TAXONOMIC HISTORY, COMPARATIVE MORPHOLOGY, AND VARIATION IN *ASTROPHYTUM MYRIOSTIGMA* AND ITS SUBSPECIES *TULENSE* (CACTACEAE)

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ABSTRACT

Astrophytum myriostigma subsp. *myriostigma* and subsp. *tulense* are distinguished by both vegetative and reproductive characters. The stem of the nominotypical subspecies is broad and depressed becoming broadly cylindrical in age, reaching a known maximum height of ca. 52 cm. In subsp. *tulense*, the stem is relatively slender and columnar and can reach a maximum height of ca. 90 cm. Both taxa show variation in the angle and profile of the ribs. In the nominotypical subspecies, the ribs are usually obtuse with a rounded or angular profile, or moderately acute with an angular profile. In subsp. *tulense*, the ribs are typically moderately to very acute with an angular profile. There are exceptions to these generalities. Both taxa have a modal number of five ribs, and both have the tendency to insert additional ribs with age, although the tendency seems more pronounced in subsp. *tulense*.

The flower of the nominotypical subspecies differs from that of subsp. *tulense* in having a significantly larger mean perianth diameter ($P \leq 0.01$), a significantly higher mean number of stigma lobes ($P \leq 0.05$), and more tepal rows (3–5 vs. 1–3). The color of the tepals is pale yellow to whitish yellow in subsp. *tulense*, but brighter yellow or golden yellow in the nominotypical subspecies. The seeds of the nominotypical subspecies are significantly larger ($P \leq 0.01$) than the seeds of subsp. *tulense*.

Morphological variation was studied in nine populations of the subsp. *myriostigma* and six populations of the subsp. *tulense*. The nominotypical subspecies displays rib angle and rib profile differences among individual plants within a population. Plants with a depressed stem and obtuse, rounded ribs are predominant at some localities. At other localities, plants with more moderately acute, angular ribs are predominant, or at least common. Populations of subsp. *tulense* show individual variation in stem morphology. The stem varies from attenuated (tapered) to non-attenuated and from relatively slender (diameter ca. 20% of height) to relatively broad (diameter ca. 77% of height).

The plants from near Mama León and adjacent localities in Tamaulipas, have very robust stems and are the least typical of the columnar subspecies. The relationships of this population to other columnar populations warrant further study. The population near Las Tablas, San Luis Potosí, shows considerable variation in the stem and rib morphology. Some plants resemble the nominotypical subspecies whereas others are similar morphologically to subsp. *tulense*. The perianth diameter is intermediate between those of the two subspecies. The evidence suggests that this is an area of past or ongoing hybridization between the two taxa; the question of hybridization warrants further investigation.

Attenuated and non-attenuated stems are the result of differential rates of vertical and lateral growth due to cellular activity in the apical and lateral meristems, respectively. The attenuated (tapered) stem is produced by a gradually increasing lateral growth rate which remains slower than the vertical rate. A non-attenuated stem is produced by the lateral growth rate exceeding the vertical rate early in development, then stabilizing at some point and not surpassing the vertical rate.

RESUMEN

Astrophytum myriostigma subsp. *myriostigma* y A.*myriostigma* subsp. *tulense* se distinguen tanto por carácteres vegetativos como reproductivos. El tallo de la subespecie típica es ancho y aplanado y se vuelve anchamente cilíndrico con la edad, alcanzando una altura máxima conocida de c. 52 cm. En la subespecie *tulense*, el tallo es relativamente delgado y columnar y puede alcanzar una altura máxima de unos 90 cm. Ambos taxones muestran variaciones en el ángulo y el perfil de las costillas. En la subespecie *myriostigma*, las costillas suelen ser obtusas con un perfil redondeado o angular, o moderadamente agudas con un perfil angular. En subespecie *tulense*, las costillas son típicamente de moderadas a muy agudas con un perfil angular. Hay excepciones a estas generalidades. Ambos taxones tienen un número modal de cinco costillas, y ambos tienen la tendencia a insertar costillas adicionales con la edad, aunque la tendencia parece más pronunciada en subespecie *tulense*.

La flor de la subespecie *myriostigma* difiere de la de la subespecie *tulense*, al tener un diámetro medio del perianto significativamente mayor ($P \leq 0.01$), un número medio significativamente mayor de lóbulos del estigma ($P \leq 0.05$) y más filas de tépalos (3–5 vs. 1–3). El color de los tépalos es de amarillo pálido a amarillo blanquecino en subespecie *tulense*, pero amarillo más brillante o amarillo dorado en la subespecie nominotípica. Las semillas de la subespecie nominotípica son significativamente más grandes ($P \leq 0.01$) que las semillas de la subespecie *tulense*.

Se estudió la variación morfológica en nueve poblaciones de la subespecie *myriostigma* y seis poblaciones de la subespecie *tulense*. La

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subespecie nominotípica muestra diferencias en el ángulo y el perfil de las costillas entre plantas individuales dentro de una población. En algunas localidades predominan las plantas de tallo aplanado y costillas obtusas y redondeadas. En otras localidades, las plantas con tallos más elevados y costillas angulares moderadamente agudas son predominantes, o al menos comunes. Poblaciones de subespecie *tulense* muestran variaciones individuales en la morfología del tallo. El tallo varía de cónico atenuado a no atenuado y de relativamente delgado (diámetro del 20% de la altura) a relativamente ancho (diámetro del 77% de la altura).

Las plantas de cerca de Mama León y quizás de localidades adyacentes en Tamaulipas, tienen tallos muy robustos y son las menos típicas de la subespecie columnar. Las relaciones de esta población con las de áreas adyacentes merecen un estudio más profundo. La población cercana a Las Tablas, San Luis Potosí, muestra una variación considerable en la morfología del tallo y las costillas. Algunas plantas se parecen a la subespecie nominotípica y otras son similares morfológicamente a la subespecie *tulense*. El diámetro del perianto es intermedio entre el de ambas subespecies. La evidencia sugiere que esta es un área de hibridación pasada o en curso entre los dos taxones; la cuestión de la hibridación merece una mayor investigación.

Los tallos más o menos atenuados son el resultado de tasas diferenciales de crecimiento vertical y lateral debido a la actividad celular en los meristemos apicales y laterales, respectivamente. El tallo atenuado (ahusado) se produce por una tasa de crecimiento lateral que aumenta gradualmente y que permanece más lenta que la tasa vertical. Un tallo no atenuado se produce cuando la tasa de crecimiento lateral excede la tasa vertical en las primeras etapas del desarrollo, luego se estabiliza en algún punto y no supera la tasa vertical.

INTRODUCTION

The Bishop's Cap, *Astrophytum myriostigma*, is represented by three morphologically divergent and geographically defined groups of populations (Hoock 1990; Montanucci & Kleszewski 2019). One group is represented by plants with a broad, depressed stem with obtuse, rounded ribs and large flowers; these plants conform, more-or-less, to Lemaire's (1839) original description of the species. This group occurs on the Central Plateau, approximately in the north-central area of San Luis Potosí. A second group consists of plants with small flowers and a columnar growth habit; these populations are geographically adjacent to the first group, occupying the northern and eastern parts of the Central Plateau. A third group is geographically isolated in the Jaumave Valley at the eastern edge of the Sierra Madre Oriental. Unlike the other two groups, the Jaumave plants, as seedlings, generally have rather long black spines which are later lost; also, as seedlings they display a columnar growth habit, but as they mature, they develop a globose, or sub-globose stem which eventually becomes broad, short columnar with age. The flower is smaller, on average, than that of the nominate subspecies. Montanucci and Kleszewski (2019) provided statistical data on the morphological variation in vegetative and reproductive characters for populations in the Jaumave Valley. They also reviewed the nomenclatural history of these populations and concluded that the subspecific epithet *quadricostatum* (H. Möller) Kayser is the correct name for these plants based on the rules of priority. Inasmuch as this taxon has already been the subject of a morphological study, it is not given further consideration here.

Locality records for the nominotypical subspecies and the "columnar" form of *Astrophytum myriostigma* indicate that they occur in proximity or are sympatric with one another in some areas of the Central Plateau. The co-occurrence of the two forms raised questions concerning their taxonomic status and relationships (Schätzle 1990, 1992). Schätzle (*op. cit.*) was uncertain whether to consider them different varieties or merely forms of a single variable species. But, at some localities, the presence of both taxa together with intermediate plants suggested that hybridization was probably occurring (Hoock 1990; Kleszewski 2001). The purpose of this paper is to review the taxonomic history of the species, and based on our further studies, to describe the comparative morphology of the nominotypical subspecies and subsp. *tulense*, including their inter- and intrapopulation variation.

TAXONOMIC HISTORY

Charles Lemaire described and named *Astrophytum myriostigma* in 1839; the original description lacked designated type material, locality, and collector information, but according to Ehrenberg (1847), the naturalist H. G. Galeotti discovered this cactus in 1837 near Hacienda de San Lázaro, San Luis Potosí. Two years later Galeotti described and named it *Cereus callicoche* (Galeotti *in* Scheidweiler 1839). Thus, two names were nearly simultaneously proposed for the species, but *Cereus callicoche* was subsequently relegated to the synonymy of Lemaire's *Astrophytum myriostigma* by G. Lawrence (1841). According to Hoock (1993) Galeotti's collection locality (Hacienda de San Lázaro) possibly corresponds to the present-day settlement of San

Lorenzo in San Luis Potosí. Hoock also mentions a more southerly literature record at Hacienda de Peñasco, and nearby to the southeast, a credible sight record at Candido Navarro (Hoock 1993; George Hinton, pers. comm., April 7, 2006).

Heinrich Möller (1927) named *Echinocactus myriostigma* subsp. *potosina* based on material originating from the state of San Luis Potosí. Later the name was recombined as *Astrophytum myriostigma* subsp. *potosinum* by Okumura (1933:195). Möller's concept of this taxon was vague, and the description provided little information as to how it differed from the nominotypical subspecies. It was characterized as having a medium large, pure yellow flower ("*mittelgrosse rein blassgelbe Blüte*"). A type specimen and type locality were not designated. Möller regarded the columnar and nude forms of the Bishop's Cap as varieties belonging to this subspecies. Kayser (1932) attempted to clarify the concept of this new taxon, referring to its broad, more rounded ribs and its green stem coloration. However, Megata (1944) synonymized the subsp. *potosinum* with the nominotypical subspecies based on his observations of imported plants (presumably undocumented) with intermediate morphology.

Backeberg (1961) treated the taxon *potosinum* as a variety and enlarged its description as follows: *"Etwas breitkugelig; Flöckchen nicht sehr dicht, der Körper daher grünlicher erscheinend; Rippen 5, scharfkantig, gerade herablaufend; Blute kleiner, nur etwa halb so groß wie beim Typus der Art, blaßgelb, viel heller als beim Typus der Art. …"* Our English translation of Backeberg's description follows: "somewhat broadly spherical; flakes not very dense, the body, therefore, appears greener; ribs 5, sharp-edged, running down straight; flowers smaller, only about half the size of the type, pale yellow, much lighter than the type of the species."

The above-mentioned descriptions indicate a variable rib morphology for this taxon, from broad, rounded ribs to more acute, angular ribs. Based on our observations and comparative data, plants with moderately acute, angular ribs occur together with plants with broader, rounded ribs, and the two morphotypes produce large flowers of similar size and hue (see also Lux & Stanik 1985, figs. 1–2). But small flowers about half the size of those of the nominate subspecies and with pale color are diagnostic characters for subsp. *tulense* (see Kayser's 1932 protologue below). Therefore, it is possible that Backeberg (1961) had inadvertently based his description of var. *potosinum* on specimens of subsp. *tulense* (that had not yet developed a columnar stem), or perhaps hybrids between *tulense* and the nominate subspecies. In any case, Backeberg considered *tulense* to be closely related to *potosinum* and treated the former as a subvariety of the latter. In his taxonomic key (Backeberg 1961), the two taxa are described as having medium-sized or small flowers but differing in stem characteristics—greener stem and straight ribs in *potosinum*, whiter stem and spiral ribs in *tulense*. Backeberg also recognized var. *columnare*, distinguishing it from the previously mentioned taxa by its columnar stem and moderately large, pale yellow flowers. In a study of the northern Jaumave Valley populations of Bishop's Caps, Hoock (1990) implicitly regarded the subsp. *potosinum* as an alternative name for the nominotypical subspecies. Ultimately, in his monographic study of *Astrophytum*, Hoock (2008) placed the subsp. *potosinum* in the synonymy of the nominotypical subspecies, presumably because he considered it an intra-populational variant. It is evident from the foregoing discussion that the diagnosis and affinities of subsp. *potosinum* remained ambiguous over many decades; the taxon was either aligned with subsp. *tulense*, or considered related to, or synonymous with, the nominotypical subspecies.

Curt Backeberg (1961) described var. *strongylogonum* which was characterized by a broad, depressed stem with obtuse, rounded ribs and a large flower. Lemaire's (1839) type material appears to have included plants with obtuse, rounded ribs, as the original description states in part: *"anguli quinque (aut sex) crassissimi, maxime convexi, semicirculum explicantes…"* Considering the similarities between the two descriptions, it is presumed that Backeberg's new variety was a junior synonym of the nominotypical subspecies. The taxon was eventually regarded as invalid by Eggli (1985) who determined that Backeberg had failed to designate and conserve a type specimen in violation of the then International Code of Botanical Nomenclature (ICBN, Article 9.5).

The columnar form of *Astrophytum myriostigma*, known since 1895 (see Hirscht 1895a, b), was first described by Karl Schumann (1898) as *Echinocactus myriostigma* var. *columnaris*. According to Schumann, it

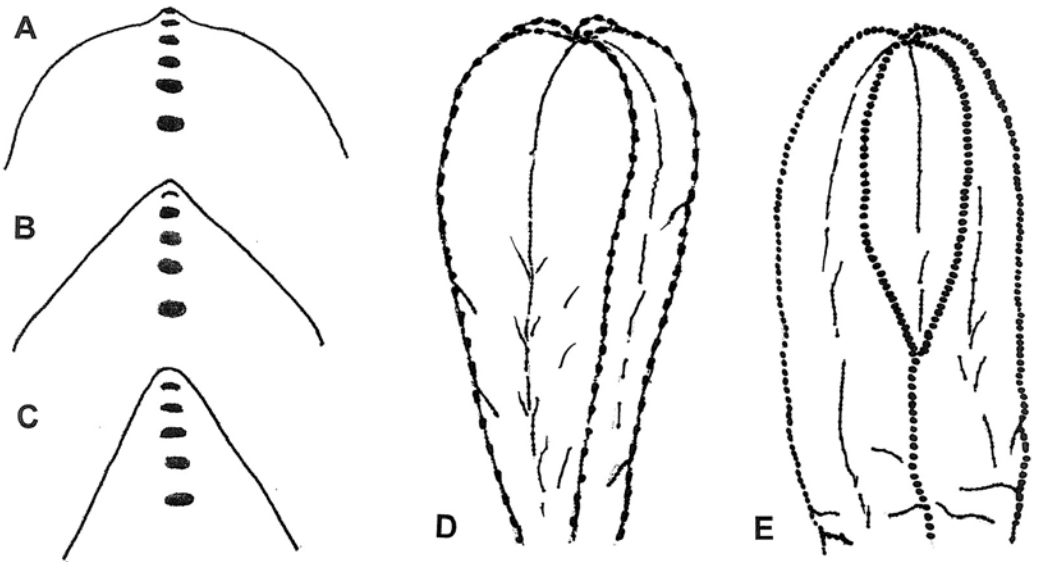

Fig. 1. Rib morphology observed in *Astrophytum myriostigma*. **A.** obtuse rib with rounded profile. **B.** obtuse rib with angular profile. **C.** acute rib with angular profile. Stem morphology of columnar plants. **D.** attenuated (tapered) stem. **E.** non-attenuated stem.

was distinguished from the nominotypical subspecies by its columnar form, small blossom (25 mm in length), and five stigma lobes. Schumann's protologue did not designate a type specimen and lacked locality information. The name was recombined as *Astrophytum myriostigma* var. *columnare* by Tsuda (1934). Megata (1944:43) followed Tsuda's taxonomy and described the flower as "very small, 3–4 cm in diameter." Decades later, another population of columnar plants came to be known largely through the collecting activities of H. W. Viereck. Plants imported in large numbers to Europe from the vicinity of Tula, Tamaulipas, were described and named *Astrophytum myriostigma* subsp. *tulense* by Konrad Kayser (1932). Kayser's protologue follows:

> *Im Jahre 1929 berichtete der Sammler Viereck von einer 'gedrechten, säulenförmigen, schneeweißen Myriostigmenform', die er in der Nähe von Tula gefunden hätte. Die Firma Fr. A. Haage importierte in den nächsten zwei Jahren große Mengen dieser subspecies Tulense. Als besonders charakteristisch möchte ich die dichte Beflockung bezeichnen, die an die subspecies koahuilense erinnert. Die Flocken sind nur viel kürzer, niemals filzig wie bei jener, die subsp. Tulense neigt im Alter wie keine der übrigen Unterarten zur Vielrippigkeit auch unter jungen Stücken finden sich häufig Sechs- und Mehrripper, sie neigen zum Säulenwachstum, bei keiner anderen Form stehen die Areolen so dicht aneinander wie hier, das hat zur Folge, daß die ältere Pflanze meist gleichzeitig mit vielen Blüten, oft 8–12, blüht. Die Blüten sind von allen Formen – auch bei großen Stücken – die kleinsten, blaßesten in Farbe. Dafür haben sie einen ausgesprochenen, intensiven Wohlgeruch, der an Rosen und Citronen erinnert. Die Luft des Kulturraumes, in dem auch nur wenige Stücke blühten, duftet deutlich nach Rosen. Die kleinen Samenkapseln sind trocken, springen in fünf Zipfeln auf. Die Zahl der Samenkörner beträgt meist nur 10–12 in der Kapsel, während wir bei den Formen aus Potosi u. Tamaulipas ca. 20–40, bei der Form aus Koahuila 60–70 finden.*

Our English translation follows, with words in brackets added for clarity:

> *In 1929 the collector Viereck reported about an "upright, columnar, snow-white form of myriostigma" that he had found near Tula. The company Fr. A. Haage imported large quantities of this subspecies tulense over the next two years. I would like to describe the dense flocking as particularly characteristic, which is reminiscent of the subspecies coahuilense. The flakes are just much shorter, never felty like those of the subspecies*

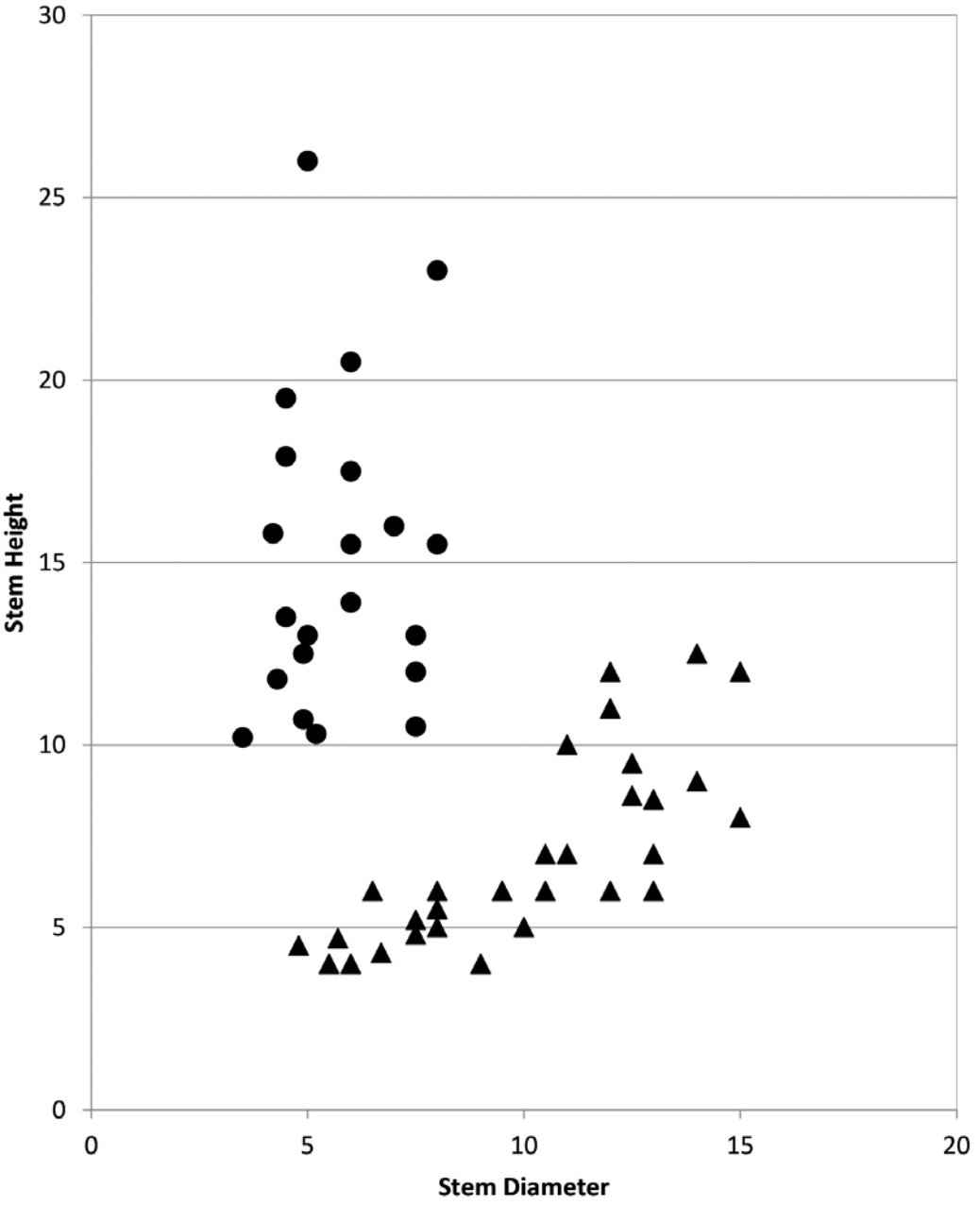

Fig. 2. Plot of stem height (cm) against stem diameter (cm) comparing a sample of columnar plants from Entronque Huizache (Huizache Junction) (circles) with a sample of the nominate subspecies from Cerritos and Villar (triangles).

[coahuilense]. In old age, like none of the other subspecies, tulense tends to be multi-ribbed, even among young specimens there are often six- and multi-ribs; they tend to have columnar growth; in no other form are the areoles so close together as here, which means that the older plant usually blooms with many flowers, often 8–12, at the same time. Of all varieties, the flowers are—even in large specimens—the smallest, pale in color. In return,

they have a pronounced, intense fragrance that is reminiscent of roses and lemons. The air of the growing area, in which only a few specimens bloomed, smells clearly of roses. The small seed pods are dry and open with five corners. The number of seeds in the capsule is usually only 10–12, while we find around 20–40 in the forms from [San Luis] Potosi and Tamaulipas, and 60–70 in the form from Coahuila.

The morphological characteristics of var. *columnare* and subsp. *tulense* were quite similar, leading Viereck (1939) to consider them synonymous. Megata (1944) recognized var. *columnare* but treated subsp. *tulense* as a synonym of the nominotypical subspecies. In stark contrast to Viereck's opinion, Sadovský and Schütz (1979:159) redescribed and elevated the two taxa to the rank of species. The authors distinguished *Astrophytum columnare* from *Astrophytum tulense* by differences in stem morphology, the former having an attenuated stem, the latter having a non-attenuated stem with the lower and upper portions of the stem approximately equal in diameter, in other words, not tapering or diminishing in diameter. The authors used the terms *"basipete attenuato"* to describe the tapered stem of *A. columnare*. We could not find *"basipete"*; the nearest Latin words we could find were *basi stipite attenuato.*

Other differences noted by Sadovský and Schütz (1979), and mentioned also in popular literature, include sharp (acute) ribs with slightly undulating (humped) edges in var. *columnare*, but somewhat wider and smoother ribs in subsp. *tulense*. The var. *columnare* has the tendency to retain five ribs later in life, but in subsp. *tulense* to add additional ribs up to six or seven even in the seedling stage. In var. *columnare* rib addition occurs primarily through bifurcation, whereas in subsp. *tulense* it occurs through bifurcation and insertion.

Hoock (1990) agreed with Viereck (1939) that the two taxa were the same and years later recognized subsp. *tulense* as the accepted name for the columnar populations (Hoock 2008). We also use the subspecific name *tulense* instead of var. *columnare* for the following reasons: The concept of a *variety* was formally defined by Du Rietz (1930) and quoted in Stace (1989:194), as "a population of one or several biotypes, forming a more-or-less distinct, local facies of a species," in other words, a local or ecological race. Our perusal of the literature on the systematics of the Cactaceae reveals that use of the term *variety* as conceptualized by Du Reitz (1930) is virtually nonexistent. In fact, the categories of *variety* and *subspecies* have been used inconsistently by many U.S. botanists (Stuessy 1990), and most troubling, in cactus taxonomy the category of *variety* has been largely used in the sense of a *subspecies*. Stuessy's (1990) concept of *variety* differed from that of Du Reitz, and he offered guidelines for the practical application of the categories of *subspecies*, *variety*, and *form*. According to Stuessy, *subspecies* should be characterized by several conspicuous morphological differences, marked multigenic genetic divergences, cohesive allopatric or parapatric distributions with natural hybridization possible along contact zones, and markedly reduced fertility in hybrids. *Varieties* should be characterized by one to a few conspicuous differences, cohesive geographic distributions which are largely allopatric (with some overlap), genetic divergences (multigenic or simple), probable natural hybridization in contact areas and reduced fertility in hybrids. It is evident that Stuessy's distinction between the categories of *subspecies* and *variety* is rather subjective, involving the degree of divergence between them. It seems that applying his guidelines for the use of the two categories would likely result in further ambiguity and confusion. Therefore, we prefer to follow the concept of a *variety* as stated by Du Reitz (1930). In our opinion use of the *subspecies* category instead of *variety* for the infraspecific taxa of *Astrophytum myriostigma* largely avoids conceptual issues. Furthermore, the nominotypical subspecies and subsp. *tulense* differ not only in vegetative morphology, but also in reproductive characters (see discussion below). Thus, in this case, the taxonomic rank of *subspecies* seems to be more appropriate than the rank of *variety* because it denotes a comparatively greater level of divergence.

METHODS

Sampled Localities.—The literature on *Astrophytum myriostigma* was reviewed to find and compile locality records and associated field numbers for this taxon. Localities represented by many field numbers indicated the potential to provide sufficient sample sizes for quantitative analysis. Localities were visited and randomly searched for plants. However, it was soon realized that random searching was less effective than efforts

concentrated in areas of slope with good drainage and associated flora especially consisting of *Agave*, *Hechtia,* and various xerophytic shrubs. Our intent was to find as many plants as possible. The discovered *Astrophytum* were photographed and measured if possible. Nine localities for subsp. *myriostigma* and six localities for subsp. *tulense* were selected based on adequate or marginally adequate samples to characterize the morphological variation of the local population. Localities from which only subjective information was collected were also tabulated because we believed the information contributed to the overall understanding of the variation in this species.

Character Analysis.—The morphological variation observed among populations of *Astrophytum myriostigma* provided a source of characters potentially useful for understanding the patterns of variation and morphological relationships among populations of this widespread species. Based on morphological variation described in the literature and our initial comparisons, the following 10 characters were selected for analysis: 1) stem proportions (stem diameter at mid-section and stem height); 2) shape of the stem base (attenuated or non-attenuated); 3) rib angle (obtuse, moderately acute, or acute); 4) rib profile (rounded or angular); 5) epidermal trichomes (flecked: a uniform, moderate to dense covering of trichomes; semi-nude: patchy or sparse flecking; nude: absence of trichomes); 6) diameter of perianth in mm; 7) number of stigma lobes; 8) number of tepal rows; 9) color of mature fruit; 10) long diameter of the seeds (to an accuracy of 0.05 mm). See Fig. 1 for representative morphotypes of rib angle and profile, and stem morphology. The variation in epidermal trichome density among populations of *Astrophytum myriostigma* is reported in greater detail by Montanucci and Kleszewski (2020).

In the following morphological analysis, statistics of dispersion for quantitative characters include the observed limits of variation, the sample mean ($\bar{x}$), ± 95% confidence limits for the sample mean, and sample size (n). Some characters, e.g., floral traits, were primarily recorded from greenhouse-grown plants due to the difficulties of field sampling. All greenhouse-grown plants have locality documentation unless stated otherwise.

RESULTS OF MORPHOLOGICAL ANALYSIS

Morphology of subsp. myriostigma.—The nominate subspecies of *Astrophytum myriostigma* has a depressed, globose to sub-globose stem in youth, which becomes a broad cylindrical stem in age. Hoock (1990) recorded a maximum stem height of 25 cm and a diameter of 20 cm. In our study, a maximum stem height of 52 cm and an estimated diameter of ca. 25 cm were recorded. The modal number of ribs is five, but with increasing age some plants acquire additional ribs, usually from six to eight; plants with four ribs are very uncommon. New ribs are added by the division of a single rib, or by insertion of an additional rib between existing ribs at the stem apex. The rib angle varies from obtuse to moderately acute, and the rib profile can be rounded to angular. The flower is relatively large, with a maximum perianth diameter of about 76 mm (Hoock 2008). We obtained a perianth diameter ranging from 38–64 mm ($\bar{x}$ = 50.5 ± 1.57 mm) in a sample of 55 flowers. The number of stigma lobes varies from 4–9 ($\bar{x}$ = 5.75 ± 0.25) in a sample of 82 flowers. The number of tepal rows in the perianth varies from 3–5, with 5 rows found in 4.8% of the sample (Montanucci & Kleszewski 2019). The mature fruit is green or pale green in color, with apical dehiscence producing four to six flaps upon opening. In some cases, the fruit, when ripe, is pink at the base, but the flaps remain green. Seedling spines, if present, are short (0.5–2 mm), usually straight, and black in color.

Morphology of subsp. tulense.—In contrast to the globose to short cylindrical stem of the nominate subspecies, the subsp. *tulense* has a columnar stem (Fig. 2). In the seedling stage, the stem is typically columnar, and this growth habit is maintained throughout life. In some seedlings, however, the stem is ± globose and gradually becomes columnar with increasing age. In old plants, the stem can reach a height of 90 cm (Sadovský & Schütz 1979). The modal number of ribs is five, but additional ribs (from 6–9) may develop, and plants with as many as 11 ribs have been found; plants with four ribs are quite rare. The rib angle varies from obtuse to acute, and the rib profile varies from rounded to angular. The perianth diameter of subsp. *tulense* is significantly smaller ($P \leq 0.01$) than that of the nominotypical subspecies. A perianth diameter ranging from

13–44 mm ($\bar{x}$ = 30.3 ± 0.76 mm) in a sample of 171 flowers was obtained. The number of stigma lobes in 250 flowers ranged from 1–8 ($\bar{x}$ = 4.7 ± 0.13). The mean number of stigma lobes in subsp. *tulense* is significantly lower ($P \leq 0.05$) than that of the nominate subspecies. The number of tepal rows in the perianth typically varies from 1–2, but in some specimens, there may be a third row. The mature fruit has apical dehiscence producing two to five flaps upon opening. In 47 fruits examined, 21 were green or pale green in color; 26 fruits were pink in color, especially around the base. The seeds of subsp. *tulense* are significantly smaller ($P \leq 0.01$) than those of the subsp. *myriostigma* (Table 1). Seedling spines, if present, are short (0.5–2 mm), usually straight, but occasionally recurved, and black in color.

Variation in samples of subsp. myriostigma.—Variation in stem morphology, including stem habitus, diameter and height of stem, number of ribs, rib angle, rib profile, variation in epidermal trichome density, and floral and seed measurements are discussed below. Categories for stem habitus at each locality are summarized in Table 2. Variation in stem habitus presumably reflects age-class composition in the local population. Young plants are globose or depressed globose but become sub-globose (slightly elevated) and eventually broadly cylindrical or barrel shaped in age. Variation in rib angle, rib profile and number of ribs among samples is summarized in Table 3. The nine sampled localities are listed alphabetically.

Cerritos, SLP.—All plants had a globose, depressed stem in which stem diameter exceeded height. Stem measurements were recorded for 13 plants. The smallest plant had a diameter of 4.8 cm and a height of 4.5 cm; the broadest plant had a diameter of 13 cm and a height of 8.5 cm. The tallest plant was 11 cm with a diameter of 12 cm. Stem diameter as a percentage of height ranged from 106–158%. All plants examined had obtuse ribs which varied from rounded to angular in profile. Seedlings grown under greenhouse conditions had acute ribs which gradually became more obtuse as the seedlings grew larger. Only one semi-nude plant was recorded; all other plants had moderate to dense covering of epidermal trichomes. Measurements were taken from 34 flowers from two cultivated plants. The perianth diameter ranged from 38–64 mm ($\bar{x}$ = 52.44 ± 2.30 mm). Schätzle (1990) reported a perianth diameter of 60 mm for the Cerritos population. Presumably, this was a maximum measurement; however, he did not provide a sample size. The average long diameter for seeds is given in Table 1.

Guadalcazar, SLP.—No stem measurements were taken at this locality, but stem habitus and rib morphology were classified subjectively based on observation. Most plants had a depressed, globose stem, but a lesser number had a globose to sub-globose (slightly elevated) stem. Only one semi-nude plant was recorded; all others had a moderate to dense covering of epidermal trichomes. Schätzle (1992) reported a perianth diameter of 55–60 mm for this population; however, he did not provide a sample size. We have no data for flower measurements.

Las Tablas, SLP.—Considerable variation in stem habitus was noted at this locality, ranging from depressed globose to sub-globose to columnar. Stem measurements were obtained from 11 plants. The tallest of these was 19.5 cm with a diameter of 12 cm and resembled subsp. *tulense*. The shortest plant was depressed, globose, with a height of 5.5 cm and a diameter of 7.5 cm. Stem diameter as a percentage of stem height ranged from 61.5–136.4%. Rib angle and profile ranged from obtuse and rounded to acute and angular. The frequency in the number of ribs varied as follows: five ribs (25 plants), six ribs (three plants), seven ribs (seven plants), eight ribs (two plants), 10 ribs (two plants), and 11 ribs (one plant). No nude plants were recorded. Measurements were obtained from 38 flowers from seven cultivated plants with globose to sub-globose (somewhat elevated) stems. Perianth diameter ranged from 27–50 mm ($\bar{x}$ = 39.26 ± 1.72 mm). The mean perianth diameter is approximately intermediate between that of subsp. *myriostigma* and that of subsp. *tulense*. Two cultivated plants from Las Tablas produced fruits that resembled those of subsp. *tulense*, i.e., pink in color when ripe.

Las Tablas, 7–10 km S, SLP.—No stem measurements were taken at this locality, but stem habitus and rib morphology were classified subjectively based on observation. Stem habitus varied from depressed globose to sub-globose and short columnar. Rib angle and profile ranged from obtuse and rounded to acute and angular. The number of ribs varied in frequency as follows: four ribs (one plant), five ribs (sixteen plants),

Table 1. Comparison of seed size between *Astrophytum myriostigma* and subsp. *tulense*. The abbreviations are sample size (*n*), observed limits of variation (OL), sample mean ($\bar{x}$), standard deviation (SD), 95% confidence limits for mean (± 95% CL).

Locality	*n*	OL	$\bar{x}$	SD	± 95% CL
subsp. *myriostigma*					
Cerritos, SLP	30	2.45–2.95 mm	2.68 mm	0.1428 mm	± 0.0511 mm
Villa de Hidalgo, SLP	30	2.60–3.35 mm	2.88 mm	0.1729 mm	± 0.0619 mm
Villar, SLP	30	2.50–3.20 mm	2.83 mm	0.1946 mm	± 0.0696 mm
subsp. *tulense*					
Entronque Huizache, SLP	30	2.25–2.80 mm	2.47 mm	0.1213 mm	± 0.0434 mm
Magdaleno Cedillo (1), TAM	30	1.90–2.65 mm	2.26 mm	0.2559 mm	± 0.0916 mm
Magdaleno Cedillo (2), TAM	30	1.95–2.40 mm	2.12 mm	0.1187 mm	± 0.0425 mm

Table 2. Summary of categories for stem habitus at sampled localities for *Astrophytum myriostigma* and its subsp. *tulense*.

subsp. *myriostigma*	*n*	Habitus (n)
Cerritos	13	globose-depressed (13)
Guadalcazar	22	globose-depressed (16); ± globose (5); subglobose (1)
Las Tablas	41	globose-depressed (11); globose-sub-globose (18); short columnar to columnar (12)
Las Tablas, 7–10 km S	26	globose-depressed (3); ± globose (14); sub-globose (7); short columnar (2)
Nuñez	19	globose-depressed (9); ± globose (7); sub-globose (3)
Puerta del Rio	10	globose-depressed (2); ± globose (4); sub-globose (4)
San Rafael	9	globose-depressed (6); ± globose (3)
Villa de Hidalgo	12	globose-depressed (7); sub-globose (4); broad-columnar (1)
Villar	37	globose-depressed (23); ± globose (8); sub-globose (5); broad cylindrical (1)
subsp. *tulense*	***n***	**Habitus (n)**
Entronque Huizache	14	sub-globose (1); columnar (13)
Noria de Las Flores	9	± globose (4); sub-globose (3); columnar (2)
Presa de Guadalupe, 12.4 km NE	9	sub-globose (1); moderately broad columnar (7); slender columnar (1)
La Perdida	31	globose (14); sub-globose (11); short columnar (4); columnar (2)
Magdaleno Cedillo	43	globose (12); sub-globose (14); columnar (17)
Mama León	21	globose-depressed (1); ± globose (9); sub-globose (7); short-columnar (3); columnar (1)

Table 3. Summary of variation in rib morphology (based on number and percentage of plants) and rib number for samples of subsp. *myriostigma* and subsp. *tulense*. OB/RD = obtuse, rounded ribs; OB/AN = obtuse, angular ribs; AC/AN = acute, angular ribs.

subsp. *myriostigma*	*n*	OB/RD	OB/AN	AC/AN	Rib Number
Cerritos	8	4 (50%)	4 (50%)	0%	5
Guadalcázar	22	5 (22.7%)	14 (63.7%)	3 (13.6%)	5–8
Las Tablas	40	4 (10%)	23 (57.5%)	13 (32.5%)	5–11
Las Tablas, 7–10 km S	26	4 (15.4%)	12 (46.1%)	10 (38.5%)	4–12
Núñez	18	9 (50%)	9 (50%)	0%	5–8
Puerta del Rio	10	2 (20%)	8 (80%)	0%	5–6
San Rafael	9	4 (44.5%)	2 (22.2%)	3 (33.3%)	5
Villa de Hidalgo	12	5 (41.7%)	7 (58.3%)	0%	5–7
Villar	18	2 (11.1%)	7 (38.9%)	9 (50%)	4–7
subsp. *tulense*	*n*	OB/RD	OB/AN	AC/AN	Rib Number
Entronque Huizache	16	0%	0%	16 (100%)	5–9
Noria de Las Flores	9	0%	2 (22.2%)	7 (77.8%)	5–8
Presa de Guadalupe, 12.4 km NE	9	0%	6 (66.6%)	3 (33.3%)	5–8
La Perdida	31	0%	4 (12.9%)	27 (87.1%)	5–7
Magdaleno Cedillo	49	0%	7 (14.3%)	42 (85.7%)	5–9
Mama León	21	1 (4.8%)	10 (47.6%)	10 (47.6%)	5–9

six ribs (five plants), seven ribs (two plants), nine ribs (one plant), and 12 ribs (one plant). The plant with 12 ribs had a broad, short columnar stem. Another plant with six ribs had a columnar stem with extensive bark development, indicating that it was an old plant. One plant was recorded as semi-nude; all other plants were densely covered with epidermal trichomes. Note: nine plants from this sample were erroneously listed as from "Ejido San Francisco" (Montanucci & Kleszewski 2020:258). As far as we have been able to determine, *Astrophytum* does not occur in the immediate vicinity of San Francisco which is situated ca. 20 km (straight line) south of Las Tablas.

Nuñez, SLP.—No measurements were obtained from plants at this locality, but stem habitus was subjectively classified based on observation. Stem habitus varied from depressed globose to ± globose; several plants were classified as sub-globose (slightly elevated). The largest plant found had a diameter of ca. 25 cm. The number of ribs varied in frequency as follows: five ribs (17 plants), six ribs (one plant), and eight ribs (one plant). The ribs were obtuse in all plants, but the profile varied from rounded to angular. One plant (a small seedling), had acute, angular ribs. Three nude plants were recorded; the other plants had moderate to dense covering of epidermal trichomes.

Puerta del Rio, SLP.—Stem habitus was subjectively classified by observation. The stem varied from depressed globose to sub-globose (slightly elevated) at this locality. Nine plants had five ribs, and one plant had six ribs. The ribs were obtuse with a rounded profile in two plants, and obtuse with an angular profile in eight plants. Two semi-nude plants were recorded; the others had a moderate to dense covering of trichomes.

San Rafael, SLP.—Stem habitus was classified subjectively by observation. The stem was globose and depressed in six plants, but not depressed or ± elevated in three plants. Rib morphology varied from obtuse with a rounded profile to moderately acute with an angular profile (Table 3). Only plants with five ribs were observed and none of the plants were of advanced age. One plant was somewhat greenish due to the sparseness of epidermal trichomes; the other plants were white.

Villa de Hidalgo, SLP.—Stem habitus ranged from depressed globose to sub-globose to broadly cylindrical. Stem measurements were obtained from 12 plants. The largest plant had a diameter of 22 cm and a height of 37 cm. The smallest plant had a diameter of 13 cm and a height of 12 cm. Stem diameter as a percentage of height ranged from 59.5–120%. The ribs varied from obtuse and rounded in profile to obtuse and angular in profile. The number of ribs varied in frequency as follows: five ribs (10 plants), six ribs (one plant), and seven ribs (one plant). Thirteen seedlings (ca. ≤ 6.5 cm in diameter) grown under greenhouse conditions had five acute ribs with an angular profile. Two seedlings (diameter 7.5 cm, height 5–6 cm) had obtuse, somewhat angular ribs. It appears that the ribs become more obtuse as the seedlings increase in size. All plants had a moderate to dense covering of epidermal trichomes. The perianth diameter ranged from 65–68 mm in three flowers produced by one cultivated plant; the flowers had 8–9 stigma lobes. The average long diameter for seeds is given in Table 1.

Villar, SLP.—Stem habitus varied from depressed globose to sub-globose to broadly cylindrical (one plant). Stem measurements were taken from 19 plants. The tallest plant had a stem height of 15.5 cm and a stem diameter of 14.5 cm. The two broadest plants both had a stem diameter of 15 cm and a stem height of 8–12 cm. The smallest plant had a stem diameter of 5.5 cm and a height of 4 cm. Stem diameter as a percentage of height ranged from 93.5–225%, the greatest percentage among the localities sampled for this taxon. The rib angle and profile varied from obtuse with a rounded profile to obtuse with a more-or-less angular profile to acute with an angular profile. The number of ribs varied in frequency as follows: four ribs (one plant), five ribs (14 plants), six ribs (one plant), and seven ribs (two plants). Among 33 seedlings (2–3 cm diameter) grown under greenhouse conditions, the number of ribs varied as follows: five ribs (29 seedlings), six ribs (one seedling), seven ribs (one seedling), and eight ribs (two seedlings). All plants at the sampled locality had a moderate to dense covering of epidermal trichomes. The average long diameter for seeds is given in Table 1.

The rib morphology of subsp. *myriostigma* for the nine samples combined (n = 146) can be summarized as follows: 1) obtuse, rounded ribs (37 plants, 25.3%); 2) obtuse, slightly rounded to angular ribs (79 plants, 54.1%); 3) ± acute, angular ribs (30 plants, 20.6%). In addition, 46 plants from 17 localities with small sample

sizes were classified and the following numbers obtained: 1) obtuse, rounded ribs (17 plants, 37%); 2) obtuse, slightly rounded to angular ribs (21 plants, 45.7%); 3) ± acute, angular ribs (8 plants, 17.3%).

Variation in samples of subsp. tulense.—Variation in stem morphology, including stem habitus, diameter and height of stem, number of ribs, rib angle, rib profile, variation in epidermal trichome density, and floral and seed measurements are discussed below. Categories for stem habitus at each locality are summarized in Table 2. Variation in stem habitus presumably reflects age-class composition in the local population. Young plants are globose or sub-globose (slightly elevated) and eventually become slender columnar or moderately broad columnar in age. Variation in rib angle, rib profile and number of ribs among samples is summarized in Table 3. The six sampled localities are listed alphabetically by placename and state.

Entronque Huizache, SLP.—Stem habitus varied from sub-globose (slightly elevated) to columnar. Stem measurements were obtained from 21 plants. The tallest plant had a stem height of 26 cm and a diameter of 5 cm. The two shortest plants had a stem height of 10.2 and 10.3 cm, and a diameter of 3.5 and 5.2 cm, respectively. Stem diameter, as a percentage of stem height in plants taller than 15 cm, ranged from 19.2–51.6% ($\bar{x}$ = 32.7%), indicating that columnar plants had a narrow to moderately broad stem. Compare stem diameter data with that from Magdaleno Cedillo (see below). All plants in the sample had acute, angular ribs; one plant had a twisted or spiral stem. The frequency in the number of ribs varied as follows: five ribs (22 plants), seven ribs (three plants), and nine ribs (one plant). Two seedlings growing in mats of *Hechtia* had tapered stems; all other plants had stems that were non-attenuated or somewhat intermediate. In this population, plants as tall as 90 cm and with eight ribs were reported by Schätzle (1990). He stated that rib bifurcation began at a height of about 40 cm. All plants examined had a dense covering of white trichomes. Schätzle (1990) reported a perianth diameter of 25 mm for this population. It is not clear if this was an average value or a maximum value, and he did not provide a sample size. Perianth measurements were taken from 91 flowers from 10 cultivated plants. Perianth diameter varied from 13–44 mm ($\bar{x}$ = 31.5 mm ± 1.35 mm). The sample mean is significantly smaller ($P \leq 0.01$) than the mean perianth diameter of the sample from Magdaleno Cedillo (see below). The average long diameter for seeds is given in Table 1.

Noria de Las Flores, SLP.—Stem morphology was subjectively classified by observation. Stem habitus varied from ± globose to sub-globose (slightly elevated) to columnar. Rib angle and profile varied from acute and angular to obtuse and angular. The frequency in the number of ribs varied as follows: five ribs (seven plants), six ribs (one plant), and eight ribs (one plant). Kleszewski and Hoock (2007) reported plants ranging in height from 8–35 cm at this locality. All plants examined had a dense covering of epidermal trichomes. Perianth diameter ranged from 23–33 mm in several flowers from plants grown in the greenhouse.

Presa de Guadalupe, 12.4 km NE, SLP.—Stem morphology was subjectively classified by observation. Stem habitus varied from sub-globose (elevated stem) to columnar. The columnar plants were slender (diameter ca. 33.8% of height) to moderately broad (diameter ca. 52% of height). The rib angle and profile varied from obtuse and angular to acute and angular. The frequency in the number of ribs varied as follows: five ribs (one plant), six ribs (three plants), seven ribs (two plants) and eight ribs (three plants). All plants examined had a moderate to dense covering of epidermal trichomes.

La Perdida, TAM.—Stem morphology was subjectively classified based on observation. Stem habitus varied from globose to sub-globose (slightly elevated) to columnar. The rib angle and profile were predominantly acute and angular, but four plants had obtuse ribs with an angular profile. The number of ribs varied in frequency as follows: five ribs (28 plants), six ribs (two plants), and seven ribs (one plant). Schätzle (1988) reported 8–11 ribs in plants with a height of about 30 cm. Schätzle (1990) also stated that columnar plants as tall as 30 cm had at least five ribs and began to acquire additional ribs beyond this height. All plants examined had a dense covering of white epidermal trichomes. However, two plants had exposed green epidermis near the stem base presumably due to mechanical disturbance. All seedlings had a non-attenuated globose to sub-globose stem; they were found growing in exposed locations along the perimeter of *Hechtia* and *Agave* colonies. Schätzle (1990) reported a perianth diameter of only 10 mm for this population, but he did not provide a sample size. He also reported that small flowers were produced by both globose and columnar plants at this locality. One of us (KPK) visited the habitat several times and obtained perianth diameters from 25–35 mm.

We observed one cultivated plant with very small flowers like those of plants from La Perdida reported by Schatzle (1990). The plant (which lacked locality data) was slender (stem diameter ca. 13–15% of height) and occasionally produced flowers with a perianth diameter of ca. 13–17 mm, and with a pistil length of 5–6 mm and minute stigma lobes which remained closed during full anthesis. The flowers could not be successfully pollinated, and in one case dissection of the ovary revealed the absence of ovules. We cannot explain the underlying cause of the small size and aberrant ovary morphology of these flowers, although it likely could have had a nutritional basis.

Magdaleno Cedillo, TAM.—Stem habitus varied from globose to sub-globose to columnar. Stem measurements were obtained from 31 plants. The tallest plant in the sample was 30 cm in height and13 cm in diameter. Kleszewski and Hoock (2007) reported old plants reaching a height of about 50 cm at this locality. The shortest plant was 7 cm in height with a diameter of 6.5 cm. The stem diameter, as a percentage of height in plants taller than 15 cm, ranged from 20–77.4% ($\bar{x}$ = 52.7%). Rib angle and profile varied from obtuse and angular (< 15% of sample) to ± acute and angular (ca. 85% of the sample). The number of ribs varied in frequency as follows: five ribs (24 plants), six ribs (12 plants), seven ribs (seven plants), eight ribs (five plants), and nine ribs (one plant). Among 40 cultivated seedlings ranging in height from 5–9 cm, 37 had five ribs, one had six ribs, and two seedlings had seven ribs. All plants at this locality had a moderate to dense covering of epidermal trichomes, with the majority being very white. However, some old plants lacked trichomes on the lower portions of the stem, possibly due to mechanical disturbance. Schätzle (1988) reported a perianth diameter of 25–30 mm, but he did not provide a sample size. In our study, measurements of 33 flowers were taken from three cultivated plants. The perianth diameter ranged from 30–48 mm ($\bar{x}$ = 37.03 ± 1.78 mm). The average long diameter for seeds is given in Table 1.

Mama León, TAM.—Stem morphology was subjectively classified by observation. Stem habitus varied from depressed globose to sub-globose (elevated) to columnar. Most plants had a robust stem habitus, more like the nominate subspecies rather than like subsp. *tulense*. Stem measurements were taken from the tallest plant in the sample; it was 39 cm in height and 19 cm in diameter; its diameter as a percentage of height was 48.7%. The number of ribs varied in frequency as follows: five ribs (14 plants), six ribs (two plants), seven ribs (three plants), eight ribs (one plant), nine ribs (one plant). The rib angle and profile varied from obtuse and rounded, to obtuse and angular, to acute and angular. Two plants examined had a slightly greenish appearance due to a reduction in density of epidermal trichomes. In the habitat, nine seedlings associated with a maternal plant were examined, but not measured. The stem diameter of the seedlings appeared to exceed the height somewhat, giving them a depressed habitus; the ribs were obtuse with an angular profile. Two flowers were examined from plants in the habitat; they were not in full anthesis and so were not measured. Both flowers had 7 stigma lobes with 3 and possibly 4 (one flower) rows of tepals. By contrast, the flower of one cultivated plant had two rows of tepals. Another cultivated plant produced a flower with a perianth diameter of 25 mm. A plant in bloom near Calabacillas produced a flower with apparently three tepal rows and five stigma lobes. Epidermal trichomes varied from moderately sparse to dense, giving the Mama León plants a greenish to white appearance.

Variation in the rib morphology for the six samples of subsp. *tulense* combined (including several additional plants) (n = 141) is summarized as follows: 1) obtuse, rounded ribs (two plants, 1.4%); 2) obtuse, angular ribs (30 plants, 21.3%); 3) acute, angular ribs (109 plants, 77.3%).

DISCUSSION AND CONCLUSIONS

Astrophytum myriostigma subsp. *myriostigma* and subsp. *tulense* are distinguished by both vegetative and reproductive characteristics. This study has provided additional data that further characterize the two taxa and provide a better understanding of their morphological variation.

The stem.—The stem of the nominate subspecies is broad, globose, and usually depressed early in life, becoming broadly cylindrical or barrel-shaped in age and reaching a known maximum height of 52 cm. Plants of this exceptional size were found in the mountain slopes south of Tanque de Los Angeles, SLP. In

subsp. *tulense*, the seedlings have a globose or sub-globose (elevated) stem which gradually becomes columnar; this growth habit is maintained through life and in age the stem can reach a maximum height of ca. 90 cm (Sadovský & Schütz 1979; Schätzle 1990). Plants of this height were reported historically from the vicinity of Entronque Huizache, SLP, (Schätzle *op. cit* , and Steven Brack pers. comm. Oct. 5, 1990). Subjective comparisons of plants of subsp. *tulense* from Calabacillas, Nicolas Medrano and Mama León indicate that these plants have rather broad, robust stems and thus bear close resemblance to the nominate subspecies. Our measurement data (stem diameter as a percentage of stem height) also reveal that the plants from Magdaleno Cedillo are, on average, more robust than the plants from Entronque Huizache.

Our study of the stem morphology among plants from different localities revealed that a non-attenuated stem is generally common across the sampled populations. The attenuated (tapered) stem was recorded in relatively few plants, particularly some from Magdaleno Cedillo and Entronque Huizache. We were not able to study plants from Dr. Arroyo, Nuevo Leon, the Type locality of var. *columnare* as restricted by Sadovský and Schütz (1979) and cannot provide data for plant stem morphology from that area.

The ribs.—The two taxa display differences as well as variation in the number, angle, and profile of the ribs. In subsp. *myriostigma* the ribs are usually obtuse, and the rib profile varies from rounded to more-or-less angular. The acute rib angle and angular profile is generally less common in the nominotypical subspecies, except for the sample from Villar. Plants with a broad, depressed stem and obtuse angular or rounded ribs predominate at some localities, including Cerritos, Guadalcazar, and Nuñez. Plants with this morphology have also been found at Guaxcama, and in lesser numbers at Buenavista, Charco Blanco, Derramaderos, El Tepozan, Joya de Luna, La Hincada, La Muralla, and Trojes, although most of these named localities remain largely unstudied. Plants with the highest number of ribs were found at Las Tablas and 7–10 km south (Table 3).

In contrast to the nominate subspecies, the subsp. *tulense* typically has acute, angular ribs. This morphology predominates at Entronque Huizache, Noria de las Flores, La Perdida, and Magdaleno Cedillo. Obtuse, angular ribs are less common in local populations except for the samples from NE of Presa de Guadalupe and Mama León (Table 3), and this rib morphology was also noted in plants from Calabacillas and Nicolas Medrano. Only a small proportion (4.8%) of the sample from Mama León was represented by plants with obtuse, rounded ribs.

The flower.—The flower of the nominotypical subspecies differs from that of subsp. *tulense* in having a significantly larger mean perianth diameter ($P \leq 0.01$), a significantly higher mean number of stigma lobes ($P \leq 0.05$), and usually more tepal rows (3–5 vs. 1–2 [3]). The color of the tepals is pale yellow to whitish yellow in subsp. *tulense*, but brighter yellow or golden yellow in the nominate subspecies.

There is variation in perianth diameter and number of tepal rows among samples of subsp. *tulense*. The sample from Magdaleno Cedillo has a significantly larger mean perianth diameter ($P \leq 0.01$) than the sample from Entronque Huizache. Typically, the number of tepal rows varies from one to two, but plants from Mama León and Calabacillas may produce flowers with up to three or four rows of tepals. However, our data are inadequate to describe these populations in more detail.

The seeds.—The seeds of the nominate subspecies are significantly larger ($P \leq 0.01$) than the seeds of subsp. *tulense*. The mean long diameter of seeds was taken for samples of the nominate subspecies from Cerritos, Villa de Hidalgo, and Villar; the samples did not differ significantly from each other ($P \geq 0.01$). However, in subsp. *tulense*, the seeds from plants from Entronque Huizache had a significantly larger mean long diameter ($P \leq 0.01$) than the mean of samples from Magdaleno Cedillo (Table 1).

Hybridization.—Kleszewski (2001) reported that the nominate subspecies and subsp. *tulense* could be sympatric and possibly hybridizing in the vicinity of Las Tablas. The additional data presented herein support this hypothesis. Some plants have a depressed globose stem with obtuse, rounded ribs, whereas others have a columnar stem resembling the morphology of subsp. tulense. The mean perianth diameter for the flower sample from Las Tablas is intermediate between that of the nominate subspecies and that of subsp. *tulense*. Other geographic locations may support populations composed of hybrids and parental types, and it seems reasonable that subsp. *tulense* and the nominate subspecies may have experienced a history of hybridization

and genetic introgression. Analytical methods using molecular genetic markers will probably be necessary to identify hybrids and assess the extent of hybridization between the two taxa.

Stem morphogenesis.—Undoubtedly, both genetic and environmental factors influence stem morphogenesis in nature. In culture, it is possible that photoperiod, light intensity, and nutrients may influence stem morphogenesis, but these factors have not been studied experimentally and cannot be discussed in detail. However, we have raised seedlings of both stem forms to maturity and have recorded our observations concerning stem morphogenesis. The cactus stem is classified as a sterile long shoot that shows indeterminate growth because the apical meristem remains active (Powell & Weedin 2004). Vertical growth of the stem is the result of cell divisions within the apical meristem, and the stem increases in diameter due to activity in the lateral meristem (Sinnott 1960; Gibson & Nobel 1986). Seedlings of subsp. *tulense* that initially develop a tapered, columnar stem, maintain this morphology throughout life, resulting in adult plants with the "classic" var. *columnare* appearance. Our observations suggest that a tapered, columnar stem is produced when lateral growth proceeds at a slower but gradually increasing rate relative to vertical growth; the lateral growth rate eventually stabilizes, more-or-less, and does not surpass the vertical rate. A non-tapered, columnar stem is the result of the lateral growth rate surpassing the vertical rate early in development to produce a globose, more-or-less depressed stem with a given diameter, at which point the lateral rate stabilizes or slows, and is surpassed by the vertical growth rate. The globose stem may reach a diameter of ca. 6.5–11.5 cm or more before significant vertical growth is initiated by the apical meristem.

The attenuated and non-attenuated stems represent morphologies at the opposite limits of the range of variation. This variation is non-discrete because there are intermediate forms among individuals in the population. In the habitat we observed that the stem is tapered and columnar in a few seedlings emerging up through mats of *Hechtia*, but in larger plants portions of the stem in full sunlight are more even in diameter. Competition for light and relatively high levels of organic nutrients could influence development of the tapered, columnar stem of seedlings growing within mats of *Hechtia*. Plants growing in exposed locations near the margins of *Hechtia* and *Agave* colonies (e.g., at La Perdida, Magdaleno Cedillo) tend to remain globose when young until vertical growth begins to overtake lateral growth. Incidentally, individuals of subsp. *tulense* in the globose growth stage resemble the nominate subspecies and can be easily misidentified. We also noted variation in the growth pattern of the diameter of the columnar stem. In some large plants, the diameter is remarkably even along the length of the stem. In others, the stem diameter increases gradually along the length of the stem. Less often, an alternating increase and decrease of the diameter was noted along the length of the stem, possibly due to intermittent conditions not conducive to growth.

Problems with stability potentially arise as the plant becomes large, especially for plants with an attenuated stem base. Only two toppled plants were found during this study. One was ca. 30 cm tall with a diameter of ca. 10 cm. The stem base was attenuated over a relatively short distance. The second columnar plant found toppled was not measured. Because the stem base had started to decay, its morphology could not be determined. Toppling is sporadic and may be non-fatal, and generally occurs late in the reproductive life of the plant and therefore is not considered a significant selective force.

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