*, which are at the base of the Hypericifolia Clade and occur in the Trans-Pecos. The species within the Hypericifolia clade that occur in the Trans-Pecos are: *E. astyla*, *E. jejuna*, *E. nutans*, *E. hyssopifolia*, *E. vermiculata*, *E. glyptosperma*, *E. serpillifolia*, *E. maculata*, *E. villifera*, *E. serrula*, *E. stictospora*, *E. prostrata*, *E. ophthalmica*, and *E. indivisa*. Of these, all but two, *E. astyla* and *E. jejuna*, are relatively widespread throughout the rest of the United States and/or Mexico, with five occurring on at least two other continents. Both of the major clades can be divided several more times, but the focus will remain in the Peplis Clade, as that is where the majority of the Trans-Pecos species are. The Peplis Clade can be subdivided into two major groups. One is primarily composed of Sonoran Desert species with a few that occupy nearby regions. The species that occur in the Tran-Pecos include *E. abramsiana*, *E. capitellata*, *E. albomarginata*, and *E. serpens*. All four also occur in the Sonoran Desert. It is useful to split the other major group into three. The most basal branch includes seven species of primarily sand dune endemics, and four of these taxa, *E. carunculata*, *E. missurica*, *E. parryi*, and *E. geyeri* var. *geyeri*, occur in the Trans-Pecos. *Euphorbia geyeri* var. *wheeleriana* presumably belongs to this group, but its inclusion has not been verified phylogenetically. The other branch includes the last two groups. One group includes 10 species that range throughout

the Southwestern United States into Mexico, including five species that occur in the Trans-Pecos: *E. lata*, *E. revoluta*, *E. setiloba*, *E. arizonica*, and *E. micromera*. The other group includes seven species that, with the exceptions of *E. fendleri* and *E. chaetocalyx*, occur exclusively in the Chihuahuan Desert; for succinctness, this group will be referred to as the Fendleri Clade.

The seven taxa in the Fendleri Clade studied by Yang and Berry (2011) were: *E. fendleri*, *E. chaetocalyx*, *E. perennans*, *E. simulans*, *E. theriaca* var. *spurca*, *E. theriaca* var. *theriaca*, and *E. golondrina.* The Fendleri Clade probably includes *E. chaetocalyx* var. *triligulata*, *E. cryptorubra*, *E. fruticulosa* Engelm. ex Boiss. (both var. *fruticulosa* and var. *hirtella* M.C. Johnst.), and may include *E. crepitata* L.C. Wheeler, based on similarities in characters and distribution, though *E. crepitata* may better fit with the clade that includes *E. arizonica*. *Euphorbia fruticulosa* and *E. crepitata* are only known to occur in Mexico. Members of this group are easily separated from most other members of sect. *Anisophyllum* that grow in the same locations by their overall lack of hairs (except occasionally on the stipules and inside cyathia), leaves that are entire and not linear, stipules on the ventral side of stems that are usually united (at least basally) into linear to lanceolate appendages, styles that are branched, and seeds that are subtriangular to quadrangular in cross section with angles protruding beyond the faces instead of continuing them (i.e., not “plump”). This set of characteristics excludes all other species in the places where members of the Fendleri Clade occur, except for *E. micromera* and potentially *E. polycarpa* Benth. (in the US, distributed in Arizona and California), which are both difficult to exclude from this group as a whole based on morphology but are generally hairier. Of the eight taxa, five are restricted to the Trans-Pecos region of Texas. All but *E. fendleri* and *E. chaetocalyx* are restricted to five counties, of both Texas and New Mexico, bordering the Rio

Grande. The counties in Texas are Brewster, Presidio, Hudspeth, and El Paso Counties. The county in New Mexico is Dona Ana County. Two taxa, *E. golondrina* and *E. chaetocalyx* var. *triligulata*, are considered rare (Poole et al., 2007).

As shown above, the considerable diversity of sect. *Anisophyllum* in the Trans-Pecos offers a unique opportunity to study many representative groups. However, this diversity has often led to difficulty in identification and misidentification, even among experienced botanists. This can be especially problematic when considering the overall small size of the plants being studied. Furthermore, there are still discoveries to be made. This thesis will discuss a few discoveries and notes that have been made over the last few years by the author and give an overall key to avoid future confusion in the group.

CHAPTER II

METHODS AND MATERIALS

When this investigation began, the Sul Ross State University herbarium (SRSC) was consulted to gain an initial understanding of the species of *Euphorbia* sect. *Anisophyllum* in the Trans-Pecos region of Texas. After a preliminary understanding was gained, research took place in both herbaria and the field during the same timeframe. This was especially easy since a total of 12 species were found growing on Sul Ross State University (SRSU) campus and adjacent Hancock Hill allowing for the study of live material and herbarium specimens simultaneously. Specimen records at SRSC and satellite images on Google Earth were consulted in determining field locations. For herbaria other than SRSC, *Symbiota* portals such as *SEINet* and databases in herbarium websites were consulted to help determine what herbaria to visit. In both herbarium and field studies, multiple characteristics were consulted to form the conclusions in the following chapters. All work took place between 2014 and 2016.

HERBARIUM AND FIELD WORK

Herbarium specimens were examined at the following herbaria: SRSC, University of Texas at El Paso (UTEP), University of Texas at Austin (TEX-LL), S.L. Welsh (BRY), and Colorado State University (CS). The three Texas herbaria had many specimens of sect. *Anisophyllum* from the Trans-Pecos region of Texas. The other Texas herbarium that might have had specimens from the region was the Botanical Institute of Texas (BRIT). This herbarium should be searched in the future. The other two herbaria (BRY and CS) were opportunistically visited and held many specimens of *Euphorbia fendleri* s.l. Specimens from various other herbaria were also examined on *Tropicos*, *Global Biodiversity Information Facility* (*GBIF*), and

various *Symbiota* portals such as *SEINet*. The specimen photographs examined in *Symbiota*, *Tropicos*, and *GBIF* were from the following herbaria: New York Botanic Gardens (NY), Royal Botanic Gardens (K), Missouri Botanic Gardens (MO), Smithsonian Institution (US), California Academy of Science (CAS), University of California at Berkley (UC), Gray Herbarium (GH), Muséum National d'Histoire Naturelle (P), and Herbarium of G.B. Hinton (GBH). Out of the herbaria listed above, SRSC was frequented the most due to location and abundant specimens of sect. *Anisophyllum* from the Trans-Pecos. All specimens of sect. *Anisophyllum* at SRSC were examined. In total, SRSC had 1,867 specimens of sect. *Anisophyllum*, and the vast majority (at least 1,700) were from the Trans-Pecos. Nine hundred fifty-one of these specimens were imaged and uploaded with skeleton data (i.e., catalog/barcode number, scientific name, country, state, and county) to Symbiota (via Consortium of Northern Great Plains Herbaria); 257 specimens of sect. *Anisophyllum* were databased; and 200 sect. *Anisophyllum* specimens were georeferenced.

At least one type of each species in the Fendleri Clade was observed (except *E. theriaca* var. *theriaca*, the Holotype of which is held at GH) as follows: *E. fendleri*, Holotype (photo: NY), Isotype (specimen: UT; photos: K, MO, US); *E. chaetocalyx* var. *chaetocalyx* (basionym: *E. fendleri* var. *chaetocalyx*), Isotype (photos: NY); *E. perennans* (basionym: *Chamaesyce perennans*), Isotype (specimen: SRSC); *E. simulans* (basionym: *Euphorbia polycarpa* var. *simulans*), Isotype (photos: CAS, US); *E. theriaca* var. *spurca*, Holotype (specimen: LL), Isotype (photo: MO); and *E. golondrina*, Holotype (photo: US), Isotype (specimen: TEX). The following type specimens of species probably in the Fendleri Clade (not including *E. crepitata*) were observed: *E. cryptorubra*, Holotype (specimen: SRSC), Isotype (specimen: TEX, BRIT); *E. chaetocalyx* var. *triligulata* (as *E. fendleri* var. *triligulata*), Isotype (photos: NY); *E. fruticulosa*

var. *fruticulosa*, Isotype (photo: MO, NY); and *E. fruticulosa* var. *hirtella*, Holotype (specimen: TEX).

Plants were visited in the field at various locations. The most relevant were: the Quitman Mountains, Hudspeth County, Texas; the Guadalupe Mountains, and the gypsum flats between the Guadalupe Mountains and Orla, Culberson County, Texas; Big Bend National Park, Study Butte, and Alpine, Brewster County, Texas; the Glass Mountains, and Hwy 18 between Ft. Stockton and the Pecos River, Pecos County, Texas; the sand dunes on FM 1053 between the Pecos River and Interstate 20 Highway, Crane County, Texas; Tucson, Pima County, Arizona; and Hamburger Rock, San Juan County, Utah. Field observations were important in determining characters such as leaf ornamentation (*E. abramsiana*), habit, and general habitat. Also, plants observed in the field often look considerably different from herbarium specimens. For instance, leaf margins of some species often appear revolute in specimens due to rolling inward quickly on drying (*E. abramsiana* and others). Observations were made during spring, summer, and fall months. All collections were deposited at SRSC, totaling about 95 within *Euphorbia* sect. *Anisophyllum*. The specimens at SRSC and the observations of living plants allowed for the evaluation of several characters.

ELABORATION OF CHARACTERS FOR IDENTIFICATION

A quite thorough explanation of important characters, terms, and general characteristics of *E.* sect. *Anisophyllum* is presented by Wheeler (1936a and 1941), as explained below. The stems are interrupted (sympodial or pseudodichotomous branching) and have two sides: a dorsal or upper side (the side of the stem facing the sky) and a ventral or lower side (the side of the stem facing the ground). The long side of inequilateral leaves is always on the dorsal side of the stems. The stipules and hairs (Millspaugh, 1914) may be different on the dorsal side from those

on the ventral side, making differentiation between these two sides useful. Leaves are simple, toothed or entire, with inequilateral bases. Hairs are always simple, and typically multicellular. The stipules on the ventral side are more often united than those on the dorsal side. The stipules are also more often distinct on apical stems. On the involucre of each cyathium, there are typically four glands held on stipes. The sinus is the location where a rudimentary fifth gland occurs, which is large in many other *Euphorbia* species (e.g., *E. wrightii*). The sinus is often U-shaped and depressed. The glands next to the sinus are considered proximal glands and the other two are considered distal glands. The proximal glands are typically larger. Between any two glands is a single lobe of the involucre (the sinus has two; one on each side of the fifth gland), each of which represents the apex of its modified leaf. The androphores (or andropeds) are the pedicels that hold the monandrous staminate flowers. The staminate flowers are held in five fascicles. There are two rows of staminate flowers per fascicle in species that have 10 or more stamens. These fascicles surround a single pistillate flower held on a gynophore (or gynoped) that often curves into the sinus so that the fruit hangs downward. Typically, neither the staminate nor pistillate flowers have sepals or petals (though the pistillate flower may have a rudimentary perianth). A row of bractioles is present on either side of each fascicle, and a single bracteole is present for each androphore (though the bracteoles may be reduced or be more numerous if staminate flowers are reduced). The seeds are quadrangular (four-sided in cross-section) and have four facets (sides or faces) (Fig. 1). Even seeds that are triangular have four distinct facets. The raphe is the line on the proximal angle (Fig. 1C and Fig. 2C) that faces the collumnella in the center of the fruit. Opposite the raphe is the dorsal angle (or back of the seed) (Fig. 1A and Fig 2A). The lateral angles are the two angles that are neither the proximal nor the dorsal angles (Fig. 1B and Fig. 2B). Radial measurements are those made from the raphe to the

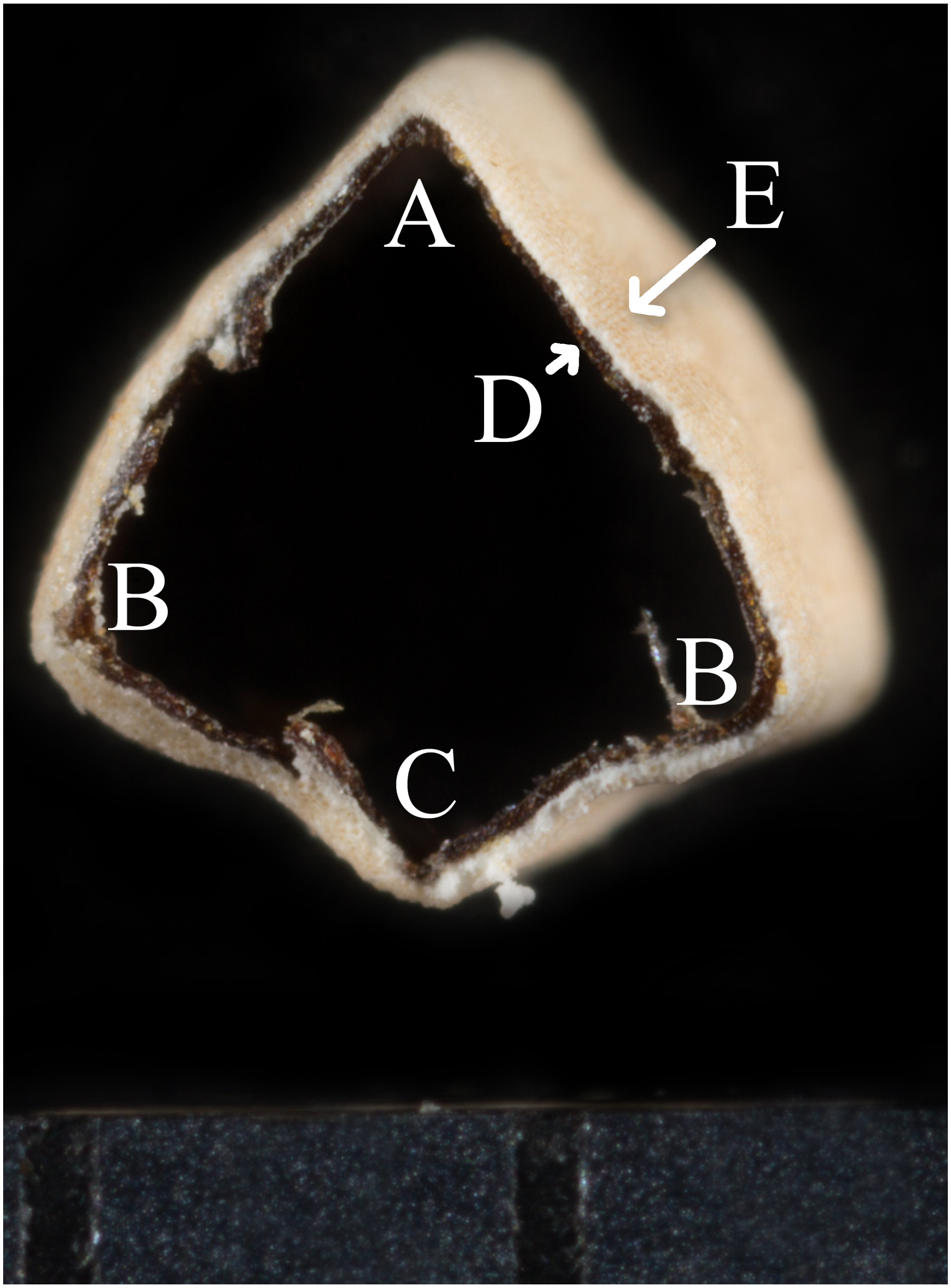

Figure 1. Euphorbia acuta seed cross section. Taylor 132, Texas, Pecos Co. ca. 7.2 km north of Interstate 10 Highway on Highway 18, 10 May 2013. Scale in millimeters. A. Dorsal angle. B. Lateral angles. C. Proximal angle. D. Dark colored testa. E. Light colored mucilaginous layer. Photo by Nathan C. Taylor.

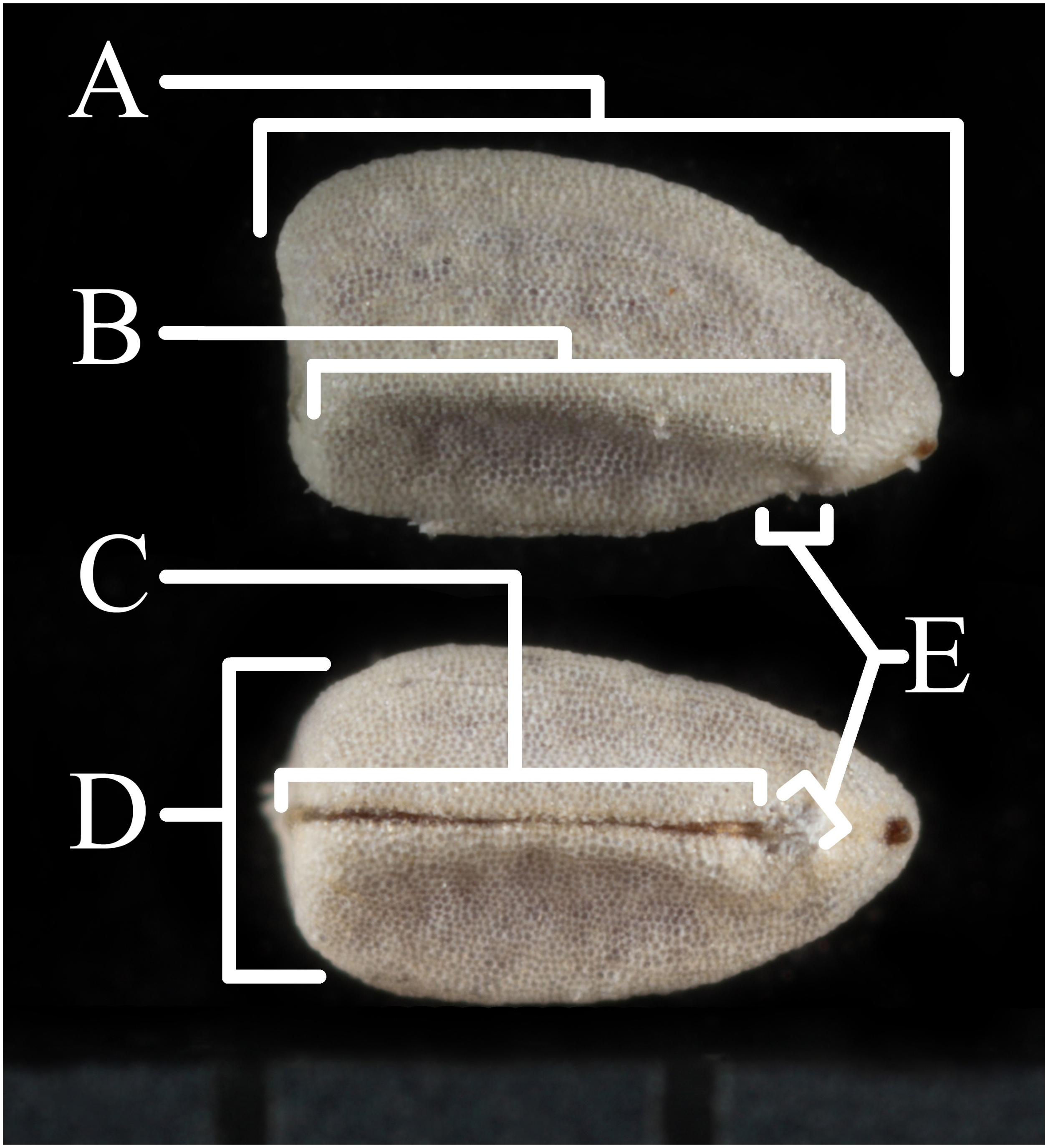

Figure 2. *Euphorbia lata* seeds. *Taylor 800*, Texas, Gaines County ca. 0.97 km north of Highway 180 on County Road 141, 15 Aug 2016. Scale in millimeters. A. Dorsal angle. B. Lateral angle. C. Raphe on proximal angle. D. Chalazal end of seed. E. Hilum. Photo by Nathan C. Taylor.

dorsal angle. Tangential measurements are those made from one lateral angle to the other. Occasionally, ridges include the angles — meaning that the ridges cause the angles to be ridged. This can be contrasted with ridged seeds that do not include the angles — meaning that the angles have a relatively smooth curve. Seed coats of most members of sect. *Anisophyllum* become mucilaginous when wet. When dry, this mucilaginous layer is a white coat overlaying, and often obscuring, the black, brownish, or tan testa (Fig. 1D–E).

Wheeler (1936a) notes that plant duration (i.e., the distinction between "annual" and "perennial") and the use of “rough or smooth” to differentiate seeds are not adequate for identification as most species bloom their first year and seeds may vary from smooth to wrinkled in the same species. While it is true that duration is not helpful for first-year plants and should not be used alone, it is very useful in making identifications of large populations of plants of the same species. It is also not uncommon in the Trans-Pecos region of Texas to be able to consult many plants of the same species in a small area. Likewise, there are a few species, primarily *E. geyeri*, *E. missurica*, *E. carunculata*, and *E. parryi*, that always have smooth seeds. While it is true that these characters should be used with caution, they should not be altogether excluded. Wheeler (1936a) also notes that the presence or absence of glandular appendages should be used with caution. The appendage may indeed be prominent or absent in the same species but can be useful under certain circumstances. Gland and seed shape, number of androphores, presence of the fifth gland, the sinus depression, and stipule and hair types are all listed as useful characters by Wheeler (1936a).

In addition to the characters above, maculation and habit can be useful but to a limited degree. The maculation is typically an oval to oblong reddish spot along the midvein that may branch to smaller veins. A maculation may also be broken into an irregular shape or narrowed to

a narrow red line. In the species that produce maculations, it is not always present (especially in shade or late in the year). However, the presence of a maculation can be useful in eliminating species that are not known to produce them. The shape of maculations can also be useful as explained in chapter III on *E. abramsiana*.

Habit can be quite useful for the determination of some taxa. While it is nearly impossible to know with absolute certainty what the habit of a plant was that is mounted on a herbarium sheet, there are somewhat reliable ways of knowing if a plant is prostrate or ascending to erect. Stems that are erect or ascending will usually be pressed with stems above the rootstock, sometimes bending down below the level of the rootstock in low ascending plants but not overlapping the rootstock. Stems that are prostrate will usually be pressed in a way that the stems overlap the rootstock or at least bend well below the rootstock. These rules of thumb do not work for young plants and should not be used for individual plants, but are useful in the consideration of entire populations where there are large numbers of specimens such as *E. fendleri* Torr. & A. Gray and *E. chaetocalyx* (Boiss.) Tidestr.

Among the most important factors to consider when identifying members of *E.* sect. *Anisophyllum* is when the plants become etiolated due to the effects of shade and dense competition from other plants. Etiolated plants tend to lack maculations regardless of species, develop ascending to erect stems regardless of typical habit (except apparently in *E. albomarginata* Torr. & A. Gray and *E. serpens* Kunth), produce narrower stems than typical, develop longer gynophores and androphores, have different hair densities than non-etiolated plants, and sometimes possess atypically shaped leaves. All the affected characters can be quite useful in identification under normal circumstances, which makes etiolated plants much more difficult to identify. One way to determine if a plant is etiolated is by examining the leaves. If

the Kranz anatomy (as described in the introduction) is easily visible, the plant is likely etiolated. (Kranz anatomy will also be easily visible in crushed leaves of plants that are not etiolated.) The method does not work well for all plants, especially those with densely hairy leaves, most hardy perennials, and *E. acuta* Engelm. and *E. angusta* Engelm., the only two species in the Trans-Pecos that lack C_4 photosynthesis. The characters least affected by etiolation are those listed by Wheeler (1936a) as reliable characters: gland and seed shape, number of androphores, presence of the fifth gland, the sinus depression, and stipule and hair types. In addition to fruit size and shape, the aforementioned characters should be considered relatively reliable for identifying etiolated plants.

Habit is also influenced by weather. When non-etiolated plants of prostrate species of sect. *Anisophyllum* start to dry out, long stems become decumbent and short stems become ascending. If plants become completely dry, the stems can become erect. The leaves also fold dorsally so that the two opposite leaves almost meet on the upper sides of stems. The habit of plants with leaves positioned in that manner should be considered unreliable. When etiolated plants dry out, they typically shrivel and the stems often collapse. The effect on non-etiolated plants can be compared to the effect of drying on stems of *Selaginella lepidophylla* (Selaginaceae) that curl upward and towards the center as the plants dry (though the curling effect is less dramatic in sect. *Anisophyllum*). This curling may also be problematic if the plant starts to dry out before pressing. Specimens pressed after the plants have started drying are characterized by nearly all leaf pairs overlapping and curled stems. Specimens pressed after drying out are difficult to use without dissection, as dorsal stipules, cyathia, fruits, and upper sides of leaves are often obscured.

Another factor affecting habit that should be considered is the health of the plant. A certain rust, presumably *Uromyces proëminens* (DC.) Lév. based on the observations of Standley (1916), causes stems to become strictly erect (even in *E. albomarginata*). Plants infected with the rust are easy to spot and are ordinarily noticeably infected on only a few branches. The infested stems are typically taller than healthy stems even in species with ascending stems. Another condition, likely a disease known as aster yellows, causes the ovaries to become vegetative buds, stamens to become leaves, and bracts to become more leaf-like. Often associated with this is the presence of a fasciation, and whorled leaves. The aster yellows condition is caused by phytoplasmas, which are bacteria that lack cell walls (McCoy et al., 1989). Plants infected with either disease are more difficult to identify and are less useful taxonomically.

Based on these observations, the information in the following chapters has been determined. Two of these chapters have been published. Chapter III concerning *Euphorbia abramsiana* L.C. Wheeler is published by Taylor and Terry (2015) in *Phytoneuron*. Chapter IV concerning *Euphorbia cryptorubra* N.C. Taylor & M. Terry is published by Taylor and Terry (2016) in the *Journal of the Botanical Institute of Texas*. In Taylor and Terry (2015) the spelling *E. serpyllifolia* is now known to be a misspelling of *E. serpillifolia* (Berry et al., 2016; Persoon, 1806).

CHAPTER III

EUPHORBIA ABRAMSIANA (EUPHORBIACEAE): NEW TO TEXAS

ABSTRACT

Euphorbia abramsiana L.C. Wheeler is a prostrate annual found throughout southern California, Arizona, the southwest corner of New Mexico, and adjacent Mexico. This report documents its occurrence in Trans-Pecos Texas. Misidentified *E. abramsiana* specimens, mostly confused with *E. glyptosperma* and *E. serpyllifolia*, have been found from locations mainly in and near Big Bend National Park and Big Bend Ranch State Park. *Euphorbia abramsiana* differs from *E. glyptosperma* and *E. serpyllifolia* by the presence of very short, stiff hairs on the stems, distinct pale lines following the pattern of the pinnate venation on the leaf blades, leaf blade maculation consisting of a series of spots along and near the midvein, and an abrupt protrusion on the chalazal end of the seed.

INTRODUCTION

Euphorbia abramsiana L.C. Wheeler (subg. *Chamaesyce* sect. *Anisophyllum*) is a prostrate desert annual (Fig. 3) previously known from southern California, Arizona, the southwestern corner of New Mexico, and adjacent Mexico. The species is now documented for Texas, represented by eight specimens in the Sul Ross State University Herbarium (SRSC) and two from the University of Texas herbarium (TEX-LL). All were collected in and near Big Bend National Park (BBNP) and Big Bend Ranch State Park (BBRSP), with one seemingly out-of-place record in Reeves County (Fig. 4).

Figure 3. *Euphorbia abramsiana*. *Morey 197*, Madera Canyon River Access, Big Bend Ranch State Park, Texas, 22 Sep 2014. Photo by Roy Morey; used with his permission.

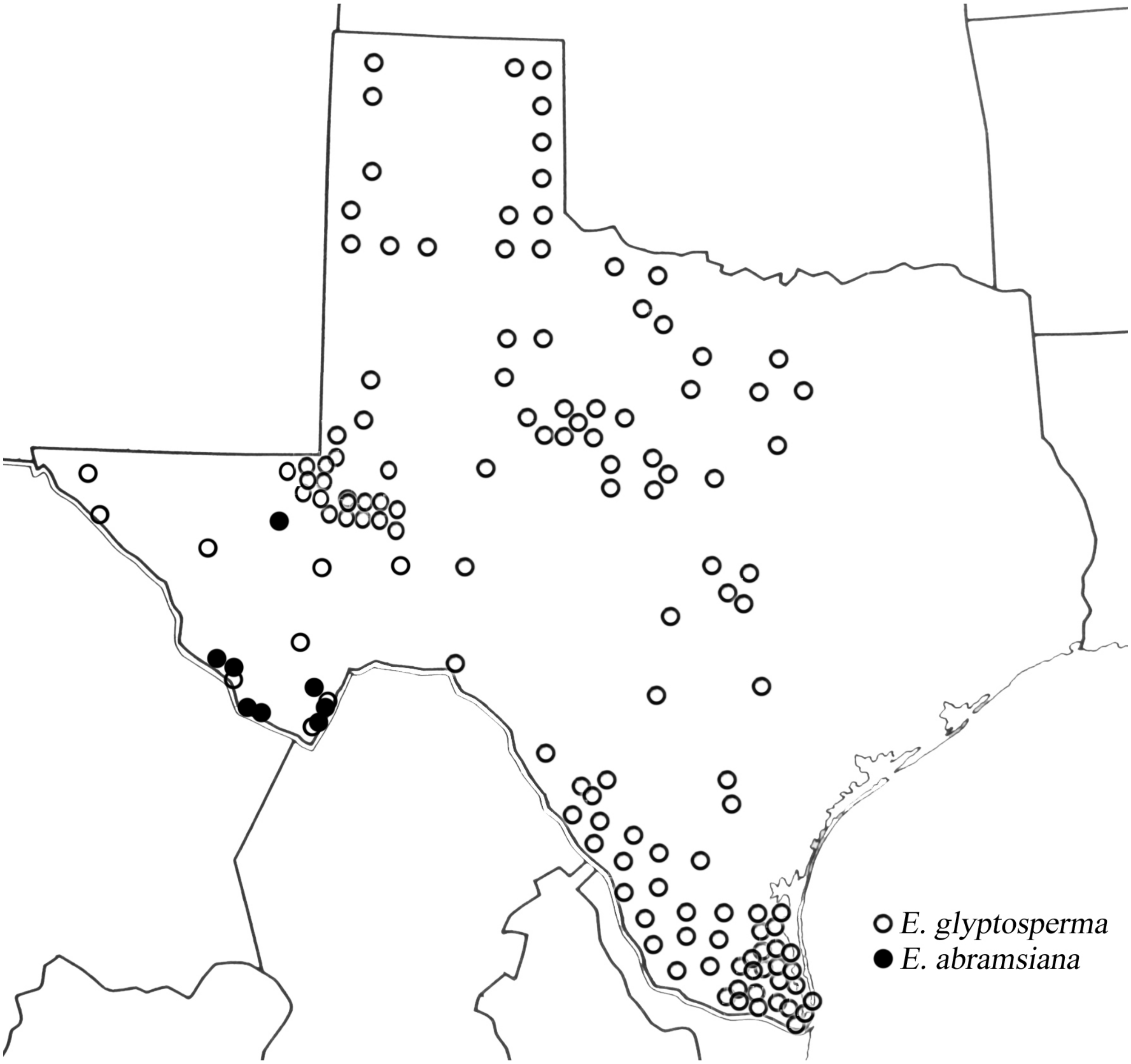

Figure 4. Distribution of *Euphorbia abramsiana* and *E. glyptosperma* in Texas (distribution of *E. glyptosperma* outside Trans-Pecos Texas from Turner et al. 2003).

TEXAS SPECIMENS OF *EUPHORBIA ABRAMSIANA* EXAMINED

UNITED STATES. Texas. Reeves Co.: Frequent annual; limestone soil along highway about 15 mi S of Pecos toward Saragosa, alt. 457 m, 9 Sep 1951, *Warnock 10181* (TEX-LL). **Presidio Co.**: BBRSP, Terneros Creek crossing on road to Sauceda, 579814 E, 3269720 N, alt. 920 m, 30 Sep 2014, *Morey 207* (SRSC); BBRSP, Madera Canyon River Access, near 605018 E, 3240801 N, alt. 720 m, 22 Sep 2014, *Morey 197* (SRSC; Fig. 3); BBRSP, 1 mi W of Lajitas on Rio Grande, 616973 E, 3237502 N, 710 m, 23 Sep 2014, *Morey 198* (SRSC); 6.1 km N of Presidio on Hwy 67, 4 Sep 1999, *McRae 41* (SRSC). **Brewster Co.**: BBNP, Mesa de Anguila Trail, off trail just E of Comanche Creek, 27 Sep 2014, *Morey 203* (SRSC); BBNP, frequent annual on sandy soil at head of Boquillas Canyon, alt. 579 m, 12 Aug 1966, *Warnock 20951* (SRSC); BBNP, gravel-topped yellow marl hills near San Vicente, 29°9' x 103°1', alt. ca. 579 m, 16 Nov 1958, *Johnston 3625* (SRSC); BBNP, infrequent annual in limestone soil in Avery Canyon, alt. 975 m, 23 July 1950, *Warnock 9135* (SRSC); BBNP, muddy banks of Rio Grande near San Vicente, 26 Aug 1915, *Young s.n.* (TEX-LL).

DESCRIPTION OF TEXAS SPECIMENS OF *EUPHORBIA ABRAMSIANA*

Prostrate to ascending annual; stems pubescent with very short, stiff hairs, at least basally, often glabrous toward the apices; leaf blades oval to oblong, oblong-ovate, oblong-lanceolate (often the short side is semi-oval and the long side is semi-oblong), to 10 mm long, 4 mm wide, sometimes pubescent, bases unequal; blades green in shade to dark green in bright sunlight in living plants, with pale stripes following the pattern of the pinnate venation (though not veins themselves; stripes fade after blades dry); blade maculation comprised of a series of spots, usually of different sizes, arranged along and near the midrib (spots sometimes branching or merging to form an irregular shape), or occasionally one or a few spots along and near major

veins away from the midrib; blade margins entire to toothed at the apex and along the long side of the margins; stipules divided several times into filaments; cyathia solitary at the nodes; involucral glands mostly circular, occasionally oblong, with appendages entire to bilobed; involucral lobes between glands usually divided into a few segments; staminate flowers 3–5; styles divided and short; capsules globose triangular, slightly elongated, 1.8 mm long, 1.5 mm wide, glabrous; seeds quadrangular in cross section, white, 1.2–1.3 mm long, ca. 0.5 mm wide, with markedly raised, rounded transverse ridges, with the angles appearing entire or inconspicuously notched between some transverse ridges, the transverse ridges appearing mostly continuous with the angles, and the chalazal end of the seed with an abrupt protrusion, less than 0.1 mm long.

The description above of *Euphorbia abramsiana* is mostly consistent with others published for the species (Jercinovic 2007; Wheeler 1934; Wheeler 1941), but we have provided more details here on leaf morphology and seeds. Steinmann and Felger (1997) described minute teeth on the margins of the leaf blade large enough to be seen only with aid of magnification, compared to *E. serpyllifolia* with conspicuous teeth often large enough to be seen without magnification. We find that *E. abramsiana* can have larger teeth than *E. serpyllifolia*, albeit rarely. Apart from some specimens with relatively deep incisions between the teeth, the Texas specimens cited above display all other characters of *E. abramsiana*. The Texas specimens also look very similar to an isotype (*Abrams 4097*, MO, digital image via tropicos.org).

The *Euphorbia abramsiana* specimens from Texas were previously identified as *E. glyptosperma* (Fig. 5), *E. serpyllifolia* (Fig. 6), and one as *E. golondrina*, with four specimens bearing annotations by M.C. Johnston. Johnston annotated these specimens as “atypical” and belonging to *E. glyptosperma*. Correll and Johnston (1970) similarly noted that some “aberrant”

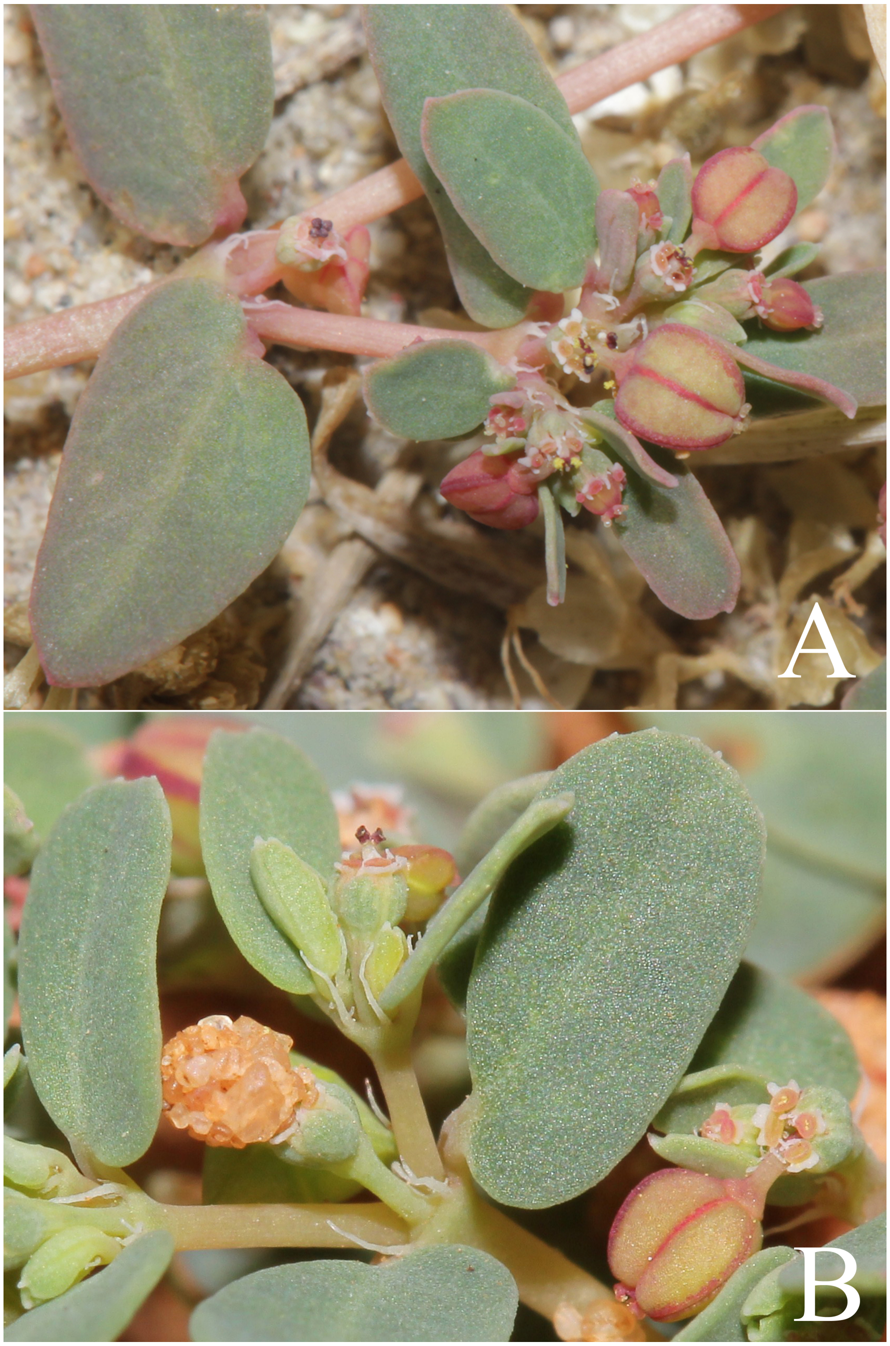

Figure 5. *Euphorbia glyptosperma*. Leaf blades without lines or splotches. *Euphorbia glyptosperma* specimens from the Trans-Pecos often display characteristics similar to those of *E. abramsiana*, compared to *E. glyptosperma* specimens in other parts of Texas. A. Tornillo Creek, Big Bend National Park, Texas, 12 Oct 2014. B. Gaines Co., Texas, 5 Oct 2011. Photos by Nathan C. Taylor.

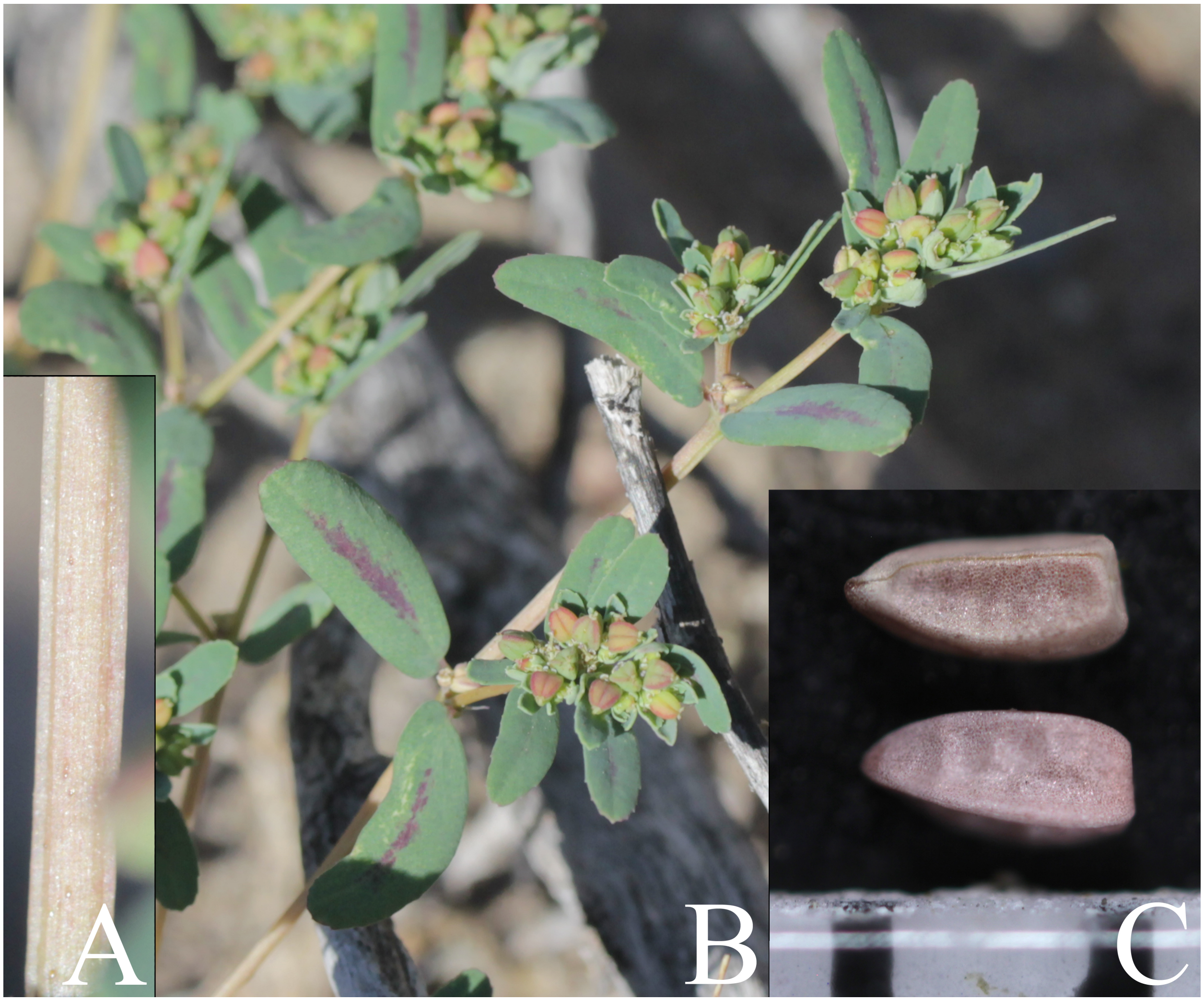

Figure 6. *Euphorbia serpyllifolia*. Stems usually ascending and winged; leaf blades with or without a continuous, linear splotch; seeds pitted, wrinkled, or with low transverse ridges. A. and B. Tornillo Creek, Big Bend National Park, Texas, 12 Oct 2014. C. Solitario Overlook, Big Bend Ranch State Park, Texas, 4 Sep. 2014, *Morey 182*. The distance between the two wide black vertical lines at bottom of figure is 1 millimeter. Photos by Nathan C. Taylor.

specimens of *E. glyptosperma* are pubescent. *Euphorbia glyptosperma* and *E. serpyllifolia* are both common throughout Trans-Pecos Texas. *Euphorbia glyptosperma* is found throughout Texas except in the eastern part of the state (Fig. 4) and seems to prefer sandy, disturbed soils, whereas *E. serpyllifolia* is seemingly restricted to the Trans-Pecos and is found mostly in rocky soils. In the USA as a whole, *E. glyptosperma* and *E. serpyllifolia* are reported throughout except the southeastern states (even entering Canada). *Euphorbia golondrina* is restricted to Trans-Pecos Texas and is much less widespread, apparently confined to certain sandy habitats. *Euphorbia abramsiana*, *E. glyptosperma*, *E. serpyllifolia*, and *E. golondrina* are all sympatric in Trans-Pecos Texas.

Many *Euphorbia glyptosperma* specimens from the Trans-Pecos differ slightly in certain characters from *E. glyptosperma* specimens from other parts of Texas (Fig. 5). In many Trans-Pecos specimens of *E. glyptosperma* the seeds are longer, the leaf blades are usually more oval, bases of blades are less unequal, the cyathial glands are more circular, and the glandular appendages are more often 2-lobed. All these traits approach those of *E. abramsiana*, suggesting hybridization between these two species in the Trans-Pecos region where they are sympatric.

KEY TO *EUPHORBIA ABRAMSIANA* AND SIMILAR SPECIES

1. Upper stipules (those on the side of the stem facing upward or mostly upward) not united and mostly entire, forming 2 linear segments; lower stipules (those on the side of the stem facing downward or mostly downward) united into a single linear segment; seeds greater than 1.5 mm long, lacking markedly raised transverse ridges .... **Euphorbia golondrina**

1. Upper and lower stipules divided, often into more than 2 linear segments; seeds less than 1.5 mm long, with or without transverse ridges.

  2. Stems usually ascending and somewhat winged, giving the plant a shriveled appearance;

seeds smooth, pitted, wrinkled, or with low transverse ridges (Fig. 6)

.... **Euphorbia serpyllifolia**

2. Stems prostrate (except in shade or dense competition with other plants), not winged; seeds with markedly raised transverse ridges.

   3. Stems pubescent with short stiff hairs (often only basally); leaf blades often with pale stripes following the pattern of the pinnate venation in living plants; maculation interrupted, consisting of many small circular or irregular spots (Fig. 7); seeds concolorous, white; seeds with an abrupt protrusion at the chalazal end (Fig. 8A)

   .... **Euphorbia abramsiana**

   3. Stems glabrous; leaf blades lacking pale stripes; maculation rarely present but, if present forming a single, continuous, linear spot along the midvein; seeds often slightly bicolorous when mature, with mostly light tan ridges and slightly paler areas (sometimes with a pale reddish tint) between ridges; seeds without an abrupt protrusion at the chalazal end (Fig. 8B) .... **Euphorbia glyptosperma**

ACKNOWLEDGEMENTS

We thank A. Michael Powell for providing valuable comments that improved this paper and for providing continual access and use of the Sul Ross State University Herbarium. We acknowledge Tom Wendt and Billie Turner for welcoming access to the University of Texas Herbarium. We also thank Guy Nesom for improvements made to this paper.

Figure 7. *Euphorbia abramsiana*. Leaf blades often have pale lines in the position of pinnate venation and a central splotch broken into many smaller spots. A. Hot Springs Trail, Big Bend National Park, Texas, 12 Oct 2014. B. Tucson, Arizona, 7 Aug 2014. Photos by Nathan C. Taylor.

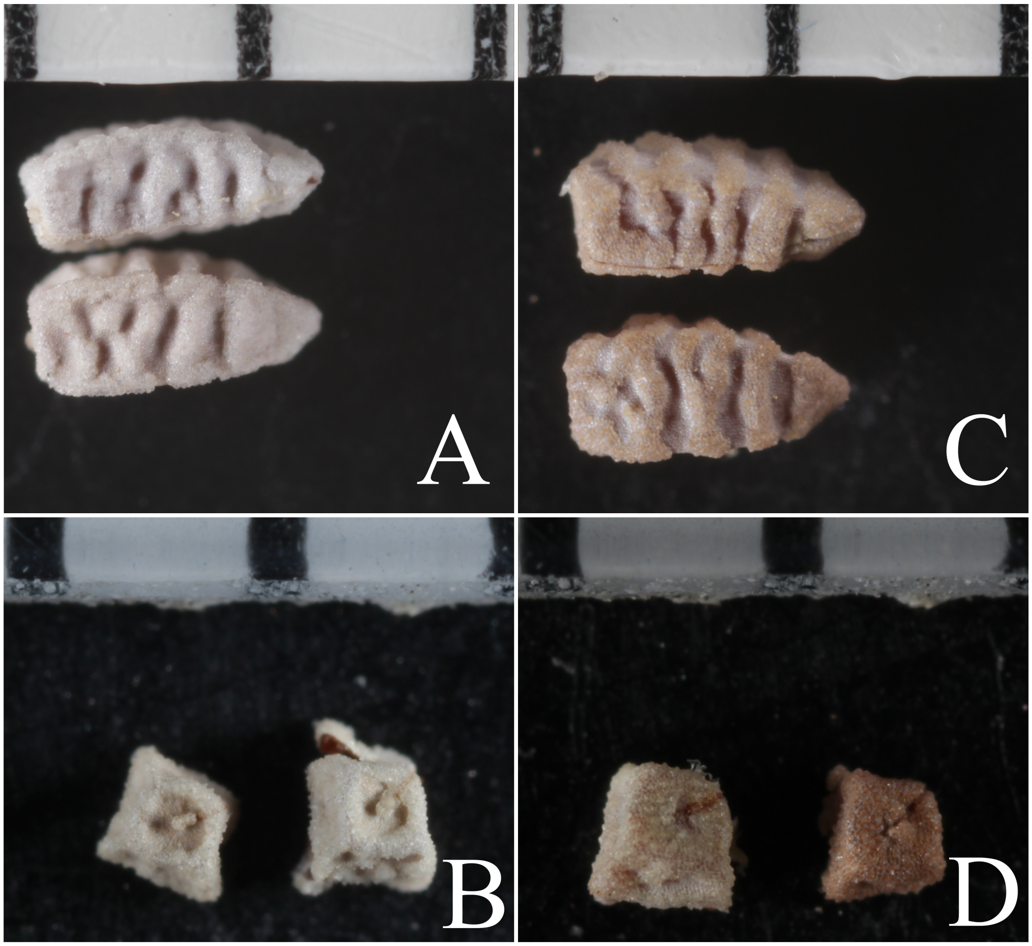

Figure 8. A. *Euphorbia abramsiana* seeds have transverse ridges appearing mostly continuous with the rest of the seed; angles (four corners of seeds in cross section) less noticeably notched between ridges (*Warnock 9135*, SRSC). B. Chalazal end of *E. abramsiana* seed showing a protrusion often visible from the side of the seed (*Warnock 9135*, SRSC). C. *Euphorbia glyptosperma* seeds have transverse ridges that appear distinct from the areas between notches and often appear as a slightly different color; angles noticeably notched between ridges (*Warnock & Parks 8762*, SRSC). D. Chalazal end of *E. glyptosperma* seed mostly flat or only slightly bulging and not typically visible from the side of the seed (*Warnock & Parks 8762*, SRSC). Seed differences between *E. abramsiana* and *E. glyptosperma* are somewhat inconsistent in ridge characters but consistent in characters on the chalazal end of seeds, at least in specimens collected in the Trans-Pecos. Scale in millimeters. Photos by Nathan C. Taylor.

LITERATURE CITED

Correll, D. S. and M. C. Johnston. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, Texas, USA.

Jercinovic, E. 2007. The status of the genus *Chamaesyce* in New Mexico. *The New Mexico Botanist Newsletter* 40: 1–14.

Steinmann, V.W. and R.S. Felger. 1997. The Euphorbiaceae of Sonora, Mexico. *Aliso* 16: 1–71.

Turner, B.L., H. Nichols, G. Denny, and O. Doron. 2003. Atlas of the vascular plants of Texas. Vol. I–Dicots; Vol. II–Ferns, Gymnosperms, Monocots. Sida, Bot. Misc. 24, 1 and 2.

Wheeler, L.C. 1934. California *Euphorbia* notes. *Bulletin of the Southern California Academy of Sciences* 33: 109–110.

Wheeler, L.C. 1941. *Euphorbia* subgenus *Chamaesyce* in Canada and the United States exclusive of southern Florida. *Rhodora* 43: 97–154, 168–205, 223–286.

CHAPTER IV

EUPHORBIA CRYPTORUBRA (EUPHORBIACEAE), A NEW SPECIES IN *EUPHORBIA* SUBGENUS *CHAMAESYCE* SECTION *ANISOPHYLLUM* FROM TEXAS, U.S.A. AND CHIHUAHUA, MEXICO

ABSTRACT

Euphorbia cryptorubra sp. nov. is described here as a new species. It is a glabrous annual belonging to subgenus *Chamaesyce* Raf. section *Anisophyllum* Roeper. It is currently known from two locations, one southeast of the Quitman Mountains, Texas, U.S.A. and the other near Ojinaga, Chihuahua, Mexico. Specimens of the new species are most similar to those of *E. theriaca* L.C. Wheeler, *E. simulans* (L.C. Wheeler) Warnock & M.C. Johnst., and *E. golondrina* L.C. Wheeler due to their similarities in habit, vestiture, leaf margins, stipules, styles, and some general seed characters but can be differentiated by leaf shape and specific seed characters. Specimens of *E. cryptorubra* key to *E. golondrina* in Manual of the Vascular Plants of Texas, but differ in their smoother seed coats, shorter, mostly oblong-oval leaf blades, habitat, and distribution.

INTRODUCTION

Euphorbia L. subg. *Chamaesyce* Raf. sect. *Anisophyllum* Roeper is a diverse group in the Trans-Pecos region of Texas. This taxon is taxonomically equivalent to the genus *Chamaesyce* Gray, but has recently been treated as a monophyletic group nested within a more broadly circumscribed *Euphorbia* by Steinmann & Porter (2002), Bruyns et al. (2006), Park & Jansen (2007), Zimmermann et al. (2010), Horn et al. (2012), and Yang et al. (2012). With about 35 species and three varieties (two of which have been treated as species), the Trans-Pecos region of

Texas includes more species of sect. *Anisophyllum* than any single state in the United States (compared to about 30 in Arizona and 23 in Florida). One of the species, *E. golondrina* L.C. Wheeler, is particularly uncommon and seemingly restricted to the sands of Boquillas Canyon and its vicinity. Thus, it was interesting to find specimens identified as *Euphorbia golondrina* collected from the south end of the Quitman Mountains, Hudspeth County (approximately 300 km northwest of Boquillas Canyon). Even more interesting is that the Hudspeth County specimens are morphologically quite different from the *Euphorbia golondrina* of Boquillas Canyon though they keyed to *E. golondrina* in *Manual of the Vascular Plants of Texas* (Correll & Johnston 1970). Observations of living plants in the field, and specimens from the United States and Mexico in the Sul Ross State University Herbarium (SRSC), the University of Texas Herbarium, Austin (TEX-LL), and the University of Texas Herbarium, El Paso (UTEP) have led to the conclusion that this is, in fact, an undescribed species.

Many species of *Euphorbia* sect. *Anisophyllum* have asymmetrical leaves, though the degree of asymmetry differs greatly among species. It is useful to define this asymmetry by describing the width of the petioles at their connection with the blades and the shape of each half of the leaf blade (as divided along the midvein) separately (Fig. 9). Conveniently, the new species and all the species it has been confused with typically have a prostrate or low ascending habit and leaves that rotate to face the sky. Thus, the longitudinal halves of the blades can be identified in relation to the stem (i.e., the margin in the apical direction of the stem and the margin in the basal direction of the stem). We use seed terminology as found in Wheeler (1941).

Euphorbia cryptorubra N.C. Taylor & M. Terry, sp. nov. (Figs. 10–12). TYPE: U.S.A. Texas. Hudspeth Co.: 17 km NW of Indian Hot Springs ranch entrance, common in deep

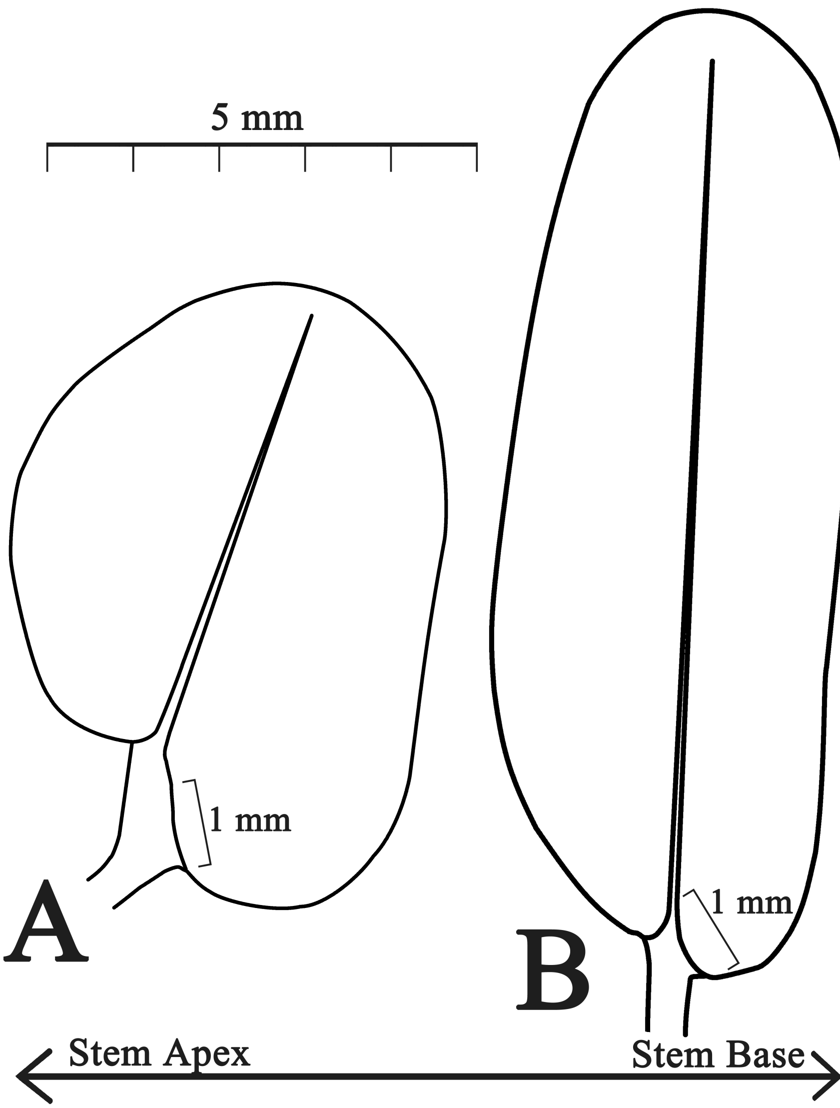

Figure 9. Large mid-stem leaves of *Euphorbia cryptorubra* (A) and *E. golondrina* L.C. Wheeler (B) showing difference in size and shape of the two halves of the leaf blades and flared petioles at the attachment with the blades. Leaf halves to the left of the midvein are in the direction of the stem apex. Leaf halves to the right of the midvein are in the direction of the stem base. Scale in millimeters. A. Blade half with the margin facing the stem apex mostly semi-oval; blade half with the margin facing the base of the stem mostly semi-oblong to semi-oblong-oval. Based on *N.C. Taylor 635*. B. Both blade halves mostly semi-oblong. Based on *W.R. Carr 12199*.

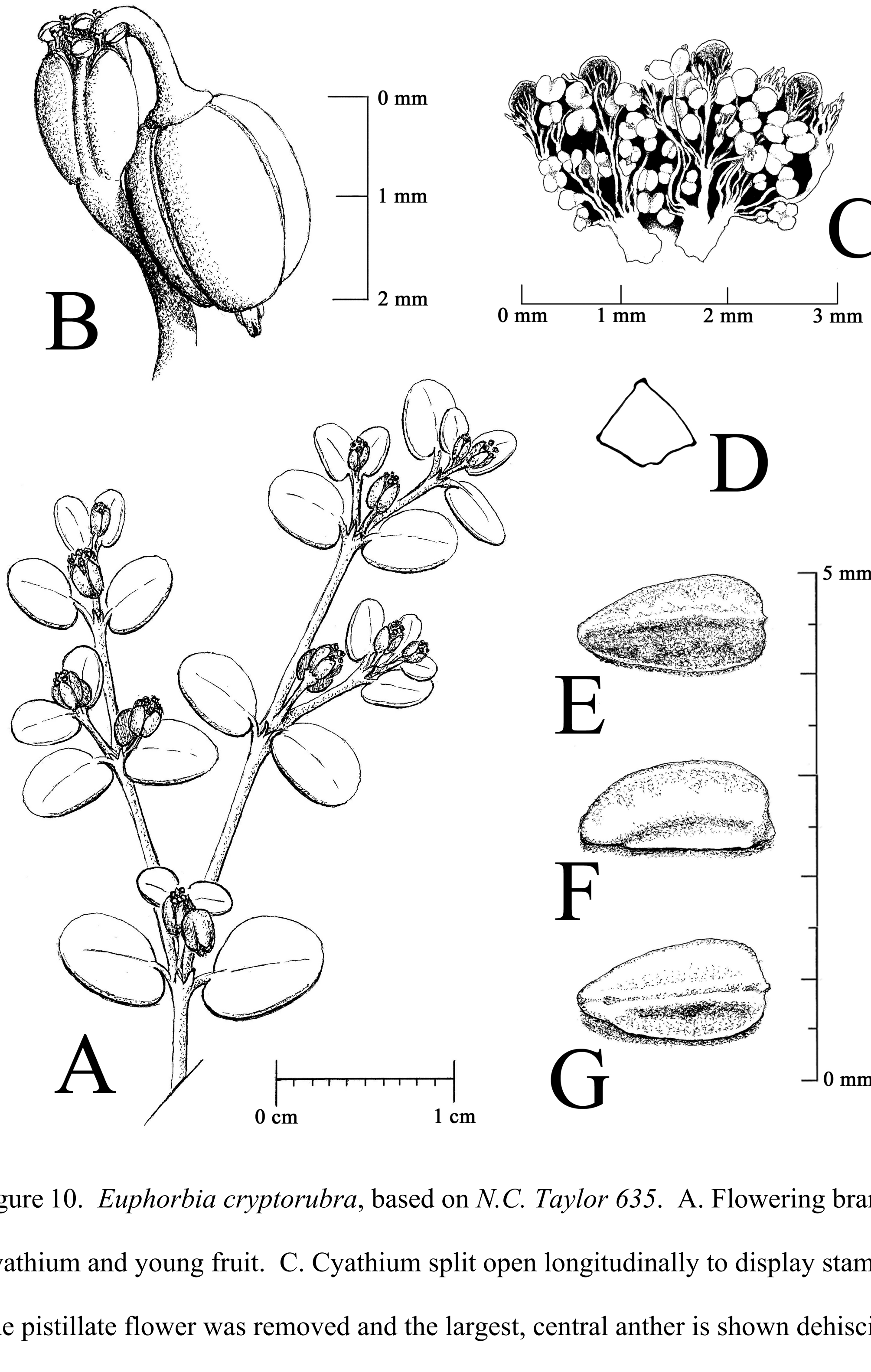

Figure 10. *Euphorbia cryptorubra*, based on *N.C. Taylor 635*. A. Flowering branch. B. Cyathium and young fruit. C. Cyathium split open longitudinally to display staminate flowers. The pistillate flower was removed and the largest, central anther is shown dehiscing. D. Seed, cross-section. E. Seed, dorsal view. F. Seed, lateral view. G. Seed, ventral view. Illustrated by Philip Taylor.

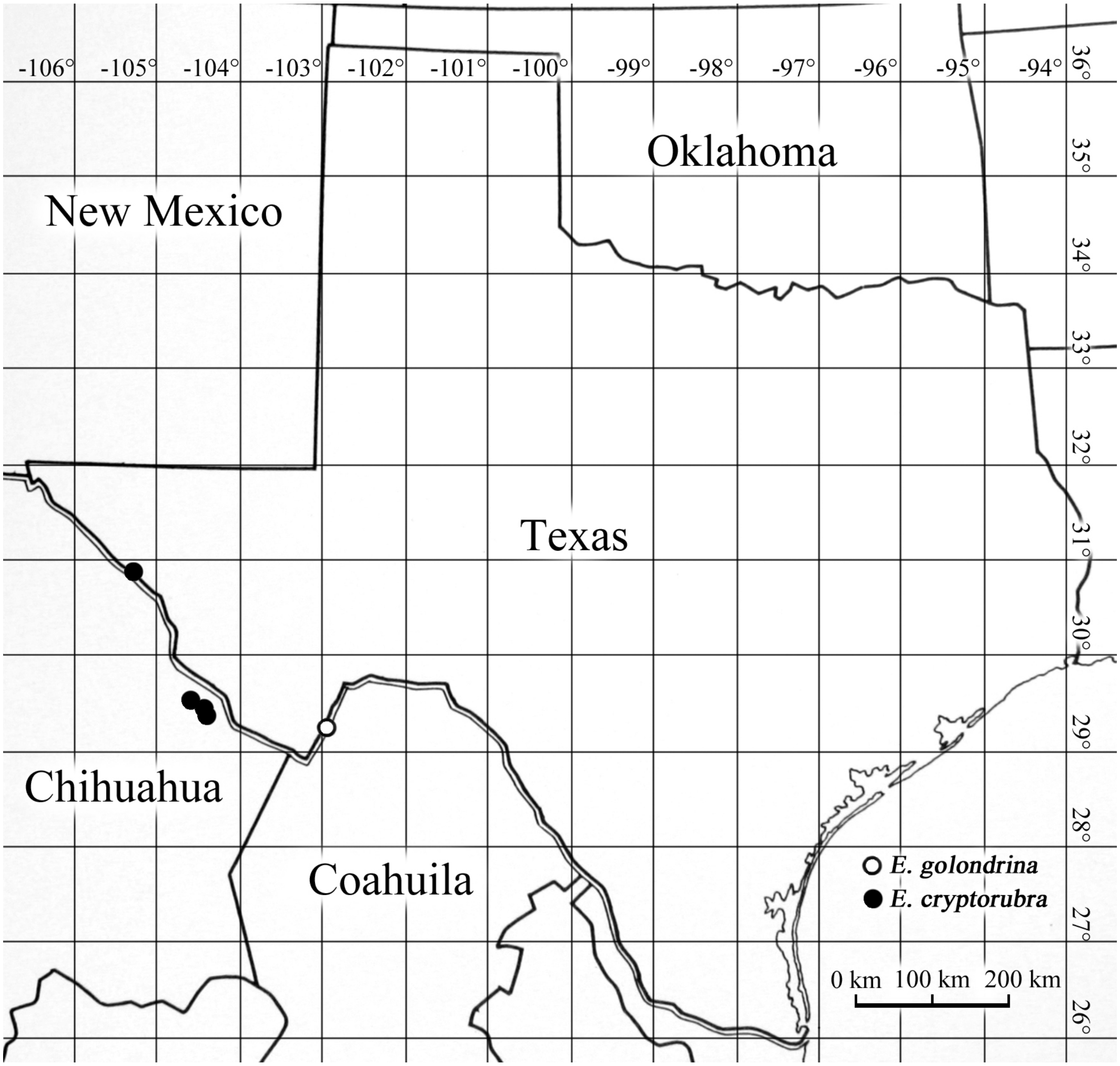

Figure 11. The known distribution of *Euphorbia cryptorubra* and *E. golondrina* L.C. Wheeler.

Figure 12. *Euphorbia cryptorubra* habit and substrate; purplish colored leaves turning red when dried (inset). Photos by Nathan C. Taylor.

calcareous Benevides shale, 30.937167° N, 105.463783° W, elev. 1075 m, 27 Jul 2015, *N.C. Taylor 635* (Holotype: SRSC; Isotypes: TEX, BRIT).

Prostrate annuals, glabrous; leaves mostly oval-oblong, oblique, to 7 mm long; cyathia solitary to 2 mm long; glands circular usually unappendaged, 0.2–0.4 mm in diameter; seeds smooth or with low wrinkles, broadly lanceolate-elliptic in outline, 1.8–1.9 mm long.

Plants glabrous mat-forming annual herbs from slender taproots (10–)15–20(–greater than 33) cm across. **Stems** 5–10(–33) cm long, breaking easily at basal nodes, usually yellowish even when leaves start turning red (color difficult to see except when dried). **Leaves** opposite, slightly succulent, petiolate, petioles 1–2 mm long, 0.5 mm in diameter, unequally attached to the two halves of the blade, attachment with blade flared up to 1.5 mm wide on larger mid-stem leaves, blades oval-oblong to suborbicular, notably asymmetrical, but often shriveling or folding after drying to appear oblong, oval, oblanceolate, or spatulate on specimens, (3.5–)6–7(–7.5) x (2–)4–5.5 mm, green to red when dried, lacking maculation, apex rounded, margin entire, slightly revolute, blade half (as divided along the midvein) with the margin facing the stem apex mostly semi-oval with semi-rounded base, and half of blade with the margin facing the base of the stem mostly semi-oblong to semi-oblong-oval with semi-cordate to semi-truncate base, lobe at base of blades extending up to 1.5 mm from the center of petiole attachment, 0.3 mm beyond where the margin of the petiole meets the blade nearest the lobe; stipules glabrous 0.7–0.9 mm long, lanceolate to occasionally linear-lanceolate, with distinct lobes on dorsal side (side facing upward) of stems, mostly united to apically distinct on ventral side (side facing downward) of stems**.** **Cyathia** solitary, 1–2 mm long, 0.5–1.5 mm wide, glands short-stipitate, circular or subcircular, concave, yellow, 0.2–0.4 mm in diameter (0.4–0.5 in living plants), unappendaged or with a narrow white to pink semi-lunate (bib-like) appendage. **Staminate flowers** 30–36 per

cyathium with up to 7(–8) exserted at one time. **Pistillate flowers** glabrous; style branches 3, 0.5 mm long, each divided 1/2–2/3 its length; gynophore reflexed, exserted 1–1.5 mm at maturity. **Capsule** 2–2.5(–3) mm long, 1.8–2.1(–2.5) mm wide at widest point before dehiscence, widest in the middle, short-oval-oblong in outline, triangular in cross-section, septa slightly impressed (more impressed at the apical half), keels rounded, each capsule containing 3 seeds. **Seeds** 1.8–1.9 mm long, 0.8–1 mm wide at widest point, mucilaginous when wet, elongated, white, smooth or with low transverse wrinkles, subquadrangular to nearly triangular in cross-section, broadly lanceolate-elliptic in outline as viewed dorsally, angles protruding from the edges of the faces (keeled), lateral angles converging at the apex, appearing to curve to meet nearly at the hylum 0.2–0.3 mm from apex, then straightening until reaching the apex, raphe (proximal angle) impressed with the testa raised and rounded along each side, dorsal faces (2 faces meeting at the dorsal angle) slightly convex and 0.6–0.7 mm wide at widest point, ventral faces slightly concave and ca. 0.4 mm wide at widest point, chalazal end with a low bulge with slight bump at the start of the raphe 0.4 mm from the start of the dorsal angle.

OTHER SPECIMENS EXAMINED

UNITED STATES. Texas. Hudspeth Co.: Gypsum hills, Rio Grande flood plains, 40 km about [sic] Indian Hot Springs, 1097 m, 29 Sep 1963, *B.H. Warnock 19310* (SRSC), *19311* (TEX); near entrance to Indian Hot Springs, SE side of Quitman Mountains, 8 Oct 2004, *B.L. Turner 24-525* (SRSC); 16 km NW of Indian Hot Springs, SE side of Quitman Mountains, 8 Oct 2004, *B.L. Turner 24-529* (SRSC, TEX); near Rio Grande at a point 16 air km NW of Indian Hot Wells, growing on shale outcrop (Cretaceous Benevides Formation), arroyo bank, 31° [sic; should be 30°] 56’N, 105°27’30”W elev. 1059 m, 3 Sep 1979, *R.D. Worthington 5174* (TEX, UTEP); near Rio Grande 21.7 road km (16 air km) NW of Indian Hot Springs on the Cretaceous

Benevides formation of calcareous shale, 31° [sic; should be 30°] 56'N, 105°27'30"W, elev. 1059 m, 27 Oct 1985, *R.D. Worthington 13841* (UTEP). **MEXICO. Chihuahua:** 16 km S of Ojinaga, silty flat base of low hills, road from Ojinaga S to Alamos Chapo; across Upper Cretaceous beds abounding in soft saline and gypseous shales, 9-10 Aug 1941, *I.M. Johnston 8026* (LL); ca. 9 km W of Ojinaga on the highway to Chihuahua City, desert scrub, gravelly marly hills 29°34'40"N, 104°28'W, elev. 820 m, 20 Oct 1972, *F. Chiang 9718* (LL); Camargo Road 10.5 km S of Ojinaga, in gypseous-clay soil, 5 Apr 1971, *A.M. Powell 2011* (TEX).

ETYMOLOGY

Cryptorubra ("hidden red") refers to the tendency for a dull red coloration in the leaves (seemingly caused by excessive exposure to sun or drought) to be "hidden" until dried. Though not a unique character, it is particularly prominent in *E. cryptorubra*. It can often be difficult to tell which leaves will turn red when a living plant dries.

GEOGRAPHY

Most collections have been made from a relatively small area NW of Indian Hot Springs Ranch located at the SE end of the Quitman Mountains, near the Rio Grande in Hudspeth County, Texas. The remainder of collections were made near Ojinaga, Chihuahua, Mexico. The Texas records represent the northernmost collection of *E. cryptorubra*. The southernmost collection of *E. cryptorubra* is currently 16 km S of Ojinaga. The latter record also represents the greatest distance from the Rio Grande (also about 16 km) depending on what is meant by "about" for the collections by B.H. Warnock. The notable disjunction of approximately 170 km may be explained by the lack of *Euphorbia* sect. *Anisophyllum* specimens collected from the Rio Grande flood plains in Mexico between the two populations. Alternatively, large disjunct ranges

are not unheard of within the section and several examples may be found. One such example is found in the range of *E. carunculata* Waterf. (a large mat forming species), which is distributed northeast of the Pecos River in the sand dunes of Loving, Winkler, Ward, Crane, Hardeman, and Wilbarger Counties in Texas, the Mescalero Sands of New Mexico, Little Sahara State Park, Oklahoma, and southeast of Samalayuca, Chihuahua, with no known populations between the populations of Texas and Oklahoma (a disjunction of about 250 km), between the Pecos River and the Rio Grande (a distance of more than 250 km), nor on the High Plains of Texas (representing a separation of over 400 km). Also, the specimens of *E. cryptorubra* from Chihuahua are more widely dispersed than those in Texas, potentially suggesting a wider distribution than is currently documented. Further exploration within the Rio Grande flood plains in Mexico will likely yield a wider distribution within northern Chihuahua if suitable habitat exists. A significantly wider distribution in Texas is probably less likely based on the numerous collections of *E. cryptorubra* at the southeastern end of the Quitman Mountains, and the relatively abundant collections of more widespread (but still inconspicuous) species along the Rio Grande such as *E. simulans* (L.C. Wheeler) Warnock & M.C. Johnst., *E. micromera* Boiss., and *E. theriaca* var. *spurca* M.C. Johnst.

At the Texas locality, *E. cryptorubra* is found almost exclusively in hills of deep Benevides Shale (as determined using the map in Jones & Reaser 1970) and nearby calcareous clay in Chihuahuan Desert scrub habitat. There are two notable associated species found in shallow Benevides Shale but not in other substrates in the immediate area: *Anulocaulis leiosolenus* var. *leiosolenus* (Torr.) Standl. (Nyctaginaceae), and a population of intermediates between *Euphorbia chaetocalyx* (Boiss.) Tidestr. and *E. fendleri* Torr. & A. Gray sensu Berry et al. (2016). In the specific habitat that *E. cryptorubra* prefers, even these two associates are

uncommon or absent. Based on the substrate at the type locality and label data from the specimens in Chihuahua, *E. cryptorubra* seems to be restricted to calcareous and gypseous clays and shales.

SIMILAR SPECIES

Euphorbia cryptorubra readily keys to *Euphorbia golondrina* L.C. Wheeler (Fig. 13) in Correll & Johnston (1970), and Johnston (1975), but it might also be keyed to *E. geyeri* if the seeds are interpreted as being "plump" (explanation below under *E. geyeri*). *Euphorbia cryptorubra* keys to *E. ocellata* Durand & Hilg. in Wheeler (1941) which is not known east of Arizona and has seeds similar to *E. geyeri* Engelm. Specimens of *E. cryptorubra* have been identified as *E. golondrina*, *E. geyeri* var. *wheeleriana* Warnock & M.C. Johnst., *E. simulans* (L.C. Wheeler) Warnock & M.C. Johnst., and *E. theriaca* L.C. Wheeler. *Euphorbia cryptorubra* can be distinguished from these species using the following key:

1. Seeds smooth with the angles continuing the convex faces (plump; without keeled angles) ______ **E. geyeri**

1. Seeds smooth, wrinkled, or ridged with angles protruding from the edges of the faces OR all faces concave (not plump; angles keeled) ______ 2

    2. Seeds markedly ridged ______ **E. theriaca**

    2. Seeds smooth or wrinkled, not ridged ______ 3

        3. Stems prostrate to low ascending; most glands oval to oblong; seeds shorter than 1.5 mm ______ **E. simulans**

        3. Stems generally prostrate; most glands circular or subcircular; seeds longer than 1.5 mm ______ 4

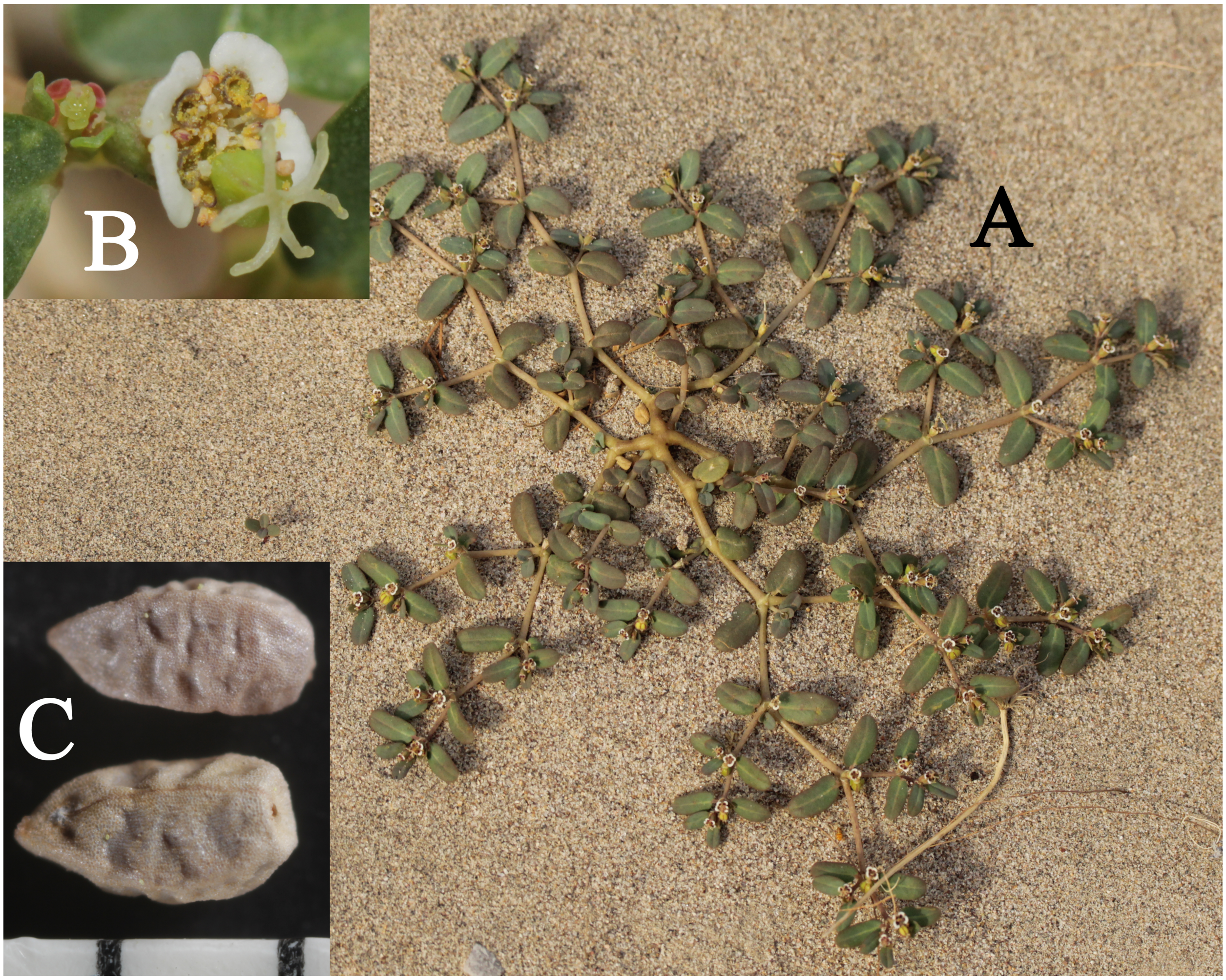

Figure 13. *Euphorbia golondrina* L.C. Wheeler on the sandy banks of the Rio Grande at Boquillas Canyon, Big Bend National Park, Texas. A. Habit and substrate. B. Cyathium. C. Seeds. Photos by Nathan C. Taylor.

4. Most mature leaf blades oblong overall, larger mid-stem blades typically 7–12 mm long; appendages prominent; seeds 1.6–1.7 mm long, visibly wrinkled with some wrinkles typically overlapping the angles ______________________ **E. golondrina**

4. Most mature leaf blades oval-oblong overall, larger mid-stem blades typically 6–7 mm long; appendages absent or inconspicuous; seeds 1.8–1.9 mm long, smooth to inconspicuously wrinkled, without wrinkles overlapping the angles ____ **E. cryptorubra**

Euphorbia geyeri grows in sandy soils NE of the Pecos River, El Paso County, and the northern half of Hudspeth County, TX. *Euphorbia theriaca* grows primarily in rocky or gravelly soils along the Rio Grande W of Terrell County, TX, to southern NM. *Euphorbia simulans* grows primarily in rocky or gravelly soils in southern Brewster and Presidio Counties, TX. *Euphorbia golondrina* is restricted to sandy soil around Boquillas Canyon, Big Bend National Park, Brewster County, TX.

Euphorbia cryptorubra is almost certainly more closely related to *E. theriaca*, *E. similans*, and *E. golondrina* than to *E. geyeri* which belongs to a group with distinctive seeds that appear more rounded than those in other species. Excluding *E. geyeri*, the remaining four species share many characters in common, including: generally prostrate habit, glabrous vestiture (except occasionally on stipules and inside cyathia), entire leaf margins, entire and distinct stipules on dorsal sides of the stem, united or distinct stipules on ventral sides of stems, relatively high numbers of staminate flowers, and bifid styles.

Based on a comparison of characters, *E. cryptorubra* most resembles *E. golondrina*. The characteristics they share are semi-succulent leaves, circular glands, and similar seed length.

They differ in the characters provided in the key and the degree of asymmetry in the leaves. The leaf blades of *E. golondrina* have semi-oblong halves on both sides of the midvein while those of *E. cryptorubra* have a semi-oval half on the side in the direction of stem apices (Fig. 9). The petioles of *E. golondrina* flare up to 1(–1.1) mm wide at the connection with the blades while those of *E. cryptorubra* flare up to 1.5 mm wide. *Euphorbia golondrina* appears to be restricted to areas near Boquillas Canyon in both Texas and adjacent Coahuila. All other occurrences previously identified as *E. golondrina* have proven to be *E. simulans*, *E. cryptorubra*, or something else entirely. This is not to say that *E. golondrina* does not occur elsewhere. It only means that no specimens have been found outside this range at the herbaria visited by the first author. The specimens collected by Warnock at Avery Canyon, Big Bend National Park as *E. golondrina* are different from the plants at Boquillas Canyon and appear to be more closely related to *E. simulans* or *E. theriaca* var. *spurca* with shorter seed length and differently shaped, non-succulent leaves. These may be hybrids but require further study before any conclusions can be made regarding their taxonomy.

ACKNOWLEDGMENTS

We thank A. Michael Powell, Paul Berry, and two anonymous reviewers for numerous revisions and suggestions that greatly improved the paper. We also thank the SRSC, UT-LL, and UTEP herbaria and their respective curators, A. Michael Powell, Tom Wendt, and Richard Worthington, for generous access to the specimens that made this publication possible. Lastly, we greatly appreciate Philip Taylor for providing the beautiful illustrations on figure 2.

LITERATURE CITED

Berry, P.E., J.A. Peirson, J.J. Morawetz, V.W. Steinmann, R. Riina, Y. Yang, D. Geltman, and N.I. Cacho. 2016. *Euphorbia*. Flora of North America Editorial Committee, eds. Flora of North America North of Mexico. Vol. 12. New York and Oxford.

Bruyns, P.V., R.J. Mapaya, and T. Hedderson. 2006. A new subgeneric classification of *Euphorbia* (Euphorbiaceae) based on ITS and psbA–trnH sequence data. *Taxon* 55: 397–420. doi:10.2307/25065587.

Correll, D. S. and M. C. Johnston. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, Texas, USA.

Horn, J. W., B. W. van Ee, J. J. Morawetz, R. Riina, V. W. Steinmann, P. E. Berry, and K. J. Wurdack. 2012. Phylogenetics and the evolution of major structural characters in the giant genus Euphorbia L. (Euphorbiaceae). *Molecular Phylogenetics and Evolution* 63: 305–326. doi:10.1016/j.ympev.2011.12.022.

Johnston, M.C. 1975. Studies of the *Euphorbia* species of the Chihuahuan Desert region and adjacent areas. *Wrightia* 5: 120–143.

Jones, B.R. and D.F. Reaser. 1970. Geology of the southern Quitman Mountains, Hudspeth County, Texas. Geologic quadrangle No. 39. Bureau of Economic Geology, University of Texas, Austin, Texas, USA.

Park, K.R., and R.K. Jansen. 2007. A phylogeny of Euphorbieae subtribe Euphorbiinae (Euphorbiaceae) based on molecular data. *Journal of Plant Biology* 50: 644–649. doi:10.1007/BF03030608.

Steinmann, V.W. and J.M. Porter. 2002. Phylogenetic relationships in Euphorbieae (Euphorbiaceae) based on ITS and ndhF sequence data. *Annals of the Missouri Botanical Garden* 89: 453–490.

Wheeler, L.C. 1941. *Euphorbia* subgenus *Chamaesyce* in Canada and the United States exclusive of southern Florida. *Rhodora* 43: 97–154, 168–205, 223–286. http://biodiversitylibrary.org/page/607893

Yang, Y. and P. Berry. 2011. Phylogenetics of the Chamaesyce Clade (Euphorbia, Euphorbiaceae): Reticulate evolution and long-distance dispersal in a prominent C4 lineage. *American Journal of Botany* 98: 1486–1503. doi:10.3732/ajb.1000496.

Yang, Y., R. Riina, J.J. Morawetz, T. Haevermans, X. Aubriot, and P.E. Berry. 2012. Molecular phylogenetics and classification of *Euphorbia* subgenus *Chamaesyce* (Euphorbiaceae). *Taxon* 61: 764–789. http://www.jstor.org/stable/41679308

Zimmermann, N.F.A., C.M. Ritz, and F.H. Hellwig. 2010. Further support for the phylogenetic relationships within *Euphorbia* L. (Euphorbiaceae) from nrITS and trnL–trnF IGS sequence data. *Plant Systematics and Evolution* 286: 39–58. doi:10.1007/s00606-010-0272-7.

CHAPTER V

DISCUSSION

Considering its area, the Trans-Pecos region of Texas includes a large number of described species in *E.* sect. *Anisophyllum*. Despite this, there are still new taxa being discovered with the potential for several more in the region. Among the recent discoveries are *Euphorbia abramsiana*, not previously known for Texas, and *E. cryptorubra*, a recently described species; both of which are discussed above. The discoveries and potential discoveries that are unpublished at this time are discussed below.

OTHER NOVELTIES AND NOTES

What follows are discussions of three additional species new to the Trans-Pecos region of Texas (one new to Texas) that have gone unnoticed, and discussion on two species complexes. The species complexes represent areas of future research.

Euphorbia vermiculata Raf.

Euphorbia vermiculata occurs in the southwestern and northeastern United States. In the Southwest, the species has previously been reported only for Arizona and New Mexico. Within the past 12 years, *E. vermiculata* has been found in lawns around Alpine, Texas, probably imported with ornamentals. *Euphorbia vermiculata* is not known from any other location in Texas. The Alpine specimens were previously identified as *E. serpillifolia*, which they superficially resemble. *Euphorbia vermiculata* differs in that it usually has some hairs on the stems and leaves, and a black (rather than tannish) seed testa (most easily observed when wet). When characters are compared, *E. vermiculata* is most similar to *Euphorbia nutans* but displays a prostrate growth habit and leaves that are widest at the base.

Specimens observed: **UNITED STATES. Brewster Co.:** Alpine, common prostrate weed in lawn grass on Sul Ross University campus, 8 Sep 2014 *B.L. Turner 24-432* (SRSC); common weed in campus lawns Sul Ross State University, 1 Oct 2004, *B.L. Turner s.n.* (SRSC); Sul Ross State University, common in campus lawns, 21 Sep 2014, *Nathan C. Taylor 360* (SRSC).

Euphorbia ophthalmica Pers.

Known in the Trans-Pecos region of Texas from a single collection in a landscaped yard in Marfa. The individual was likely brought in with potted plants as the species has been observed in potted plants from nurseries in Lubbock, Midland, and Austin. *Euphorbia ophthalmica* is common in Austin but apparently hasn't become established in Lubbock or Midland except in potted plants (not even known from garden beds yet). Because of this, it seems unlikely that the species will become established in the Trans-Pecos. *Euphorbia ophthalmica* differs from other species in the Trans-Pecos by its serrated leaves; yellow, pilose hairs; cyathia being held in dense glomerules, which terminate the branches; and lack of appendages on the involucral glands.

Specimen observed: **UNITED STATES. Texas. Presidio Co.:** Marfa, landscaped backyard, fill dirt?, Aug 2015, *J. Fenstermacher s.n.* (SRSC).

Euphorbia hypericifolia L.

In the Trans-Pecos, currently known only from new garden beds put in at Sul Ross State University, Alpine in 2016. *Euphorbia hypericifolia* was brought in with other cultivated plants. Establishment seems more likely than that of *E. ophthalmica* since many plants were observed and all had considerable numbers of fruits and gynophores holding only columnellae (the

columnella is the central part of a fruit that remains on the gynophore after the rest of the fruit has dehisced). However, establishment is not yet guaranteed. *Euphorbia hypericifolia* has been observed in gardens in both Midland and Lubbock. *Euphorbia hypericifolia* is a glabrous annual that is most similar to *E. hyssopifolia*. Unlike *E. hyssopifolia*, the stipules of *E. hypericifolia* are long (often over 2 mm) and glabrous, and the cyathia are held in dense glomerules.

Specimen observed: **UNITED STATES. Texas. Brewster Co.:** Alpine, Sul Ross State University, new beds put in this year behind the Warnock Science Building, 31 Aug 2016, *Nathan C. Taylor 805* (SRSC).

Euphorbia golondrina L.C. Wheeler

Euphorbia golondrina is a plant first described from the sands of Boquillas Canyon, Big Bend National Park. The specific epithet has been applied to many specimens that are not representative of the species, which has thus become somewhat of a catchall group. Along with *Euphorbia abramsiana* and *Euphorbia cryptorubra*, two other potential novelties have been identified and filed as *Euphorbia golondrina* but require further inquiry for any formal determinations.

One such form appears to be more closely related to *E. simulans*, but is more prostrate and has stipitate, appendaged glands. This form may be a hybrid since it is quite variable and appears sporadic in distribution among the five specimens that represent it. The understanding of this form would be aided by further field studies (especially how it looks in full sun compared to shade), and potentially by greenhouse experiments. Molecular work could also be extremely helpful in explaining whether this form is indeed a hybrid or separate species. Morphometrics might also be helpful, especially if a higher sample size could be obtained.

Specimens observed: **UNITED STATES. Texas. Brewster Co.:** Limestone soil in Avary Canyon, Big Bend National Park, 23 Jul 1950, *B.H. Warnock 9129* (SRSC), *2135* (TEX); yellow clay hills near Chisos Pens, Big Bend National Park, 29°18' x 103°23', 16 Nov 1958, *M.C. Johnston 3620* (SRSC); Igneous soil, near turn off to the Wilson Ranch, Chisos Mountains, 27 Nov 1958, *B.H. Warnock 17719* (SRSC), *17734* (SRSC).

The other "*E. golondrina*" form in need of resolution occurs in Hudspeth County, southeast of Esperanza. It differs in that the number of staminate flowers per cyathium is 10 or fewer, which is far less than the minimum for *E. golondrina*. The plant is smaller than the *E. golondrina* from Boquillas Canyon overall, but otherwise looks extremely similar. This may prove to be a new species or a diminutive form of *E. golondrina*. Either will prove to be a noteworthy occurrence. This form is represented by only one gathering, making its determination problematic. More collections of the vicinity of Esperanza, Texas, are needed for any conclusions to be made.

Specimen observed: **UNITED STATES. Texas. Hudspeth Co.:** Ca. 1 mile E of intersection with hiways [sic.] 192 and 34; sandy soils along dry stream bed, ca. 15 miles SE of Esperanza, 8 Aug 2004, *B.L. Turner 24-* (SRSC).

Euphorbia fendleri s.l.

A fundamental problem exists with the taxonomy of *Euphorbia fendleri* s.l. (primarily concerning *E. fendleri* and *E. chaetocalyx*). In the Trans-Pecos, *E. fendleri* (in the current sense) and *E. chaetocalyx* grow sympatrically but also appear to intergrade throughout the Southwestern U.S. If a biological species concept is to be applied to each, the taxonomy appears oversimplified.

For the purposes of disentangling *E. fendleri* and *E. chaetocalyx*, the discussion of the history of the two species will be limited to sources that include both species. These documents are the most relevant to the Trans-Pecos and point out interesting concepts that often display geographic bias but nonetheless provide an interesting understanding of population variability within *E. fendleri* and *E. chaetocalyx*. Boissier (1862) first described *E. fendleri* var. *chaetocalyx*, noting a taller plant with elongated internodes, oblong or elliptic acute apical leaves, and oblong triangular appendages. Wooton and Standley (1913) later made a new combination, calling the taxon *Chamaesyce chaetocalyx*. Their reasoning for elevating the taxon to species level was based on field observations. The main character that differs from Boissier (1862) is the idea that *C. chaetocalyx* has erect stems while those of *C. fendleri* are prostrate (Boissier noted that *E. fendleri* could have erect or prostrate stems). Wheeler (1936b and 1941) made a new combination, calling the taxon *E. fendleri* var. *chaetocalyx*, without explanation. Wheeler does give another distinction, saying that *E. fendleri* var. *typica* has obtuse, crenate appendages while those of *E. fendleri* var. *chaetocalyx* are narrowly deltoid and entire. Though Wheeler does not give explanation for this taxonomy, Kearney and Peebles (1942) indicate that the two varieties intergrade in Navajo and Coconino Counties in Arizona. Wheeler was likely aware of this apparent intergradation. Correll and Johnston (1970) maintain the combination of Wheeler, but Johnston (1975) later splits them into two separate species without much explanation as to why. In both texts, it is noted that the appendages of *E. fendleri* are short (shorter than gland is wide) or absent, and that those of *E. chaetocalyx* are as long as wide or longer. Johnston (1975) also notes the difference in chromosome numbers of *E. fendleri* (n = 14) and *E. chaetocalyx* (n = 26) under the discussion of *E. fruticulosa*. Berry et al. (2016) maintain that the two are separate species and that there are hybrids.

To summarize, the current sense of *E. fendleri* notes primarily the broad ovate to lanceolate leaves. Other attributes (depending on the reference) include prostrate stems and absent or short appendages, but apply only to the Texas or New Mexico concepts and do not satisfactorily explain the multitude of *E. fendleri* identifications given to plants with long appendages and ascending stems to the west of the Rocky Mountains. *Euphorbia fendleri* in this current sense occurs throughout the Great Plains and western U.S., including eastern California, Nevada, Arizona, Wyoming, Utah, Colorado, New Mexico, South Dakota, Nebraska, Kansas, Oklahoma, and Texas. The current sense of *Euphorbia chaetocalyx* has more uniformity in morphological concept than *E. fendleri*, with the main characteristics being narrow leaves (linear to oblong to oval), ascending to erect stems, and long appendages with little exception. The changes in concept that have occurred represent treatment at the varietal or species level but maintain little disagreement in important characters. *Euphorbia chaetocalyx* occurs in Arizona, New Mexico, and Texas.

There are some geographic trends in plants identified as *E. fendleri* (Fig. 14). In the Great Basin Desert and the northern end of the Colorado Plateau, plants are mostly broad-leafed and prostrate with medium length appendages (about as long as the gland is wide). On the Colorado Plateau, plants are usually broad-leafed and ascending with long appendages (longer than the gland is wide). On the southern edges of the Colorado Plateau, plants appear to grade from those of the Colorado Plateau to narrow-leafed (at least at the apices) plants with ascending to erect stems and long appendages (*E. chaetocalyx*). If the narrow-leafed plants have broad leaves, than there are clearly two different sets of leaves with the broad leaves occurring only prior to the production of cyathia. In the Trans-Pecos (New Mexico and Texas), broad-leafed plants are, with few exceptions, prostrate with short (shorter than gland is wide) or absent

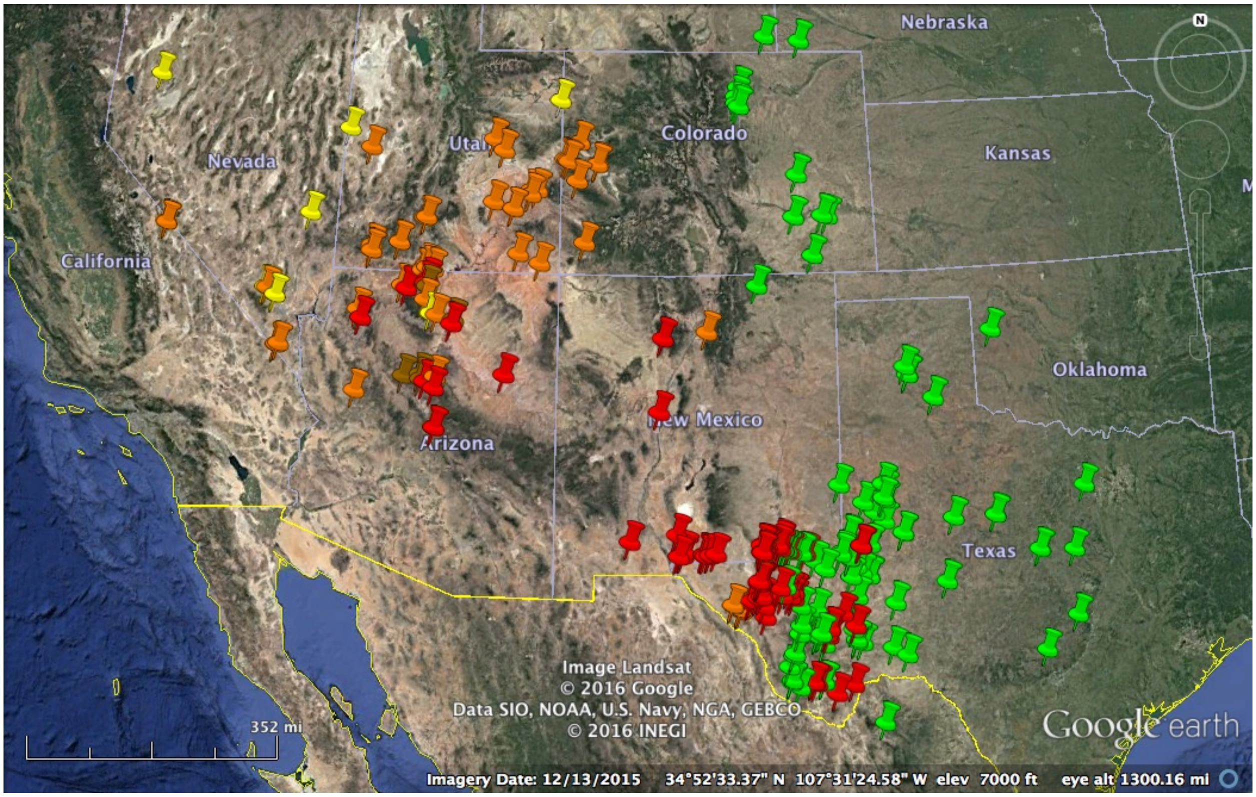

Figure 14. Map of *Euphorbia fendleri* s.l. Yellow: Great Basin concept with prostrate stems, broad leaves, and medium length appendages; Orange: Colorado Plateau concept with ascending stems, broad leaves, and long appendages; Red: Southwest desert concept (*E. chaetocalyx*) with erect stems, narrow leaves, and long appendages; Brown: intermediate between Colorado Plateau concept and Southwest Desert concept; and Green: Great Plains concept with prostrate stems; broad leaves and short or absent appendages. Intermediates between the Great Basin concept and the Colorado Plateau concepts exist but are not mapped here.

appendages and typically shorter internodes. These prostrate broad-leafed plants occur sympatrically with narrow-leafed erect plants with long appendages. Also in the Trans-Pecos is the occasional form strongly resembling the Colorado Plateau plants (broad-leafed and ascending with long appendages). East of both the Pecos River and the Rocky Mountains (primarily the Great Plains), all broad-leafed plants are prostrate with short or absent appendages. Narrow-leafed erect plants are almost entirely absent east of the Pecos River.

In most of Texas, the concept of *E. fendleri* is that of the plants east of the Pecos River (plants lacking or having very short glandular appendages, wide leaves, and prostrate stems). In the Trans-Pecos, the situation is more complicated, with the addition of *E. chaetocalyx* (narrow-leafed erect plants with long appendages). Both species can be observed growing sympatrically in at least two localities: the gypsum hills between the Guadalupe Mountains and Orla, Texas (Culberson Co.), where they have been observed within 10 meters of each other (*N.C. Taylor 579* and *N.C. Taylor 580*), and the Glass Mountains (Pecos Co.) where they have been observed within 6 meters of each other (*N.C. Taylor 769* and *N.C. Taylor 770*). In these two localities and throughout most of Trans-Pecos Texas, *E. chaetocalyx* and *E. fendleri* are easily distinguished and do not appear to intergrade. There are likely more locations where the two species occur sympatrically, but they have yet to be located.

There are some potential exceptions to the apparent lack of intergradation, including those that possess broader leaves basally, a more ascending habit, much longer and wider internodes, and an overall larger size. These are the plants originally described as *E. fendleri* var. *chaetocalyx* by Bossier (1862) and occur most commonly in El Paso and Culberson counties. The appendages and apical leaves are identical to those of normal narrow-leafed specimens. These long-internode plants should probably be interpreted as robust individuals of the narrow-

leafed plants, as there is a continual grade represented in herbaria of various internode lengths. Also, many plants tend to be much smaller in restricted soil as in rock crevices, where the more typical forms of *E. chaetocalyx* grow. It seems logical that plants that typically grow in tight soils would grow larger in looser soils.

Some other possible specimens that could be interpreted as intergradation between *E. fendleri* and *E. chaetocalyx* appear in the southern end of the Quitman Mountains, Hudspeth Co. (*N.C. Taylor 634*), possibly in Guadalupe Canyon, Culberson Co. (*B.H. Warnock 5377*), and possibly El Paso county (*G.R. Vasey 445*). These plants look exceedingly similar to those of the Colorado Plateau, with broad leaves even at the apices of stems. At the Quitman Mountains locality, only the broad-leaved ascending plants with long appendages are present and they are abundant. Broad-leafed prostrate plants and narrow-leafed erect plants are both absent at this locality. Both the Guadalupe Canyon locality and El Paso County locality are each represented by one specimen and appear to have erect stems (though there does seem to be a general trend of all leaves becoming broader overall or more broad leaves per plant, the farther northwest one goes). These areas appear to be primarily populated by narrow-leafed erect plants and may just be atypical specimens. If not, they may have originated from the Quitman Mountains population.

One possible explanation for all this confusing diversity is that the populations from the areas of apparent intermediates represent historic hybrid populations that became isolated from their parent populations and became successful. This hypothesis is compelling and can explain the Quitman Mountains population, as the nearest collection of either parent (*E. chaetocalyx*) was at the north end of the mountain range. It could also explain the other individuals in both the Guadalupe Mountains and El Paso County as occasional hybrids that don't persist. However, it

does not explain why there are apparently no examples that can be readily identified as hybrids in Brewster, Jeff Davis, and Pecos Counties, where both species are ubiquitous and are sympatric in some areas, though generally in separate soil types. *Euphorbia fendleri* will grow in a variety of soils that are well drained while *E. chaetocalyx* grows almost exclusively in limestone rock. Though this difference generally keeps them apart, it is unlikely that the gypsum flats west of Orla and the Glass Mountains are the only places the two species are sympatric. Furthermore, the Quitman Mountains population is very near the western range edge of *E. fendleri*, making hybridization unlikely unless it was historically common in the area. The hypothesis also does not explain the striking similarities between the Quitman Mountain specimens and the *E. fendleri* plants of the Colorado Plateau.

Another possible hypothesis is that all the long-appendaged individuals are one species and the unappendaged or short-appendaged individuals represent another. Following this logic, leaf shape is relatively unimportant and *E. chaetocalyx* would become a variety of a larger *E. fendleri* concept west of the Rocky Mountains, that is, a separate species from the *E. fendleri* concept of the Great Plains and Texas east of the Pecos River. The *E. fendleri* of the Great Plains would likely represent an undescribed species, since the type of *E. fendleri* was collected near Santa Fe, New Mexico, and has long appendages and broad leaves. The habit of the *E. fendleri* type also appears to be ascending (though it is difficult to tell from the specimen). This suggests that the *E. fendleri* east of the Rocky Mountains is different from the concept to the west, and that *E. chaetocalyx* is a variety of this western concept. Under this hypothesis, it is likely that *E. chaetocalyx* is an inherently distinct variety. If it were just an environmentally induced form, the Quitman Mountains population would likely be like *E. chaetocalyx*, as the conditions are not that different from other populations. Though there is some unique geology

where the broader leafed form occurs, it also occurs in limestone cliffs of the region, which is the typical substrate of *E. chaetocalyx*.

More evidence for the hypothesis of different western and eastern species and *E. chaetocalyx* being a part of the former, is that there are frequent examples of *E. chaetocalyx* (throughout its range) behaving similarly to the plants on the Colorado Plateau early in the growing season. Plants that later become classic examples of *E. chaetocalyx* will often possess broad basal leaves (e.g., *A.M. Powell 2992*) and cyathia with short, broadly lobed appendages, appearing very similar to plants found on the Colorado Plateau. Plants in both populations appear to "grow out" of this condition later in the year, typically producing longer and narrower appendages that are entire and often acute. Some older plants may occasionally produce appendages that are bilobed or rarely trilobed, but not broadly lobed. Also, appendages of older plants that are not acute are rare in the narrow leafed *E. chaetocalyx* but common in *E. fendleri* plants of the Colorado Plateau, which often remain rounded. It is not yet clear whether all plants "grow out" of their short, lobed appendages north of the Trans-Pecos, but many certainly do. Meanwhile the plants representing the concept of *E. fendleri* east of the Pecos River show no noticeable changes with time of year.

It is still unclear whether the plants in the Great Basin Desert and at the north end of the Colorado Plateau are the same as the plants of the Colorado Plateau. Some specimens at the north end of the Colorado Plateau in northwestern Colorado, northeastern Utah and Wyoming look almost identical to those of the Great Plains. More populational studies are needed on the northern and western edges of the Colorado Plateau. Future work will focus in this area, as well as on gaining a better understanding of the geography and morphology of the specimens from New Mexico. Ideally, phylogenetic analysis (morphometrics using primarily the appendages and

leaves, and especially molecular characters) would constitute the best means of resolving the questions presented, especially since all forms are morphologically similar and populations west of the Pecos River and Rocky Mountains are quite variable. Specimens would also be mapped using GIS so that the geography could be studied more carefully.

A discussion of *E. fendleri* s.l. would be incomplete without mentioning *E. chaetocalyx* var. *triligulata* and *E. fruticulosa* Engelm. ex Boiss. *Euphorbia chaetocalyx* var. *triligulata* is a rare variety known only from limestone in the vicinity of Boquillas Canyon, Brewster Co., Texas and northwestern Coahuila, Mexico. Variety *triligulata* differs from *E. chaetocalyx* var. *chaetocalyx* in its often (but not always) shrubby habit and deeply parted glandular appendages. Variety *triligulata* has been treated as a variety by most authors (Wheeler, 1936b and 1941; Correll and Johnston 1970; Johnston 1975; Mayfield, 1993; Turner, 2016; Berry et al., 2016) but has also been treated as a species (Turner et al., 2003). Berry et al. (2016) and Turner (2016) go into some details but far less than is preferable to satisfactorily say whether *triligulata* should be treated as a species or variety. Turner (2016) goes into the most detail but his views appear to be entirely based on an unpublished note on a herbarium specimen left by James Henrickson making his conclusions difficult to assess without looking at the note in person. Also, Turner considers the Hudspeth Co. plants as intermediate between *E. chaetocalyx* var. *chaetocalyx* and *E. chaetocalyx* var. *triligulata*, presumably because of its occasional woody stems, shallowly lobed appendages in early plants, or the rare presence of lobed appendages later in the growing season (which can be seen throughout the entire range of *E. chaetocalyx* and in many plants on the Colorado Plateau). Going by this definition, many if not most of the plants of the Colorado Plateau would be considered an intermediate to variety *triligulata*, making this view unlikely. In Texas, *triligulata* appears to be reproductively isolated, though *E. chaetocalyx* var. *chaetocalyx*

occurs within 24 km. of *triligulata*. The more conservative *E. chaetocalyx* var. *triligulata* is recognized here until a better understanding can be obtained. At the most accessible location (Boquillas Canyon entrance, Brewster Co. Texas), fewer than 100 plants were observed after two thorough examinations of the cliffs accessible by foot. While this location represents a small fraction of potential and known habitat, it includes the type locality, and future collections made here should be conservative.

Euphorbia fruticulosa is a shrubby species found primarily in gypsum of Coahuila and Nuevo León, Mexico. *Euphorbia fruticulosa* resembles a robust version of the Great Plains concept of *E. fendleri* that is hairy in one variety. The most thorough explanation of *E. fruticulosa* was provided by Johnston (1975). The species appears to be most closely related to one of the two concepts of *E. fendleri* found in the Trans Pecos rather than *E. chaetocalyx* var. *triligulata* as suggested by Johnston (1975). This suggestion is based primarily on leaves (and lack of appendages if the Great Plains concept is the closer relative). It is clear that *E. fruticulosa* is a part of what is being described here as *E. fendleri* s.l. However, more study is required before any further determinations can be made as to how *E. fruticulosa* relates to *E. fendleri*. There are two varieties, *E. fruticulosa* var. *fruticulosa* and *E. fruticulosa* var. *hirtella*. The only known difference is that var. *hirtella* is hairy while var. *fruticulosa* is glabrous.

More than 800 specimens have been observed by this author; it would be impractical to cite them all here. What follows are a selected few specimens that represent the various populations.

Representative specimens: ***E. fendleri*** **(Great Plains form). UNITED STATES. Texas. Brewster Co.:** Alpine, SR hill, various slopes to determine morphological variability, 11–13 Apr 2015, *N.C. Taylor 508* (SRSC). **Culberson Co.:** 17.5 km SE of Hwy 180/62 on CR

652, growing within 10 m of *E. chaetocalyx*, 28 May 2015, *N.C. Taylor 580* (SRSC). **Pecos Co.:** Glass Mountains near roadside park 43.3 km N of Hwy 90, growing within 6 m of *E. chaetocalyx*, 23 Jun 2016, *N.C. Taylor 770* (SRSC). ***E. fendleri* (Colorado Plateau form). UNITED STATES. New Mexico. Santa Fe Co.:** arid hillsides about Santa Fe, May to Jul 1847, *Fendler 800*, TYPE of *Euphorbia fendleri* (NY; TEX; MO; K). **Texas. Hudspeth Co.:** 17.1 km NW of Indian Hot Springs ranch, 27 Jul 2015, *N.C. Taylor 634* (SRSC). **Utah. San Juan Co.:** Hamburger Rock campsite, just E of camp, 4 Jul 2015, *N.C. Taylor 603* (SRSC); Hamburger Rock campsite, E of camp under *Artemisia filifolia*, etiolated and almost identical to *E. chaetocalyx*, 4 Jul 2015, *N.C. Taylor 603* (SRSC). ***E. fendleri* (Great Basin form). UNITED STATES. Colorado. Moffat Co.:** north side of Hog Lake, Brown's Park, 8 Jun 1983, *J.S. Paterson 83-138* (CS). **Nevada. Clark Co.:** Lee Cañon, Charleston Mountains, 4 Aug 1913, *A.A. Heller 11058*, TYPE of *Chamaesyce goodingii* (UC). **Lincoln Co.**: 20.9 mi E of junction 375/93 along Hwy 93, 8 Jun 1991, *D. Atwood 15382* (BRY). ***E. chaetocalyx* var. *chaetocalyx*. UNITED STATES. Texas. Culberson Co.:** 17.5 km SE of Hwy 180/62 on CR 652, growing within 10 m of *E. fendleri* (Great Plains form), 28 May 2015, *N.C. Taylor 579* (SRSC); frequent and widespread in Guadalupe Canyon, Guadalupe Mountains, 2 May 1947, *B.H. Warnock 5377*, broad-leaved form (SRSC). **El Paso Co.:** El Paso, 1881, *G.R. Vasey s.n.*, broad-leaved form (P); rocky limestone slopes near the head of Martin Canyon, Hueco Mountains, 12 Jul 1976, *A.M. Powell 2992* (SRSC). **Pecos Co.:** Glass Mountains near roadside park 43.3 km N of Hwy 90, growing within 6 m of *E. fendleri* (Great Plains form), 23 Jun 2016, *N.C. Taylor 769* (SRSC). ***E. chaetycalyx* var. *triligulata*. UNITED STATES. Texas. Brewster Co.:** Cliffs above Boquillas Canyon, 12 Jul 1931, *J.A. Moore 3444*, TYPE of *E. chaetocalyx* var. *triligulata*; Big Bend National Park, Boquillas Canyon, 24 Jun 2015, *N.C.

Taylor 590 (SRSC); Big Bend National Park, Marufo Vega trail area, 14 Apr 2006, *J. Fenstermacher 1695* (SRSC). **MEXICO. Coahuila:** San Antonio de los Alamos, eastern base of the volcanic Sierra de San Antonio, 20 Aug 1941, *I.M. Johnston 8261* (LL). ***E. fruticulosa* var. *fruticulosa*. MEXICO. Coahuila:** Mount Ridge between Azufrora and Perros Bravos, 22 Sep 1848, *J. Gregg 506*, TYPE of *E. fruticulosa* (MO); Valle del Sobaco, 9 km S of restaurant El Mezquite, 14 Jun 1972, *Chiang 7789*; **Nuevo León:** San José de la Popa, 13 Nov 2004, *G.B. Hinton 28307* (GBH). ***E. fruticulosa* var. *hirtella*. MEXICO. Coahuila:** Approximately 30 km NE of Torreon, 2.6 mi E of Coyote by winding road, 16 Aug 1974, *R. Spellenberg 3769*, TYPE of *E. fruticulosa* var. *hirtella* (TEX).

KEY TO THE MEMBERS OF *EUPHORBIA* SECTION *ANISOPHYLLUM* OF THE TRANS-PECOS REGION OF TEXAS AND ADJACENT AREAS

Other keys covering most of the Trans-Pecos species of *E.* sect. *Anisophyllum* include Wheeler (1941), Correll and Johnston (1970), Johnston (1975), and an unpublished manuscript by A.M. Powell at SRSC. Parts of the following key share attributes or are modified from the aforementioned keys.

A. Stems hairy (leaves usually hairy)

1. Fruits glabrous ____ 2

1. Fruits hairy ____ 7

2. Seeds smooth (shallowly pitted at the most), tannish or white, leaves less than 1.5 cm long _ 3

2. Seeds variously roughened, ridged or wrinkled, tannish, black, or white, leaves various ____ 4

3. Fruits deeply lobed; seeds under 1.5 mm long; habit usually ascending; uncommon perennial ____ **E. villifera** Scheele

3. Fruits shallowly lobed; seeds over 1.5 mm long; habit usually prostrate; common weedy annual ______ **E. serrula** Engelm.

4. Seeds deeply ridged, ridges often overlapping the angles, testa tannish; habit prostrate ______ **E. abramsiana** L.C. Wheeler

4. Seeds shallowly wrinkled or with ridges, wrinkles or ridges not overlapping the angles, testa black unless immature; habit various ______ 5

5. Stems glabrous or with straight hairs as long as those present on leaves (when present); seeds with two to three transverse ridges ______ **E. hyssopifolia** L.

5. Stems with short crinkled hairs shorter than hairs on leaves (when present); seeds with more than three transverse wrinkles ______ 6

6. Plants robust, ascending to erect; internodes near base typically more than 2.5 mm in diameter; mid-stem leaf blades typically longer than 15 mm, widest at or near apex or the same width two thirds or more of the length, occasionally widest at the base in some leaves, typically two times longer than wide or greater especially in apical leaves ______ **E. nutans** Lag.

6. Plants not robust, mostly prostrate; internodes near base typically less than 2.5 mm in diameter; mid-stem leaf blades typically shorter than 15 mm, widest at base, typically two times longer than wide or less; apparently restricted to Alpine, Texas ______ **E. vermiculata** Raf.

7. Leaves entire; plants various ______ 8

7. Leaves serrated (may appear entire in *E. prostrata*); plants prostrate annuals ______ 14

8. Hairs not glandular ______ 9

8. Hairs glandular ______ 13

9. Cyathia held in dense, leafless (or leaves greatly reduced in size) glomerules; plants of primarily non-calcareous soils ______ **E. capitellata** Engelm.

9. Cyathia solitary; plants of primarily calcareous soils ________________________________ 10

10. Midstem and apical leaf blades linear, more than 3 times longer than wide, or broadest in the middle or the same width entire length of blade (leaves closest to base of stems broader, to elliptic), margins not revolute, base of blades mostly equal ____________ **E. angusta** Engelm.

10. Midstem and apical leaf blades not linear, less than 3 times longer than wide, broader at the base, if approaching 3 times longer than wide, margins revolute, base of blades markedly unequal ____ 11

11. Leaf apices acuminate; hairs pilose ______________________________ **E. acuta** Engelm.

11. Leaf apices rounded; hairs short and appressed ___________________________________ 12

12. Leaf margins not revolute; blades mostly ovate throughout, not falcate ____ **E. cinerascens** Engelm.

12. Leaf margins strongly revolute; blades deltoid to lanceolate (even on same plant), often falcate ____ **E. lata** Engelm.

13. Appendages entire ____ **E. arizonica** Engelm.

13. Appendages deeply lobed, each lobe coming to a point _____________ **E. setiloba** Engelm.

14. Cyathia held in dense, leafless (or leaves greatly reduced in size) glomerules; known from one collection in Marfa ____ **E. ophthalmica** Pers.

14. Cyathia solitary ____ 15

15. Appendages unequal, two longer appendages at least 1.5 times longer than the other two; typically not weedy _____________________________________ **E. indivisa** (Engelm.) Tidestr.

15. Appendages equal or if unequal, the two longer appendages less than 1.5 times longer than the other two; common weedy species in disturbed habitats ___________________________ 16

16. Seeds pitted, style entire (3 style branches) ____________________ **E. stictospora** Engelm.

16. Seeds transversely ridged, styles bilobed (6 style lobes in total) ______________________ 17

17. Hairs on fruits appressed; seed ridges rounded; leaves mostly oblong, often with a single oblong maculation in the center ____ **E. maculata** L.

17. Hairs on fruits generally not appressed; seed ridges coming to a sharp edge; leaves mostly oval to rotund, maculation lacking ___________________________________ **E. prostrata** Aiton

B. Stems and leaves glabrous (ignore stipules)

1. Leaves linear (at least apically), margins entire ______________________________________ 2

1. Leaves not linear or if narrow, margins not entire ____________________________________ 4

2. Leaf margins revolute; seeds with transverse ridges or wrinkles; internodes near base typically less than 1.5 mm in diameter; plants of rocky and gravelly soils, not sand _ **E. revoluta** Engelm.

2. Leaf margins not revolute; seeds smooth; internodes near base of plants typically greater than (and often much greater than) 1.5 mm in diameter; plants of deep sand dunes _______________ 3

3. Plants erect or ascending; appendages long and spreading; distribution primarily east of the Guadalupe Mountains ____ **E. missurica** Raf.

3. Plants prostrate; appendages ascending or absent; distribution west of the Guadalupe Mountains ____ **E. parryi** Engelm.

4. Leaves serrated ____ 5

4. Leaves entire ____ 7

5. Seeds with two to three ridges, testa black at maturity; plants ascending to erect; internodes near base typically more than 2.5 mm in diameter; mid-stem leaf blades typically longer than 1.5 mm ____ **E. hyssopifolia** L.

5. Seeds with more than three ridges or not ridged, testa tan at maturity; plants prostrate or ascending; internodes near base typically less than 2.5 mm in diameter; mid-stem leaf blades typically shorter than 1.5 mm ____ 6

6. Seeds smooth or wrinkled, angles entire; leaves in some forms oblong-linear; stems often winged ____ **E. serpillifolia** Pers.

6. Seeds transversely ridged, ridges often overlapping the angles; leaves always broader than oblong-linear; stems without wings ______________________ **E. glyptosperma** Engelm.

7. Styles entire and round (three round style branches); plants strong perennials __________ 8

7. Styles bifid and linear (six style lobes in total); plants various ____________________ 9

8. Appendages entire; petioles erect and mostly appressed to the stem making the leaf blades appear sessile; known only from Pecos Co. in the United States ___ **E. astyla** Engelm. ex Boiss.

8. Appendages lobed; petioles spreading; known from Brewster, Terrell, and Val Verde Counties in the Trans-Pecos ___________________________ **E. jejuna** M.C. Johnst. & Warnock

9. Stipules fused into a broad, white (sometimes pink in *E. serpens*), glabrous scale on both sides of stems; plants prostrate and rooting at the nodes ______________________________ 10

9. Stipules distinct into two lobes at least on the dorsal sides of stems; plants various, not rooting at the nodes ____ 11

10. Plants strong perennials, main taproot rough and woody with age; stamens more than 11 ____ **E. albomarginata** Torr. & A. Gray

10. Plants annual or weak perennials, main taproot smooth; stamens less than 11 ____ **E. serpens** Kunth

11. Seeds longer than 3.5 mm long; oval in cross-section; large prostrate plants of sand dunes, often forming mats over 0.5 m in diameter ___________________ **E. carunculata** Waterf.

11. Seeds shorter than 3.5 mm long; triangular or quadrangular in cross-section; smaller plants of various habits and habitats, rarely forming mats over 0.5 m in diameter __________________ 12

12. Stipules divided into at least three narrow segments ______________________________ 13

12. Stipules divided into two segments or fused into a single segment ___________________ 15

13. Seeds ridged; leaves greatly inequilateral; long half of leaf blade with semi-cordate base, short half of blade with semi-cuneate to semi-rounded base; plants of disturbed soils, including fine sand ____ **E. glyptosperma** Engelm.

13. Seeds smooth; leaves mostly equilateral or slightly inequilateral; both blade halves with rounded to semi-cordate base; plants of courser sands _______________________________ **14**

14. Appendages present; plants east of the Guadalupe Mountains **E. geyeri** var. **geyeri** Engelm.

14. Appendages absent; plants west of the Guadalupe Mountains

__________________________________ **E. geyeri** var. **wheeleriana** Warnock & M.C. Johnst.

15. Plants strong perennials from thick, often rough or woody bases or rhizomes; leaves widest at the basal half or apices acute ____ 16

15. Plants annuals or weak perennials from narrow, smooth bases; leaves widest at or above middle or oblong, apices rounded or stipules densely hairy (apices subacute in *E. micromera*)

____ 20

16. Plants small shrubs or subshrubs; appendages present and deeply parted to the gland into at least 3 linear segments; plants of limestone cliffs of Boquillas Canyon, Marufo Vega Trail, and adjacent Mexico __________________________ **E. chaetocalyx** var. **triligulata** L.C. Wheeler

16. Plants herbaceous or with a thick woody caudex, above ground stems rarely persistent; appendages present or absent, if present, not parted to the gland or linear to filiform; plants widespread or restricted, not known from Boquillas Canyon __________________________ 17

17. Fruits greater than 2.5 mm long; plants robust; leaves ovate to nearly deltoid; plants of southern Brewster County _______________ **E. perennans** (Shinners) Warnock & M.C. Johnst.

17. Fruits less than 2.5 mm long; plants not robust; leaves various; plants widespread _______ 18

18. Plants prostrate in full sun; appendages absent or, if present, longest one shorter (and typically much shorter) than the gland is wide; leaves mostly ovate to lanceolate ___________________________ **E. fendleri** Torr. & A. Gray (form east of the Rocky Mountains)

18. Plants ascending to erect in full sun; appendages present, entire or bilobed (lobed or even crenate in first cyathia of the year), longest one longer than the gland is wide; leaves ovate to lanceolate to narrowly oblong ____ 19

19. Leaves mostly ovate to lanceolate; stems mostly ascending in full sun; plants restricted to the southern end of the Quitman Mountains and some specimens of the Guadalupe Mountains and El Paso County _____________________________ **E. fendleri** (form west of the Rocky Mountains)

19. Leaves mostly lanceolate to oblong, occasionally ovate in most basal leaves; stems mostly erect in full sun; plants widespread _________________________ **E. chaetocalyx** (Boiss.) Tidest.

20. Leaves widest at base, mostly ovate; stipules and insides of cyathia densely hairy ____ **E. micromera** Boiss.

20. Leaves widest at or above middle or oblong; stipules usually glabrous or occasionally with some hairs ____ 21

21. Seeds smooth with convex dorsal faces (“plump”); largest blades typically longer than 9 mm, mostly equilateral ____________________ **E. geyeri** var. **wheeleriana** Warnock & M.C. Johnst.

21. Seeds wrinkled, ridged, or smooth with concave or slightly convex dorsal faces, (not “plump”); if seeds smooth with convex dorsal faces, largest blades shorter than 9 mm and notably inequilateral (*E. cryptorubra*) ____ 22

22. Seeds with prominent transverse ridges ____ 23

22. Seeds smooth or variously wrinkled ____ 24

23. Glands sessile, usually unappendaged ______________________ **E. theriaca var. theriaca**

23. Glands stipitate, usually appendaged _____________ **E. theriaca var. spurca** M.C. Johnst.

24. Stems prostrate to low ascending; most glands oval to oblong; seeds shorter than 1.5 mm ____ **E. simulans** L.C. Wheeler

24. Stems generally prostrate; most glands circular or subcircular; seeds longer than 1.5 mm _ 25

25. Most mature leaf blades oval-oblong overall, largest blades typically 6–7(–8.5) mm long; appendages absent or inconspicuous; seeds 1.8–1.9 mm long, smooth to inconspicuously wrinkled, without wrinkles overlapping the angles; restricted to calcareous clays and shales south of the Quitman Mountains and near Ojinaga, Chihuahua ____ **E. cryptorubra** N.C. Taylor & M. Terry

25. Most mature leaf blades oblong overall, largest blades typically 7–12 mm long; appendages prominent; seeds 1.6–1.7 mm long, visibly wrinkled with some wrinkles typically overlapping the angles; restricted to sandy soil of Boquillas Canyon _________ **E. golondrina** L.C. Wheeler

CHAPTER VI

CONCLUSIONS

The Trans-Pecos region of Texas includes 39 specific and subspecific taxa of *Euphorbia* sect. *Anisophyllum*. With 39 taxa, geographic variation, and the small nature of the plants within sect. *Anisophyllum*, identification can be quite difficult. What adds to the difficulty is that there are forms that may or may not represent undescribed species. This thesis took a morphological approach to elaborate on the plants that led to new discoveries or have the potential to lead to new discoveries, focusing primarily on the Fendleri Clade (as described in the introduction). The discoveries included finding *E. abramsiana* in Texas and describing *E. cryptorubra* as a new species. The species discussed were *E. vermiculata* (new to Texas, probably introduced), *E. ophthalmica* (new to the Trans-Pecos, almost certainly introduced), *E. golondrina* s.l. (elaboration of the forms, which may or may not be representative of the species), and *E. fendleri* s.l. (elaboration of taxonomy and forms). A few characters were discussed that have received little attention by previous taxonomists; these are primarily applicable to the Trans-Pecos but may also be applied in other locations particularly the southwestern US and northern Mexico.

The scope of this work is admittedly specific, but the groups that occur in the Trans-Pecos allow a broad understanding. The Trans-Pecos includes several taxa considered to be rare, including *E. chaetocalyx* var. *triligulata*, *E. golondrina*, *E. geyeri* var. *wheeleriana*, *E. astyla*, and *E. jejuna* (Poole et al., 2007). *Euphorbia astyla* and *E. jejuna* are potentially the only two known species of a small, isolated clade positioned basally to the Hypericifolia Clade (Yang and Berry, 2011). The Trans-Pecos region also includes *E. angusta* and *E. acuta*, two of only three species in the Acutae Clade which is positioned basally to all other members within sect. *Anisophyllum* (Yang and Berry, 2011). It appears clear that the Trans-Pecos is an important

region for the diversity of sect. *Anisophyllum*. Indeed, even Wheeler as early as 1941 points out that a fifty-mile radius centered around Elephant Mountain, Brewster Co., Texas is a center for diversity within the US. Since 1941, four species and two varieties have been described and many others found in the Trans-Pecos region of Texas that were not known to the region at that time. But, there is still the potential for undescribed species of sect. *Anisophyllum* to be found in the Trans-Pecos as explained in chapter V. When considering the information within this thesis, it seems clear that, as a place for studying sect. *Anisophyllum*, the Trans-Pecos region of Texas represents an exceptionally rich geographic area.

LITERATURE CITED

Boissier, E. 1862. *Euphorbia* sect. *Anisophyllum*. In A.P. de Candolle [ed.], Prodromus systematis naturalis regni vegetabilis, vol. 15, part 2, 11–52. Victor Masson and Fils, Paris, France.

Brown, R. 1818. Observations on the natural family of plants called Compositae. *Transactions of the Linnean Society of London* 12: 76–142.

Berry, P.E., J.A. Peirson, J.J. Morawetz, V.W. Steinmann, R. Riina, Y. Yang, D. Geltman, and N.I. Cacho. 2016. *Euphorbia*. Flora of North America Editorial Committee, eds. Flora of North America North of Mexico. Vol. 12. New York and Oxford.

Bruyns, P.V., R.J. Mapaya, and T. Hedderson. 2006. A new subgeneric classification of *Euphorbia* (Euphorbiaceae) based on ITS and psbA–trnH sequence data. *Taxon* 55: 397–420. doi:10.2307/25065587.

Burch, D. 1965. A taxonomic revision of the genus Chamaesyce (Euphorbiaceae) in the Caribbean. Ph.D. dissertation, University of Florida, Gainesville, Florida, USA.

Correll, D. S. and M. C. Johnston. 1970. Manual of the vascular plants of Texas. Texas Research Foundation, Renner, Texas, USA.

Felger, R.S., S. Rutman, and N.C. Taylor. 2015. Ajo Peak to Tinajas Altas: A flora of southwestern Arizona. Part 13. Eudicots: Euphorbiaceae. *Phytoneuron* 2015: 1–65.

Gray, S.F. 1821. A natural arrangement of British plants, 2. Baldwin, London.

Horn, J. W., B. W. van Ee, J. J. Morawetz, R. Riina, V. W. Steinmann, P. E. Berry, and K. J. Wurdack. 2012. Phylogenetics and the evolution of major structural characters in the giant genus Euphorbia L. (Euphorbiaceae). *Molecular Phylogenetics and Evolution* 63: 305–326. doi:10.1016/j.ympev.2011.12.022.

Horn, J. W., Z. Xi, R. Riina, J. A. Peirson, Y. Yang, B. L. Dorsey, P. E. Berry, C. C. Davis, and K. J. Wurdack. 2014. Evolutionary bursts in Euphorbia (Euphorbiaceae) are linked with photosynthetic pathway. *Evolution* 68: 3485–3504.

Jercinovic, E. 2007. The status of the genus *Chamaesyce* in New Mexico. *The New Mexico Botanist Newsletter* 40: 1–14.

Johnston, M.C. 1975. Studies of the *Euphorbia* species of the Chihuahuan Desert region and adjacent areas. *Wrightia* 5: 120–143.

Jones, B.R. and D.F. Reaser. 1970. Geology of the southern Quitman Mountains, Hudspeth County, Texas. Geologic quadrangle No. 39. Bureau of Economic Geology, University of Texas, Austin, Texas, USA.

Kearney, T.H. and R.H. Peebles. 1942. Flowering plants and ferns of Arizona. United States Department of Agriculture, miscellaneous publications No. 423.

Linnaeus, C. 1753. Species plantarum. Stockholm.

Linnaeus, C. 1754. Genera plantarum. Stockholm.

Mayfield, M. H. 1991. *Euphorbia johnstonii* (Euphorbiaceae) a new species from Tamaulipas, Mexico, with notes on *Euphorbia* subsection *Acutae*. *Sida* 14: 573–579.

Mayfield, M.H. 1993. New combinations in *Chamaesyce* A. Gray (Euphorbiaceae) from Texas and the Chihuahuan Desert. *Phytologia* 75: 178–183.

McCoy, R. E., A. Caudwell, C.J. Chang, T.A. Chen, L.N. Chiykowski, M.T. Cousin, J.L. Dale, G.T.N. de Leeuw, D.A. Golino, K.J. Hackett, B.C. Kirkpatrick, R. Marwitz, H. Petzold, R.C. Sinha, M. Sugiura, R.F. Whitcomb, I.L. Yang, B.M. Zhu, and E. Seemüller. 1989. Plant diseases associated with mycoplasma-like organisms. In R.F. Whitcomb and J.G. Tully [eds.], The Mycoplasmas, vol. 5. 545–640. Academic Press, New York, USA.

McVaugh, R. 1961. Euphorbiae Novo-Galicanae. *Brittonia* 13: 145–205.

McVaugh, R. 1993. Euphorbiae Novo-Galicanae Revisae. *Contributions from the University of Michigan Herbarium* 19: 207–239.

Millspaugh, C.F. 1889. Contributions to North American Euphorbiaceae. *Proceedings of the California Academy series* 2, 2: 217–230.

Millspaugh, C.F. 1890. Contributions to North American Euphorbiaceae – II. *Pittonia* 2: 82–90.

Millspaugh, C.F. 1898a. Notes on the Euphorbias of Dr. Edward Palmer's. *Botanical Gazette* 25: 13–25.

Millspaugh, C.F. 1898b. Notes and new species of the genus Euphorbia. *Botanical Gazette* 26: 265–270.

Millspaugh, C.F. 1914. Contributions to North American Euphorbiaceae – V. *Fieldiana, Botany* 2: 383–397.

Millspaugh, C.F. 1916. Contributions to North American Euphorbiaceae – VI. *Fieldiana, Botany* 2: 401–412.

Park, K.R., and R.K. Jansen. 2007. A phylogeny of Euphorbieae subtribe Euphorbiinae (Euphorbiaceae) based on molecular data. *Journal of Plant Biology* 50: 644–649. doi:10.1007/BF03030608.

Persoon, C.H. 1806. Synopsis plantarum. Paris.

Poole, J.M., W.R. Carr, D.M. Price, and J.R. Singhurst. 2007. Rare Plants of Texas: A Field Guide. W.L. Moody Jr. Natural History Series, No. 37. Texas Parks and Wildlife Department, Austin, Texas, USA.

Powell, A.M. 1994. Grasses of the Trans-Pecos and adjacent areas. University of Texas Press, Austin, Texas, USA.

Powell, A.M. 1998. Trees and shrubs of the Trans-Pecos and adjacent areas. University of Texas Press, Austin, Texas, USA.

Powell, A.M. and J.F. Weedin. 2004. Cacti of the Trans-Pecos and adjacent areas. Texas Tech University Press, Lubbock, Texas, USA.

Rafinesque, C. S. 1817. Second decade of undescribed American plants. *The American Monthly Magazine and Critical Reviews* 2: 119–120.

Reichenbach, H.G.L. 1841. Repertorium herbarii sive nomenclator genera plantarum. Dresden.

Roeper, J. 1824. Enumeratio Euphorbiarum. Gottingen.

Sage, T.L., R.F. Sage, P.J. Vogan, B. Rahman, D.C. Johnson, J.C. Oakley, and M.A. Heckel. 2011. The occurrence of C2 photosynthesis in *Euphorbia* subgenus *Chamaesyce* (Euphorbiaceae). *Journal of Experimental Botany* 62: 3183–95. doi:10.1093/jxb/err059.

Standley, P.C. 1916. Fungi of New Mexico. *Mycologia* 8: 142–177.

Steinmann, V.W. and R.S. Felger. 1997. The Euphorbiaceae of Sonora, Mexico. *Aliso* 16: 1–71.

Steinmann, V.W. and J.M. Porter. 2002. Phylogenetic relationships in Euphorbieae (Euphorbiaceae) based on ITS and ndhF sequence data. *Annals of the Missouri Botanical Garden* 89: 453–490.

Taylor, N.T. and M. Terry. 2015. *Euphorbia abramsiana* (Euphorbiaceae): New to Texas. *Phytoneuron* 2015-24: 1–7. ISSN 2153 733X.

Taylor, N.T. and M. Terry. 2016. *Euphorbia cryptorubra* (Euphorbiaceae), a new species in *Euphorbia* subgenus *Chamaesyce* section *Anisophyllum* from Texas, U.S.A. and Chihuahua, Mexico. *Journal of the Botanical Research Institute of Texas* 10: 1–9.

Turner, B.L., H. Nichols, G. Denny, and O. Doron. 2003. Atlas of the vascular plants of Texas. Vol. I–Dicots; Vol. II–Ferns, Gymnosperms, Monocots. Sida, Bot. Misc. 24, 1 and 2.

Turner, B.L. 2016. Taxonomy and distribution of *Euphorbia chaetocalyx*, *E. crepidata* (sic.) and *E. fruticulosa* (Euphorbiaceae). *Phytologia* 98: 137–141.

Webster, G.L. 1967. The genera of Euphorbiaceae in the Southeastern United States. *Journal of the Arnold Arboretum* 48: 303–430.

Webster, G.L., W.V. Brown, and B.N. Smith. 1975. Systematics of photosynthetic carbon fixation pathways in Euphorbia. *Taxon* 24: 27–33.

Webster, G.L. 1994. Synopsis of the genera and suprageneric taxa of Euphorbiaceae. *Annals of the Missouri Botanical Garden* 81: 33–144.

Wheeler, L.C. 1934. California *Euphorbia* notes. *Bulletin of the Southern California Academy of Sciences* 33: 109–110.

Wheeler, L.C. 1936a. Revision of the *Euphorbia polycarpa* group of the Southwestern United States and adjacent Mexico, a preliminary treatment. *Bulletin of the Torrey Botanical Club* 63: 397–416. http://www.jstor.org/stable/2480946

Wheeler, L.C. 1936b. Revision of the *Euphorbia polycarpa* group of the Southwestern United States and adjacent Mexico, a preliminary treatment (concluded). *Bulletin of the Torrey Botanical Club* 63: 429–450. http://www.jstor.org/stable/2480954

Wheeler, L.C. 1941. *Euphorbia* subgenus *Chamaesyce* in Canada and the United States exclusive of southern Florida. *Rhodora* 43: 97–154, 168–205, 223–286. http://biodiversitylibrary.org/page/607893

Wooton, E.O. and P.C. Standley. 1913. Descriptions of new plants preliminary to a report upon the flora of New Mexico. *Contributions from the United States National Herbarium* 16:109–196.

Yang, Y. and P. Berry. 2011. Phylogenetics of the Chamaesyce Clade (Euphorbia, Euphorbiaceae): Reticulate evolution and long-distance dispersal in a prominent C4 lineage. *American Journal of Botany* 98: 1486–1503. doi:10.3732/ajb.1000496.

Yang, Y., R. Riina, J.J. Morawetz, T. Haevermans, X. Aubriot, and P.E. Berry. 2012. Molecular phylogenetics and classification of *Euphorbia* subgenus *Chamaesyce* (Euphorbiaceae). *Taxon* 61: 764–789. http://www.jstor.org/stable/41679308

Yarborough, S.C. and A.M. Powell. 2002. Ferns and fern allies of the Trans-Pecos and adjacent areas. Texas Tech University Press, Lubbock, Texas, USA.

Zimmermann, N.F.A., C.M. Ritz, and F.H. Hellwig. 2010. Further support for the phylogenetic relationships within *Euphorbia* L. (Euphorbiaceae) from nrITS and trnL–trnF IGS sequence data. *Plant Systematics and Evolution* 286: 39–58. doi:10.1007/s00606-010-0272-7.