A TAXONOMIC EVALUATION OF *ASTROPHYTUM MYRIOSTIGMA* VAR. *NUDUM* (CACTACEAE)

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ABSTRACT

The absence of epidermal trichomes has been used as a diagnostic character to distinguish *Astrophytum myriostigma* var. *nudum* from other infraspecific taxa. In the Huizache region of San Luis Potosí, Mexico, between the elevations of 1320 m and 1700 m, the local populations of *A. myriostigma* are polymorphic, comprised of nude, semi-nude, and flecked plants. However, this polymorphism is non-discrete as there is considerable variation and intermediacy among plants. Also, the proportion of nude plants increases gradually with elevation, which suggests clinal variation correlated with altitude. Exclusively nude populations are currently known only from near Santa Rita del Rucio (≥ 1710 m) and south of Entronque Huizache (≥ 1750 m). Farther south, flecked plants were recorded at 1726 m elevation at 6 km E of Guadalcázar, and to the north near El Realejo flecked plants occur as high as 1920 m. At localities southeast of the Sierra San Pedro (Sierra Guadalcázar), nude and semi-nude plants are absent or present at relatively low frequencies in local populations.

Epidermal trichomes provide shading and reflectance that protects the cactus stem against excessive solar radiation and moderates stem temperature. The majority of nude *A. myriostigma* growing in exposed locations at the margins of *Hechtia* colonies were found to suffer from chlorophyll degeneration due to excessive exposure to solar radiation.

A comparative morphological study did not find any characters which can be used in combination to diagnose the var. *nudum*. Given the lack of a suite of discrete, or nearly discrete diagnostic characters, and given that exclusively nude populations do not have a definable geographic distribution we suggest that the nude phenotype should be treated taxonomically as a "form" rather than as a geographical "variety," or subspecies.

RESUMEN

La ausencia de tricomas epidérmicos se ha utilizado como un carácter diagnóstico para distinguir *Astrophytum myriostigma* var. *nudum* de otros taxa infraespecíficos. En la región Huizache de San Luis Potosí, México, entre las elevaciones de 1320 m y 1700 m, las poblaciones locales de *A. myriostigma* son polimórficas, compuestas por plantas desnudas, semidesnudas y moteadas. Sin embargo, este polimorfismo no es discreto ya que existe una considerable variación e intermediación entre las plantas. Además, la proporción de plantas desnudas aumenta gradualmente con la elevación, lo que sugiere una variación clinal correlacionada con la altitud. Actualmente se conocen poblaciones exclusivamente desnudas solo cerca de Santa Rita del Rucio (≥ 1710 m) y al sur de Entronque Huizache (≥ 1750 m). Más al sur, se registraron plantas moteadas a 1726 m de altitud a 6 km E de Guadalcázar, y al norte, cerca de El Realejo, hay plantas moteadas de hasta 1920 m. En las localidades al sureste de la Sierra San Pedro (Sierra Guadalcázar), las plantas desnudas y semidesnudas están ausentes o presentes en frecuencias relativamente bajas en las poblaciones locales.

Los tricomas epidérmicos proporcionan sombra y reflectancia que protege el tallo del cactus de la radiación solar excesiva y modera la temperatura del tallo. Se descubrió que la mayoría de *A. myriostigma* desnuda que crece en lugares expuestos en los márgenes de las colonias de *Hechtia* sufre degeneración de clorofila debido a la exposición excesiva a la radiación solar.

Un estudio morfológico comparativo no encontró ningún carácter que pueda usarse en combinación para diagnosticar la var. *nudum*. Dada la falta de un conjunto de caracteres de diagnóstico discretos o casi discretos, y dado que las poblaciones exclusivamente desnudas no tienen una distribución geográfica definible, sugerimos que el fenotipo desnudo debe tratarse taxonómicamente como una forma en lugar de una variedad geográfica, o subespecie.

INTRODUCTION

As the specific epithet indicates, *Astrophytum myriostigma* Lemaire is characterized by numerous flecks of white trichomes covering the epidermis of the stem. In 1912, Rudolph Meyer named the var. *nudus* (originally named *Echinocactus myriostigma* Salm-Dyck var. *nudus*), a taxon that was described as essentially devoid of epidermal trichomes, giving the plant a smooth, green appearance. Megata (1944) recombined the name as *Astrophytum myriostigma* Lemaire var. *nudum* (Meyer). A perusal of the nomenclatural history of this taxon revealed a number of apparent synonyms, including *Astrophytum myriostigma* forma *nuda* Hort. von Roeder

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(1929) in Megata (1944), *Astrophytum myriostigma* Lemaire subsp. *potosinum* Moeller var. *nudum* Hort. Okumura (1933), *Astrophytum myriostigma* var. *myriostigma* subvar. *glabrum* Backeberg (1961), *Astrophytum myriostigma* var. *strongylogonum* subvar. *nudum* Backeberg (1961), *Astrophytum myriostigma* var. *virens* Sadovský & Schütz (1979), and *Astrophytum myriostigma* var. *strongylogonum* f. *rotunda* subf. *nuda* (Klaus 1985). It should be noted that Backeberg's (1961) var. *strongylogonum*, characterized by a broad, depressed stem with obtuse, rounded ribs and large flowers is a *nomen invalidum*. According to Eggli (1985), Backeberg failed to designate and conserve a nomenclatural type specimen in violation of the then International Code of Botanical Nomenclature (ICBN, Art. 37.1). Although a moot point, var. *strongylogonum* is also quite probably a junior synonym of the type species as Backeberg's description conforms well to Lemaire's original description: *"anguli quinque (aut sex) crassissimi, maxime convexi, semicirculum explicantes. …"*

In systematic botany, five infraspecific categories are generally recognized: *subspecies*, *variety*, *subvariety*, *form,* and *subform* (see the Shenzhen Code, Chapter I, Article 4.2). Stebbins (1950) believed that recognizing these categories created more confusion than order and argued that the "subspecies" category was sufficient to express most of the biologically significant variation observed in plants. Stebbins viewed the subspecies as a group of populations having certain morphological and physiological characteristics in common, occupying a geographic subdivision of the range of a species or a series of ecologically similar habitats, and differing in several characteristics from members of other subspecies. The different subspecies of a given species are usually interconnected genetically through intergrading populations.

Du Rietz (1930), quoted in Stace (1989:194), developed the concept of a "variety," stating that it is "a population of one or several biotypes, forming a more or less distinct local facies of a species," in other words it is a local or ecological race. Stuessy (1990) lamented that "variety" and "subspecies" categories have been used inconsistently, creating considerable confusion in U.S. systematic botany. He noted that the so-called "Californian school" of botany used "subspecies" as their preferred infraspecific category. The "Eastern school" used the term "variety" in the sense of a "subspecies," i.e., a "geographical variety" and not as conceptualized by Du Rietz (1930). Based on our perusal of the literature, use of the term "variety" as conceived by Du Reitz (op. cit.) is virtually nonexistent in the systematics of the Cactaceae.

In his monograph on the genus *Astrophytum*, Hoock (2008) recognized infraspecific taxa at the ranks of "subspecies" and "variety," but did not provide a clear distinction between the two categories. He recognized *Astrophytum myriostigma* var. *nudum* as a valid taxon based on morphological, ecological and distributional criteria which ostensibly distinguish it from the nominotypical subspecies. The purpose of our paper is to evaluate the criteria used as the basis for the recognition of this taxon and to determine if its current taxonomic rank is appropriate.

ORIGINAL DESCRIPTION

The original description of var. *nudum* from Meyer (1912) reads as follows: "*Simplex, caule fere globoso, nitente olivaceo-viridi, costis 5, latis, subrotundis, sine fasciculis lanatis, areolis 0.5–1 cm distantibus, aculeis O. Floribus adnunc ignotis.*"

"Körper einfach, halbkugelförmig bis fast kugelig, bei 17 cm Durchmesser 14 cm Höhe, mit eingesenktem mit spärlichem rotbraunem Wollfilz bekleidetem Scheitel, von glänzend olivgrüner Färbung, ohne Spur eines Wollflöckchens. Rippen fünf, 9–10 cm breit, abgerundet, durch scharfe Furchen voneinander getrennt. Areolen in den Kerben, einander sehr nahe, 0.5–1 cm entfernt, fast kreisrund, 3–4 mm lang, mit rotbräunlicher, spatter schwindender Wolle besetzt. Stachellos. Blüte noch nicht beobachtet. …" Our English translation of the German text is: "Body simple, hemispherical to almost spherical, 17 cm in diameter 14 cm in height, with sunken apex covered with sparse reddish-brown wool felt, of shiny olive-green color, without traces of woolly flecks. Ribs five, 9–10 cm wide, rounded, separated by sharp furrows. Areoles in the notches, very close to each other, 0.5–1 cm apart, almost circular, 3–4 mm long, with reddish brown wool, later lost. No spines. Blossom not yet observed ..."

Type Locality.—Hoock (2008) designated the Type Locality as Santa Rita (= Santa Rita del Rucio),

northeast of Entronque Huizache, San Luis Potosí. This taxon was originally reported from near Matehuala, and this locality was mentioned repeatedly in the early literature. However, Viereck (1939) suspected that the locality designation was an intentional deception to mislead commercial collectors. We examined one specimen from near Matehuala in the Herbario Nacional de Mexico (MEXU) collected by Helia Bravo Hollis (*HBH s.n.* 437). The specimen is partially flecked, which suggests that the original locality reports in the literature could be legitimate.

CHARACTER ANALYSIS

Epidermal Trichomes.—The var. *nudum* is ostensibly distinguished from other infraspecific taxa (except for some individuals of subsp. *quadricostatum*) by its green to dark blue-green stem lacking white, epidermal trichomes. Individuals of *A. myriostigma* can be classified, for the purpose of discussion, as nude (trichomes absent), semi-nude (patchy or sparse flecking), or uniformly flecked with a moderate to dense covering of trichomes. However, the classes in this polymorphism are not discrete and there is considerable variation and intermediacy among individual plants. Some plants are nude except for an occasional stray fleck here and there; others may have scattered patches of flecks on the stem, or the flecks may be confined to the edges of the ribs. Some plants have transverse bands of flecks alternating with bands of nude, green epidermis.

Polymorphic populations, comprised of flecked, semi-nude, and nude plants, occur in the Central Plateau as well as in the northern Jaumave Valley of Mexico. In the Sierra El Tablon, San Luis Potosí, Hoock (1993) observed uniformly flecked, semi-nude, and nude plants growing in proximity to one another, and he further reported that the nude and semi-nude plants were situated preferentially in partly shaded locations in dense shrub growth. Similar observations were made by Montanucci and Kleszewski (2019) in the northern Jaumave Valley near San Antonio, at an elevation of ca. 724 m. In both geographic areas, we observed densely flecked plants growing at sites fully exposed to the sun as well as in partial or transient shade.

Astrophytum myriostigma populations in the Central Plateau and the Jaumave Valley appear to be geographically isolated from one another, and in our opinion it is unlikely that they are connected by gene flow. In fact, the two geographical groups are recognized as members of different subspecies, the subsp. *quadricostatum* in the Jaumave Valley (Montanucci & Kleszewski 2019) and the subsp. *myriostigma* in the Central Plateau (Hoock 2008). We surmise, therefore, that the nude plants in these broadly separated populations may have evolved independently.

Hoock and Kleszewski (2004) reported that exclusively nude populations of *Astrophytum myriostigma* occur only at high elevations (NE of Santa Rita del Rucio at 1710 m and S of Entronque Huizache at 1750 m). At elevations ≤ 1700 m, the authors observed polymorphic populations comprised of flecked, semi-nude and nude plants. Near Entronque Huizache, one of us (KPK) observed that the relative numbers of nude plants in the population gradually increased with elevation. Although quantitative data were not collected, the observations suggest that the variation follows a clinal pattern correlated with altitude, with the frequency of nude plants increasing as altitude increases. If nude and flecked plants are viewed as genetically different populations, the polymorphic populations could represent a zone of hybridization (sensu lato) between them.

We compiled data on the relative frequencies of the trichome pattern classes and elevation from various localities in San Luis Potosí. The data revealed that from near Entronque Huizache northeastward to near Santa Rita del Rucio, polymorphic populations occur between 1320 and 1700 m elevation. Near Santa Rita del Rucio, nude plants were recorded at 1635 m, 1700 m, 1706 m, and 1800 m elevation, and one semi-nude plant was also recorded at 1700 m elevation. The latter record suggests that semi-nude plants may occur at low frequency in what was previously believed to be an exclusively nude population in the Sierra Noala at ≥1710 m elevation. Our data also show that nude and semi-nude plants represent relatively large percentages in the polymorphic populations occurring south of Santa Rita del Rucio. In pooled samples from La Pólvora north to San Carlos (1320 m to 1490 m), the following percentages were obtained: nude plants 9 (39.1%); semi-nude plants 6 (26.1 %); flecked plants 8 (34.8%). Near Entronque Huizache at ≤ 1400 m, the following plants were recorded: nude plants 1 (10%); semi-nude plants 7 (70%); flecked plants 2 (20%). Farther up the mountain

slope at (1400–1500 m), 5 plants were found (4 nude plants and 1 semi-nude), and at 1750 m, all plants observed by Hoock and Kleszewski (2004) were of the nude phenotype. These data, although meager, are consistent with our hypothesis of clinal variation correlated with altitude.

Farther south near Núñez, in the Sierra La Trinidad (1570–1650 m), the following percentages were obtained: nude plants 4 (22.2%); semi-nude plants 2 (11.1%), and flecked plants 12 (66.7%). At localities farther south and east, the percentages of nude and semi-nude plants were relatively low: Guadalcázar, 1600–1650 m (n = 17; semi-nude 5.8%); Estacíon Villar, 1500–1600 m (n = 16; nude and semi-nude 0%), Cerritos, 1075–1220 m (n = 12; semi-nude 8.3%); Puerta del Rio, 1145 m (n = 14; nude 7 %; semi-nude 7%). No nude or semi-nude plants were recorded from Las Tablas, 1000–1190 m (n = 39); El Sabrinas, 1062 m (n = 14) and near Ejido San Francisco, 908 m (n = 9).

Although exclusively nude populations occur at ≥ 1710 m elevation near Santa Rita del Rucio and Entronque Huizache, flecked plants were found at higher elevations farther south. We recorded flecked plants (n = 6) from 6 km E of Guadalcázar at 1726 m elevation. Also, one flecked plant was collected near El Realejo (22°39'52"N, -100°25'40"W) at 1920 m elevation (CGH 732, MEXU).

Hoock and Kleszewski (2004) reported that nude *A. myriostigma* growing in exposed locations often displayed a pale yellow, partly reddish discoloration. The authors attributed the development of olive to reddish color to the production of anthocyanin (Hoock & Kleszewski 2004, fig. 5; Hoock 2008:206). However, anthocyanin is absent in the Cactaceae; the red, magenta, and pink pigments produced in cacti are the nitrogen-containing betacyanins which have a different molecular structure from anthocyanin (Mabry & Dreiding 1968).

Gibson and Nobel (1986) reported that chlorophyll is susceptible to degeneration under stress from excessive exposure to photosynthetically active radiation (PAR). The degeneration of chlorophyll unmasks the carotenoid pigments in the chloroplasts, giving the plant a yellowish or pale reddish appearance, a process called "bleaching." A large proportion of the nude *Astrophytum myriostigma* that we observed growing in exposed locations showed stem discoloration consistent with chlorophyll degeneration. We assume that the discolored plants were stressed due to excessive exposure to PAR, and perhaps also water deficit. In the region between Santa Rita del Rucio to just south of Entronque Huizache, we classified nude and semi-nude plants as stressed or healthy using stem color as a criterion. In the polymorphic populations, 31 plants out of a total of 40 plants or 77.5% were classified as stressed. A slightly lower proportion was stressed in the nude populations above 1700 m elevation; 10 out of 16 plants or 62.5% showed significant discoloration.

Color of Wool on New Areoles.—Meyer (1912) described the new areoles in var. *nudum* as consisting of red-brown ("rotbraunem") wool, later turning grayish white and becoming sparse. Hoock (2008) described the wool on new areoles as having a rusty-red ("rostrot") color. There is variation in this character among plants assigned to var. *nudum*. While many nude plants conform to the original description, some have new wool with a more brownish hue, and rarely white. We examined and scored 30 nude plants from the following localities: near Entronque Huizache (11), near La Pólvora (3), near Nuñez (5), near Santa Rita del Rucio (7), and 4 plants without locality data. Seventeen plants (56%) had rust-red to red-brown wool on the new areoles; the other 13 plants (43%) had pale gray-brown to dark brown wool. The color of the wool on the new areoles of the nominotypical subspecies, subsp. *quadricostatum*, and subsp. *tulense* varies from yellowish white, pale pinkish brown, to dark blackish-brown. However, rust-red to red-brown wool has also been observed in some specimens of the nominotypical subspecies. Such specimens were recorded at several localities in San Luis Potosí: Buenavista, Guascama, and La Hincada. Hence the color of new wool is variable within and between infraspecific taxa, and only 56% of our sample of nude plants conforms to the original description.

Spacing of Areoles.—Meyer (1912) described the areoles on the rib edges as spaced between 5 and 10 mm apart in var. *nudum*. We noted that in small plants, the areoles tend to be widely spaced (ca. 10 mm), but as the plant grows, the areoles gradually become more closely positioned. In plants approaching 15 to 20 cm in stem height, the areoles may contact each other, or nearly so. In addition to this age-related (ontogenetic) variation, we found considerable individual variation. For example, we recorded two plants with a height of 17 cm, one

with areoles spaced about 10 mm apart, the other with areoles less than 5 mm apart. A third plant 16 cm tall had areoles mostly in contact with each other. Two smaller plants of similar height differed in the spacing of their areoles. One plant 7 cm tall had areoles 10 mm apart; the other plant was 8.5 cm tall and had areoles mostly in contact with each other. A maximum inter-areole distance of 15 to 20 mm was noted in a plant 6 cm in height and 10.5 cm in diameter. Overall, inter-areole distance shows considerable individual and ontogenetic variation and there is no apparent difference between var. *nudum* and the nominotypical subspecies.

Rudimentary Spines.—Klaus (1985), Hoock and Kleszewski (2004), and Hoock (2008) mentioned the presence of rudimentary spines (ca. 3 mm long) in var. *nudum* on areoles from which flowers had previously developed. Klaus (1985) mentioned that the spines are present in plants irrespective of their geographic location. Sadovský and Schütz (1979) considered the spines to be characteristic of nude plants and stated that the spines are "very durable." However, Hoock and Kleszewski (2004) stated that the spines are not securely attached and subject to loss by mechanical disturbance. In any case, not all nude plants bear rudimentary spines. We examined a series of nude plants (n=10) from the vicinity of Entronque Huizache, none of which had spines. Small spines were noted on a plant from a polymorphic population on a hill slope at 1458 m, ca. 8.8 km N of Crucero la Pólvora (jct. with Mex. Hwy. 80). Klaus (1985) reported rudimentary spines on broad-ribbed, nude plants but did not provide locality information. However, the plants are morphologically similar to those from near Núñez, San Luis Potosí. We also observed rudimentary spines on a flecked, cristate specimen and a densely flecked, columnar plant with eight ribs; both were imported plants without locality data. The variable presence of rudimentary spines on nude plants as well as on flecked plants diminishes their utility for diagnostic purposes. Nevertheless, the rudimentary spines are an interesting and inexplicable developmental phenomenon deserving further study.

Stem Morphology.—*Astrophytum myriostigma* shows variation in rib angle and rib number within and between local populations (Hoock 2008). We have also noted that some local populations are more variable than others, and in some cases a particular morphology may predominate at a given locality. For example, a large majority of plants from near Charco Blanco and Guadalcázar have a broad, depressed stem with obtuse, rounded ribs. A smaller proportion of the plants have a more moderate rib angle, but no plants have been found with acute ribs at those localities. We studied the stem morphology of polymorphic and nude populations from the following localities: Santa Rita del Rucio, habitats north and south of La Pólvora, east of Entronque Huizache, the mountains south of Entronque Huizache, and the mountains east of Núñez.

Hoock and Kleszewski (2004) compared the morphology of the plants from the mountains south of Entronque Huizache at 1750 m with those from the Sierra Noala (1710 m). The authors described the plants from the mountains south of Huizache as having a "compact form" with ribs that are broad and "less sharp-edged." Plants have a dark green epidermis and the stem diameter varies between 10 and 18 cm and stem height from 12 to 20 cm. The areoles are positioned about 1 cm apart. Adult plants from the Sierra Noala have a stem base that is broad, but the plant body is more "extended" (i.e. elevated), however, compact. The ribs are "sharp-edged" (i.e., acute rib angle), and the areoles are numerous and closely positioned. The stem is typically dark green to bluish green.

We reviewed the variation in stem morphology with additional samples from the two high elevation habitats as well as from intervening localities. We subjectively classified the rib angle as obtuse, intermediate, or acute. Our data are summarized as follows: mountains south of Entronque Huizache, at 1750 m (obtuse 1, intermediate 1, acute 2); mountains south of Entronque Huizache, ≤ 1400 m (obtuse 2, intermediate 12, acute 2); 1 km E Entronque Huizache, 1448 m (obtuse 1, intermediate 9); La Pólvora, 1348 m (obtuse 1, intermediate 9, acute 5); 8.8 km N Crucero La Pólvora, 1458 m (obtuse 1, intermediate 1, acute 2), Sierra Noala, 1710 m (intermediate 9, acute 4). These findings suggest that the range of variation in rib morphology among plants from the two high elevation habitats and intervening localities is more similar than previously reported. The rib angle varies from acute to obtuse, with an intermediate angle prevalent among local populations. The rib profile is typically angular and less frequently rounded. We also observed that young seedlings found in habitat usually have narrow or "sharp" ribs (acute rib angle). We assume that as the plants grow, they gradually

develop broader ribs. This assumption is supported by our observations. We crossed two broad-ribbed nude plants from the Huizache area and produced 77 seedlings, all of which had sharp ribs (acute rib angle) and a mean stem diameter of 25 mm. Also, the rib angle appears to be broadening in larger-sized seedlings. As previously mentioned (see above), we also determined that inter-areole distance varies ontogenetically; small (i.e., young) plants usually have widely spaced areoles (ca. 1 cm apart), whereas larger (older) plants have areoles that are more closely positioned, or in contact. However, there is also considerable individual variation not correlated with size.

Farther south near Núñez in the Sierra La Trinidad (1570–1650 m), nude, semi-nude and flecked plants show little variation in stem morphology; nearly all plants have a broad, depressed stem with obtuse ribs and a rib profile that is either broadly angular or rounded. The largest plants have a stem diameter of ca. 25 cm. A total of 16 plants were recorded, nine with broadly angular ribs and seven with broadly rounded ribs. The variation in rib angle among plants from the two regions is depicted in Figure 1.

Perianth Diameter.—Data for the flower of var. *nudum* were not available from Meyer's (1912) original description. Subsequently, Meyer (1913) observed flowering and stated that the flower differs little from that of the type species. Hoock (2008) tabulated and compared the perianth diameter for all *Astrophytum* taxa. His data indicated that maximum perianth diameter is largest in the nominotypical subspecies (76 mm) and smallest in subsp. *tulense* (50 mm) with var. *nudum* having an intermediate diameter (67 mm). We calculated the statistics of dispersion (sample mean ± 95% confidence interval and observed limits) for the three taxa as follows: subspecies *myriostigma* $\bar{x}$ = 62.9 mm ± 3.15 (46–76 mm); var. *nudum* $\bar{x}$ = 54.0 mm ± 2.48 (40–70 mm); subsp. *tulense* $\bar{x}$ = 38.0 mm ± 3.05 (25–50 mm); sample sizes are n = 24, 33, and 21 respectively. The differences among the sample means are statistically significant at $p \leq 0.05\%$.

Number of Stigma Lobes.—Hoock (2008) reported the maximum number and observed limits of stigma lobes as follows: the subsp. *myriostigma* 9 (5–9), subsp. *tulense* 8 (4–8), and var. *nudum* 7 (5–7). We calculated the statistics of dispersion (sample mean ± 95% confidence interval and observed limits) for the three taxa as follows: the subsp. *myriostigma* $\bar{x}$ = 6.8 ± 0.49 (5–9); var. *nudum* $\bar{x}$ = 5.6 ± 0.63 (4–8); subsp. *tulense* $\bar{x}$ = 5.9 ± 0.26 (5–7); sample sizes are n = 21, 14, and 30 respectively. The differences among sample means are not statistically significant ($p \geq 0.05\%$).

DISCUSSION AND CONCLUSIONS

The Adaptive Significance of Trichomes.—Experimental studies have demonstrated that epidermal trichomes increase reflectance and shading, thereby moderating daytime surface temperatures of the cactus stem (Nobel 1978, 1988). Densely flecked, well-hydrated individuals of *Astrophytum myriostigma* were observed growing in locations exposed to full sunlight without any indication of damage to the epidermis, except in cases in which the trichomes had been mechanically lost from portions of the epidermis. Flecked plants were also observed growing in partial or transient shade. Nude and semi-nude plants were usually found growing in sparse to moderate shade beneath xerophytic shrubs, *Hechtia*, *Agave*, etc.

Nude plants may be more shade tolerant than flecked plants because the absence of epidermal trichomes eliminates reflectance and maximizes the interception and absorption of filtered sunlight reaching the ground below shrubs. Light gradients are ubiquitous in the desert scrub habitats of *A. myriostigma,* and presumably, nude plants and flecked plants cannot perform optimally over the entire light gradient due to differences in morphological and physiological adaptations at opposite ends of the gradient. Possibly, the nude, semi-nude, and flecked phenotypes of *A. myriostigma* maximize the utilization of habitat for the species by occupying different portions of the available light gradient.

Moderately shaded sites under *Hechtia* or *Agave* appear to be the optimal microhabitat for nude *Astrophytum myriostigma*. This inference is supported by the following observations. In one case, three nude *A. myriostigma* were growing from a limestone crevice away from a colony of *Hechtia*; all three plants were pale yellowish-green with a reddish suffusion, the smallest plant being severely bleached. But nearby, two large *A. myriostigma* were sequestered in moderate shade under the *Hechtia* plants; they were dark green in color. In a

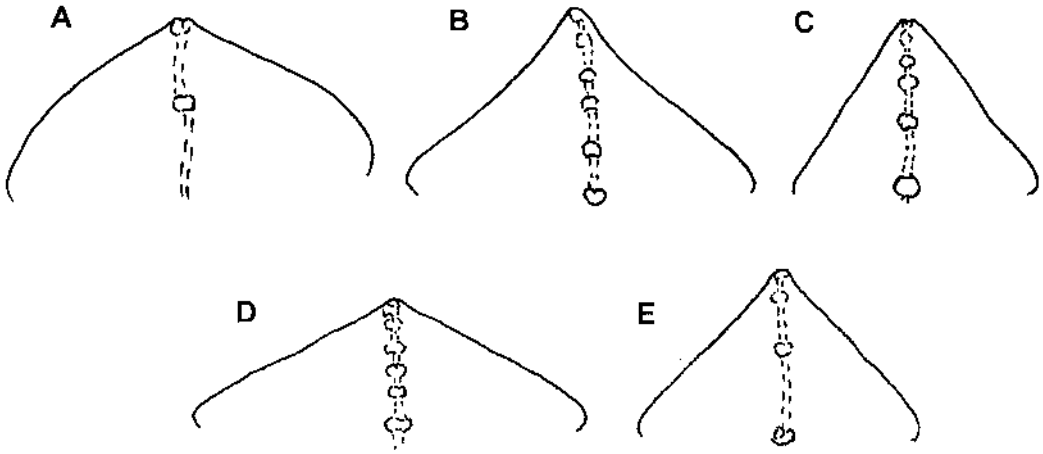

Fig. 1. Variation in rib angle and profile in *Astrophytum myriostigma* from region encompassing Santa Rita del Rucio to south of Entronque Huizache (A–C) and from Sierra La Trinidad (D–E), San Luis Potosí, Mexico.

second case, two nude plants near a clump of *Hechtia* were exposed to partial or full sunlight and were pale green with reddish suffusion along the rib edges; a third plant was in a more shaded position closer to the base of the *Hechtia* plant and it was bright green in color. A fourth plant beneath the base of a *Hechtia* plant received filtered morning sunlight, but considerable shade during the afternoon; it was dark green in color. Despite the benefit for nude *A. myriostigma* growing in protected locations, there may be a reproductive disadvantage as the plants may not be as conspicuous to pollinators as they could be in more exposed locations. Thus, the optimal growing locations for nude and semi-nude plants may be determined by a balance achieved between opposing selective pressures.

Two vegetation types occur within the distributional area of *Astrophytum myriostigma*. The microphilous desert scrub (matorral micrófilo) is composed of small leaf elements such as *Larrea tridentata, Flourensia cernua*, *Prosopis glandulosa,* etc., and it typically occurs in plains and valleys from 250 m to ca. 2000 m. The rosette desert scrub (matorral rosetófilo) is characterized by plants with a rosette growth habit including *Hechtia*, *Agave*, *Yucca*, *Dasylirion*, and *Nolina,* etc., and occupies alluvial fans, foothills and mountain slope areas from 500 m to 2600 m elevation (González-M. 2004; Medellín-L.1982). There is an obvious close association between *Astrophytum myriostigma* and the rosette-type plants. The colonies of *Hechtia* and *Agave* are especially important nurse plants for seedlings of *A. myriostigma* (Jurado et al. 2013 & references therein). Small seedlings are usually sequestered in shaded locations within stands of *Hechtia*, often near the margins of the colonies.

Hoock and Kleszewski (2004) observed that adult plants of nude *Astrophytum myriostigma* were preferentially located directly beside mats of *Hechtia*, and many in these locations were stressed. We do not believe that the stressed plants in exposed, "free-standing" locations near the mats of *Hechtia* grew from seedlings established in such open sites. Seedling survival in exposed locations seems highly improbable. We assume that the seedlings were established within colonies of *Hechtia*, perhaps near the colony border. In some cases, as the nude *A. myriostigma* grew, their stems eventually emerged from the shade provided by the *Hechtia*. In other cases, the *Hechtia* plants may have died back near the colony border, leaving the nude *A. myriostigma* completely exposed to full sunlight. Limestone slabs and outcrops often define the borders of the colonies, and *Hechtia* plants situated along these margins may be growing in relatively shallow soil and may be susceptible to periodic die offs during extended periods of drought. We observed dead *Hechtia* plants along the borders of the colonies more frequently than within the central areas of the colonies.

Astrophytum species occur in arid regions that typically experience two precipitation maxima per year (Lux & Kopunec 1992). During periods of rainfall, water uptake occurs by the root system of the plant. Under drought conditions the root system ceases to function, but water uptake is still possible by another mechanism. In arid habitats, the large differences between day and nighttime temperatures cause water vapor to condense on the cactus stem. In *Astrophytum myriostigma* subsp. *tulense*, the stem typically has a dense covering of epidermal trichomes. Microscopic examination of the trichomes revealed a pitted and porous structure that is easily wetted, suggesting its ability to retain water from the gaseous phase by condensation and adsorption (Lux & Kopunec 1992). The authors calculated through experiments that in subsp. *tulense* gaseous phase water uptake was 10 times greater than in nude *A. myriostigma*. But in the liquid phase, water uptake was greater in nude plants compared to subsp. *tulense* probably due to a greater density of stomata per unit area of the nude epidermis. But how liquid phase water uptake may be adaptive in the high elevation habitat of the nude plants is unclear.

The density of epidermal trichomes varies ontogenetically among plants in the nude and polymorphic populations. We crossed two nude plants from the Huizache region and observed that all of the seedlings were initially densely flecked. A different result was obtained when two other nude plants were crossed; the seedlings were initially polymorphic for presence of trichomes. The seedlings from these first two crosses were not raised to larger-sized plants, although we assumed that at least some of the seedlings in the first case would lose their trichomes. Subsequently, we crossed two nude plants (from a polymorphic population) and obtained 71 seeds which germinated, producing seedlings all of which were flecked. We further observed, however, that as the seedlings grew the trichomes gradually became sparse and eventually were lost in some young plants, but not in others. The differences (complete or partial loss or retention of trichomes) became evident at a stem diameter of ca. 18–20 mm. We infer that the initial presence of trichomes in small seedlings (3–5 mm in diameter) has two advantages: (i) during the first few months of growth, the seedling epidermis is tender and vulnerable to burning from direct sunlight; the trichomes provide additional protection in the partially shaded environment created by the canopy of *Hechtia* plants, and (ii) seedling survival during prolonged periods of water deficit probably depends on the ability to obtain water by condensation and adsorption. As previously mentioned, epidermal trichomes are critically important for this function.

We observed that a large proportion of the plants in the nude and polymorphic populations of *Astrophytum myriostigma* were stressed as evidenced by chlorophyll degeneration. These observations support our contention that the nude phenotype cannot perform optimally over the entire light gradient. The extent to which chlorophyll loss affects reproductive success in *A. myriostigma* is unclear. Some of the stressed plants appeared capable of reproduction as indicated by the presence of dried floral remnants. Whether stressed plants recover following the onset of rains and reduced temperatures has not been determined. However, several of the smaller plants (ca. 10.5 cm in diameter) were so adversely affected by chlorophyll loss, that recovery seemed unlikely. Water deficit and excessive exposure to full sunlight due to deterioration of the rosette canopy may be the proximate factors of stress. In turn, these events may indicate the development of an increasingly arid climate in the central and northern regions of Mexico. It is tempting to speculate that perhaps the nude populations of *A. myriostigma* occupying mountainous areas above 1700 m in the Huizache region are Pleistocene relics that previously flourished during relatively more mesic climatic periods.

The apparent absence or low-frequency occurrence of flecked and semi-nude plants at the two northern high elevation localities (near Santa Rita del Rucio and near Entronque Huizache) remains unexplained. Insufficient sampling may have failed to detect flecked and semi-nude plants, but in any case, it is reasonable to assume that there is strong selection against flecked plants at these locations. Further field work is needed to have a better concept of the distributional limits of the nude populations. Several north-south mountain ranges potentially comprise their distribution; these might include the Sierra El Picacho de Gallo (west of La Pólvora), Sierra El Coro (south of Santa Rita del Rucio), Sierra El Peñascudo (north of Santa Rita del Rucio), Sierra de Catorce (west of Matehuala), and Sierra El Azul (east of Matehuala).

Kleszewski (1994) observed semi-nude plants growing with flecked plants near Cerritos. He noticed that

some plants growing in protective vegetation were nude but had developed trichomes on the portion of the stem exposed to sunlight. His observation suggests that the presence or absence of epidermal trichomes can be environmentally induced depending on the intensity of sunlight. Other populations in the southern distribution of *A. myriostigma* may have such "facultative nudes," but we have not determined which are genetically based and which are not, among these populations. Such an assessment requires careful examination of the plants in habitat because mechanical disturbance can potentially remove flecks of trichomes. Rearing experiments under different light conditions should follow initial field studies. The plants from high elevations near Entronque Huizache and Santa Rita del Rucio are genetically determined nudes. They remain nude in exposed locations in habitat (Kleszewski 1994), and they do not develop flecks on the new growth when grown under bright sunlight in culture.

Taxonomic Conclusions.—A perusal of the taxonomic literature of the Cactaceae, indicates that use of the term "variety" as conceptualized by Du Reitz (1930) is virtually nonexistent; instead, it has been used in the sense of a "geographical variety" or "subspecies." With regard to the treatment of *Astrophytum myriostigma* var. *nudum*, two options seem to be available, namely the recognition of this taxon as a "subspecies" or its relegation to a "forma."

Application of the subspecies category requires that the taxon is diagnosable on the basis of a suite of discrete or nearly discrete characters, and that it occupies a cohesive, definable geographical distribution. Regarding the geographical distribution, Hoock and Kleszewski (2004) identified two high elevation (≥ 1700 m) populations of nude plants; the two areas are geographically restricted and widely separated. Although we have suggested other areas of potential occurrence, the fact is that the geographical distribution of exclusively nude populations remains largely unknown. Polymorphic populations (comprised of nude, semi-nude, and flecked plants) occur in adjacent, intervening areas between the two nude populations, generally at elevations below 1700 m. This polymorphism, however, is considered non-discrete as there is considerable variation and intermediacy among plants. In the polymorphic populations, the frequency of nude plants also appears to vary as a cline correlated with elevation.

We analyzed the variation in the characters used by Meyer (1912) in his original description of var. *nudum*. Color of wool on new areoles is too variable to be of diagnostic value. Inter-areole distance also shows considerable variation, both ontogenetic and inter-locality, and is not useful. The presence of rudimentary spines is variable among nude plants and in some cases these spines are also present on flecked plants. Both rib number and rib angle are variable and have no diagnostic value. The mean number of stigma lobes is not statistically different among the infraspecific taxa. However, mean perianth diameter differs significantly ($p \leq 0.05\%$) between subsp. *myriostigma*, and var. *nudum*, but there is considerable overlap in observed limits (46–76 mm) vs. (40–70 mm) respectively, thus limiting the diagnostic value of this character. Using perianth diameter, the two taxa are not likely to be distinguished on the basis of a single observation. In sum, our comparative morphological study of var. *nudum* revealed that the characters mentioned in the original description, including the absence of epidermal trichomes, are not useful for diagnostic purposes. Given the lack of a suite of discrete or nearly discrete, diagnostic characters, and given that exclusively nude populations do not have a definable distribution, we believe that the nude phenotype should be treated taxonomically as a "forma" rather than as a "subspecies."

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