

THE BIOGEOGRAPHY, ECOLOGY, AND TAXONOMY OF *LOPHOPHORA* (CACTACEAE)

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Anderson, E. F. (Department of Biology, Whitman College, Walla Walla, Washington). The biogeography, ecology, and taxonomy of *Lophophora* (Cactaceae). *Brittonia* **21**: 299–310. 1969.—*Lophophora*, commonly called peyote, has an extensive range within the Chihuahuan Desert of Texas and Mexico. Selected sites were studied and growth characteristics, soils, associated plants, and climate are described. The genus consists of two species, *L. williamsii* and *L. diffusa*. The former is both wide-ranging and highly variable morphologically, whereas the latter consists of a single, fairly small population restricted to an area in the state of Querétaro. Synonymy and types are discussed, and a key to the species is included with the descriptions.

The genus *Lophophora*, commonly called peyote or peyotl, has received much attention by both scientist and amateur because of its long history of use by Indians and because of its hallucination-producing alkaloid mescaline. However, serious botanical investigations of this wide-ranging and highly variable cactus have been relatively few in number. Coulter (1894) was the first person who attempted a systematic study of the genus. Rouhier (1927), in dealing with all aspects of the plant, included biogeographical and systematic sections in his work. Croizat (1943–1945) published a lengthy but superficial study of *Lophophora* in which few new data were used. Britton & Rose (1919–1923) and Backeberg (1961), in their cactus monographs, dealt with *Lophophora* using information compiled by previous workers. The most recent study by Bravo (1967) utilized considerable field data. The taxonomic conclusions presented in this paper are based on earlier research (Anderson, 1961), the information in this paper, and other research now nearing completion at Whitman College and the University of Oklahoma.

BIOGEOGRAPHY AND ECOLOGY

Field studies of *Lophophora* were begun in 1957, and seven trips were made to Texas and Mexico. Other significant data regarding geographical distribution were obtained from herbarium specimens. Sites have been visited throughout the geographical range of the genus, and plants have been collected for laboratory, greenhouse, and herbarium use. Of the locations reported earlier in the literature or on herbarium specimens, only two were visited that failed to yield peyote—Big Bend National Park and the region along the Pecos River in Texas. *Lophophora* was collected in Big Bend National Park by Barton C. Warnock in 1961, but my search of the locality in 1967 was unsuccessful. Warnock (oral communication) stated that Indians might have been responsible for transporting a relatively small number of plants to the area for cultivation. Although it is impossible to know whether *Lophophora* occurs naturally within the Park or was introduced by Indians in connection with their religious ceremonies, the influence of man with regard to modifying the normal distribution of this genus cannot be overlooked. There is considerable evidence, for example, that in several areas of both Texas and Mexico man has greatly reduced the number of *Lophophora* individuals or has altered the life forms of the plants by repeatedly harvesting the tops.

Extensive studies were not possible at every collection site, so ten were selected to represent *Lophophora* localities throughout its natural range. These sites (Fig. 1)

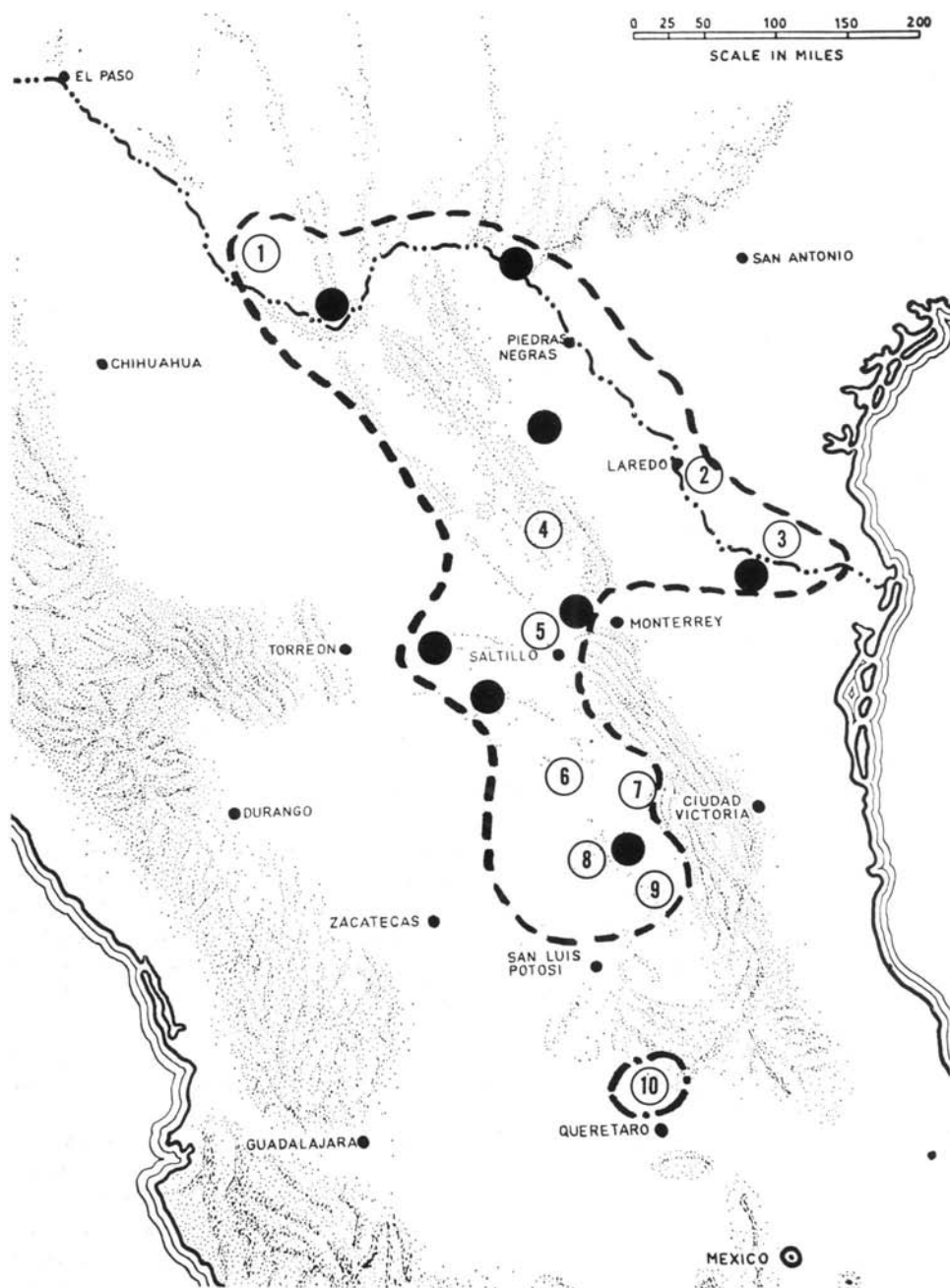


FIG. 1. Distribution of *Lophophora* (dashed line) showing major collection sites (black dots and circled numbers): (1) Shafter, Texas. (2) Mirando City, Texas. (3) Rio Grande City, Texas. (4) Monclova, Coahuila. (5) Saltillo, Coahuila. (6) Matehuala, San Luis Potosí. (7) Miquihuana, Tamaulipas. (8) El Huizache, San Luis Potosí. (9) Ciudad del Maíz, San Luis Potosí. (10) Vizarrón, Querétaro.

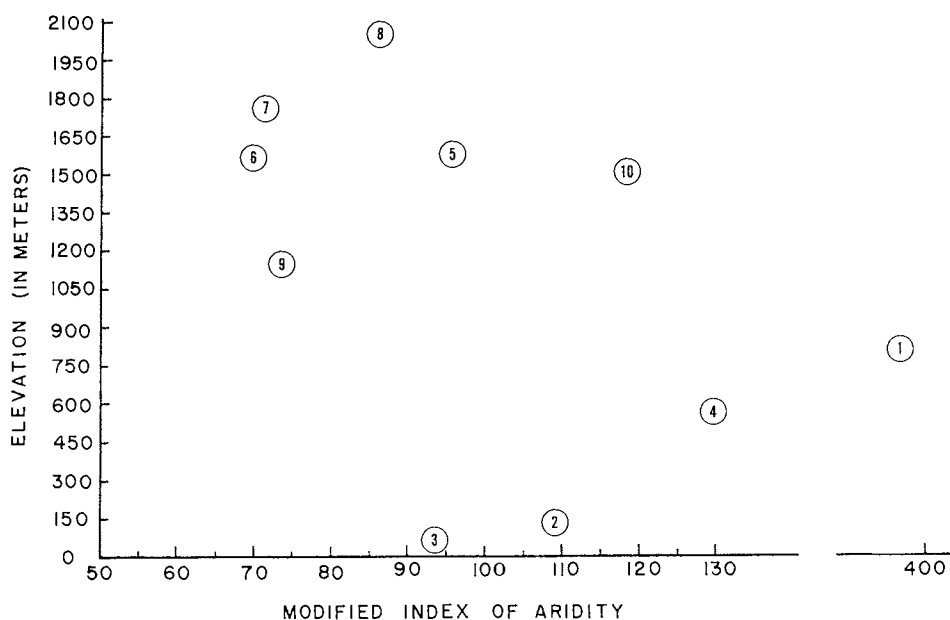


FIG. 2. Relationship of modified index of aridity to elevation. Representative localities are numbered as in Fig. 1.

not only include the geographical extremes but also represent various locations along the Rio Grande (sites 2, 3), in the low hot basins of northern Mexico (site 4), in the intermediate areas around Saltillo (site 5), on the higher central plateau (sites 6–9), and the somewhat unique zone in Querétaro (site 10).

Distribution. *Lophophora* has a latitudinal distribution of about 1200 km from 20°54' to 29°47' North Latitude. It is found along the Rio Grande drainage basin and southward into the high central plateau of northern Mexico lying between the Sierra Madre Oriental and Sierra Madre Occidental. Generally, the elevation of the localities increases to the southward. Those along the Rio Grande near Reynosa, Tamaulipas, are less than 50 m, while localities in San Luis Potosí exceed 1800 m in elevation.

Ecologists describe this large desert area of Texas and northern Mexico as the Chihuahuan Desert (Jaeger, 1957; Shelford, 1963; Shreve & Wiggins, 1964). However, within this region there is considerable variation in both topography and vegetation, which has prompted some workers (Shreve, 1939; Muller, 1947; Rzedowski, 1956, 1965) to create several subdivisions. Unfortunately, these smaller regions have not received the same names, but Rzedowski (1965) published a helpful comparative summary. *Lophophora* occurs primarily in two vegetation zones characterized by Rzedowski (1965) as (a) the microphyllous desert scrub having shrubs with small leaves or leaflets such as *Larrea divaricata*, *Prosopis juliflora*, and *Flourensia cernua*; and (b) the "rosettophyllous" desert scrub with many plants bearing rosettes of leaves such as *Agave lecheguilla* and *Yucca spp.* Probably neither of these vegetation types can be considered to be climax communities nor even formations because there is continuous mixing of the two life forms. Muller's (1947) general term "Chihuahuan Desert Shrub," therefore, which encompasses both Rzedowski groups, probably should be preferred.

The southernmost location of *Lophophora* in Querétaro is apparently well isolated from the other populations and is outside the region normally included within the Chihuahuan Desert. As shown by Rzedowski & Medellín L. (1958), however, the distribution of *Larrea* is similar to that of *Lophophora*; both genera terminate just north of the city of San Luis Potosí and then again occur together in the dry valleys of central Querétaro. Three factors are apparently responsible for this discontinuous distribution: (a) extensive saline flats in the Rio Verde region, (b) formidable mountains (the Sierra Gorda extension of the Sierra Madre Oriental), and (c) high elevation even in the broad valleys. Nevertheless, the dry Querétaro region possesses many plants similar to the Chihuahuan Desert Shrub to the north and probably should be included in it.

General characteristics of *Lophophora* populations. Peyote is not a rare cactus and in many localities is quite abundant, often forming clumps under most sizable shrubs. Caespitose individuals or even large clones are common, although single-headed plants are present in each locality as well. Injury or harvesting by man induces the formation of many stems from a single rootstock. Single clones more than 1.5 m across have been observed in San Luis Potosí, for example.

Although it is not uncommon to encounter it growing in full sunlight, *Lophophora* tends to grow under associated shrubs such as *Larrea* and *Prosopis* or in the partial shade of plants such as *Agave lecheguilla*, *Jatropha dioica*, and *Euphorbia anti-syphilitica*.

Lophophora has been observed growing in silty limestone flood plains or wedged between rocks on nearly vertical limestone cliffs, but it occurs most frequently on low limestone hills and plains composed of broken and flaky limestone.

Reproduction is primarily sexual, and often young plants can be found growing in or around mature ones. Asexual reproduction can also occur by the formation of new stems from old. These can become detached (by man, animals, wind, water, etc.), and sometimes they will root during the rainy season.

The age and size of the plant are two factors that apparently determine the number of ribs on plants of the northern population. Young plants normally have five, but mature individuals may have 5–14 or occasionally none at all. This range of rib variation can occur within the same clump, so apparently it is a growth response to various factors. *Lophophora*, especially the large northern population, exhibits a wide range of environmental morphological variations; hence, systematic conclusions based on these characters alone are hazardous.

Soils. All soils tested were limestone in origin, with a basic pH (7.9–8.3). These soils can also be characterized as having more than 150 ppm Ca, at least 6 ppm Mg, strong carbonates, and no more than trace amounts of NH_3 . The soils tested negatively for Fe, Cl, SO_4 , Mn, and Al. Four sites tested positively for NO_3 and six showed NO_2 to be present. Phosphorus and potassium varied somewhat throughout the range; no more than 3 ppm P were present at any site. Two localities, Saltillo and Matehuala, showed considerable K, whereas the other sites showed either trace amounts or none at all. Soil tests from the southernmost locality in Querétaro were not different from those of more northern soils.

Associated plants. *Lophophora* occurs in diverse habitats, and only *Larrea divaricata* is found in more than 75% of the peyote sites in which associated plants were sampled and identified. Other associated plants (and their percentage frequency) are *Jatropha dioica* (70%), *Echinocereus spp.* (70%), *Opuntia leptocaulis* (70%), *Prosopis juliflora* (70%), *Agave lecheguilla* (50%), *Echinocactus horizonthalonius* (50%), *Mammillaria spp.* (50%), *Flourensia cernua* (50%), *Acacia spp.* (40%), *Condalia spinosa* (40%), *Coryphantha spp.* (40%), *Neolloydia spp.* (40%),

Yucca filifera (40%), and *Hamatocactus spp.* (40%). *Euphorbia antisiphilitica*, *Koeberlinia spinosa*, and *Coldenia canescens* occurred in less than 40% of the sample sites. Not all perennial plants have been cited, but this information indicates that *Lophophora* occurs over a broad spectrum of vegetation types within the Chihuahuan Desert.

Climatic data and "I" index. Although many parts of Mexico lack adequate weather records, the recent publication of Soto Mora & Jáuregui O. (1965) provides considerable information about the climatic conditions in the arid zones of Mexico. They have devised an "index of aridity" for most weather stations of Mexico, and an analysis of those stations near the major collection sites of *Lophophora* shows that this genus can tolerate a wide range of climatic conditions. Precipitation reaches 175.5–556.9 mm/year, maximum temperature 29.1–40.2° C, and minimum temperature 1.9–10.2° C. Garcia (1965) noted that within the area where *Lophophora* occurs, the predominant rains fall in the late spring and early summer. However, she also stated (1964) that areas having more than 5% winter rain but less than 36% should be classified as intermediate rather than strictly summer rainfall regions. At least half of the stations near *Lophophora* sites would be intermediate in this respect.

The modified index of aridity (I), as described by Soto Mora & Jáuregui O. (1965), is an indication of the relationships of temperature and precipitation. *Lophophora* sites exhibit a wide index of aridity: 64.0–394.0. The index of aridity apparently is also related to elevation (Fig. 2). Sites 1–3 have an "I" reading of more than 100, but are less than 900 m high. Locations 5–9, on the other hand, exceed 1000 m elevation but have an "I" reading of less than 100. The two exceptions are location 3 (Rio Grande City-Reynosa), which has an "I" reading of only 93. This may be partially a result of its proximity to the coast. The other locality, site 10 (Vizarrón-Toliman, Querétaro), is at a relatively high elevation (ca. 1500 m), but the "I" reading is over 115. This southernmost site, therefore, is highly arid despite the elevation. The greater aridity may be in part the result of fairly high mountains in close proximity to the valley, thus causing a more intensified rain shadow than would be encountered in a less severe topographical situation.

TAXONOMY

LOPHOPHORA Coulter, Contr. U. S. Nat. Herb. **3**: 131. 1894.

TYPE species: *L. williamsii* (Lemaire) Coulter.

Plants low, with long fusiform roots. Stems solitary or in clusters arising from the same root system, usually rounded above, depressed in the centers; blue-green, yellow-green, and occasionally appearing reddish green; 2–7 cm high, 4–12 cm in diam. Areoles usually linearly arranged along ribs or at the apices of humplike tubercles or podaria, each bearing a tuft of soft, yellowish or whitish trichomes from which the flowers arise, 8–15 mm apart, 1–5 mm in diam; spines absent except in seedlings and then only rudimentary. Flower 1–2.2 cm in diam, 1–2.4 cm long; outer perianth segments with greenish midribs and greenish pink or whitish margins, the largest ones elliptical, 3–12 mm long, 1–3 mm broad, mucronate, marginally minutely ciliate distally; inner perianth segments pink, white, or rarely yellowish white, sometimes with greenish midribs, the largest ones elliptical, 8–22 mm long, 2–4 mm broad, mucronate or occasionally attenuate, margins ciliate or entire; filaments white; anthers yellow; pollen $\pm$ spheroidal, 0–18 colpate, 14.9–63 μ diam; style white, 5–14 mm long; stigmas 4–8 (rarely 3), 1–3 mm long, white though occasionally pinkish; ovary naked. Fruit pinkish red and fleshy at first, becoming brownish white and dry at maturity, naked, clavate, 15–20 mm long, 2–3.5 mm in diam, with the umbilicus large or the perianth parts persistent, emerging rapidly

from within the trichomes at maturity. Seeds black, tuberculate (verrucose), pyriform, 1–1.5 mm long, 1 mm broad; hilum large and flattened; cotyledons coalescent.

Flowering from March through September. Fruits mature 9–12 months after fertilization.

Widely distributed on limestone soils of low hills and flatlands in the Chihuahuan Desert of Texas, northern, and central Mexico from 50 to 1800 m elevation.

Lophophora is derived from two Greek words meaning "I bear crest," referring to the "crests" of trichomes borne on each tubercle. Common names are peyote, piote, piotl, peyotl, peote, challote, mescal, raíz diabolica, dry whiskey, dumpling cactus, and tuna de tierra. There are also numerous names in the Indian languages.

Key to the Species

Plants blue-green, usually with well-defined ribs and furrows; tufts of trichomes usually equally spaced on the ribs; flowers pinkish or rarely whitish; not in Querétaro.

1. *L. williamsii*.

Plants yellow-green, usually lacking well-defined ribs and furrows; tufts of trichomes usually unequally spaced on prominent podaria; flowers commonly whitish to yellowish white; Querétaro.

2. *L. diffusa*.

1. *L. WILLIAMSI* (Lemaire) Coulter, Contr. U. S. Nat. Herb. **3**: 131. 1894.

Echinocactus williamsii Lemaire ex Salm-Dyck in Otto & Dietr., Allgem. Gartenzeit. **13**: 385. 1845.

Anhalonium williamsii Rümpler in Förster, Handb. Cact. ed. 2. 233. 1886.

Anhalonium lewinii Hennings, Gartenflora **37**: 410. 1888.

Mammillaria williamsii Coulter, Contr. U. S. Nat. Herb. **2**: 129. 1891.

Lophophora williamsii Coulter, Contr. U. S. Nat. Herb. **3**: 131. 1894.

Ariocarpus williamsii Voss, Vilmorin Illustrierte Blumengärtneri 368. 1894.

Echinocactus lewinii K. Schumann, Nat. Pflanzenfam. **3**. Abt. 6a: 173. 1894.

Lophophora williamsii var. *lewinii* Coulter, Contr. U. S. Nat. Herb. **3**: 131. 1894.

Lophophora lewinii Rusby, Bull. Pharmacy **8**: 306. 1894.

Mammillaria lewinii Karsten, Flora Deutsch. ed. 2. **2**: 457. 1895.

Echinocactus williamsii var. *lutea* Rouhier, Trav. Labouret Mat. Med. Pharm. Galén **17** (pt. 5): 65. 1926.

Lophophora echinata var. *lutea* Croizat, Desert Plant Life **16**: 44. 1944.

Lophophora echinata Croizat, Desert Plant Life **16**: 43. 1944.

Lophophora williamsii var. *lutea* Soulaire, Cactus et Médecine 121. 1947.

Lophophora lutea Backeberg, Die Cactaceae **5**: 2901. 1961.

Lophophora williamsii var. *echinata* H. Bravo, Cact. Sucul. Mex. **12**(1): 12. 1967.

NEOTYPE: MEXICO: San Luis Potosí: on the flat lands NE of the junction of Mex. Hwys. 57 and 80 near El Huizache, 3 Jul 1958, *E. F. Anderson* 1079 (POM!).

Plants somewhat firm, blue-green and occasionally reddish green, often $\pm$ flattened on top, 2–6 cm high, 4–11 cm in diam; ribs and furrows usually present and well defined, 4–14 but highly variable and sometimes forming $\pm$ elevated podaria; areoles 0.9–1.5 cm apart, 2–4 mm in diam; flower 1–2.2 cm in diam, 1–2.4 cm long; outer perianth segments 2–3 mm broad; inner perianth segments 2.5–4 mm broad, usually pink; pollen 0–18 colpiate, 14.9–63.4 μ in diam (Fig. 3).

Occurring in Texas S of Shafter, possibly in Big Bend National Park and at the mouth of the Pecos River, and from Laredo SE to McAllen. In Mexico in the state of Coahuila S from the border, W and N of Saltillo, extending E and S into Nuevo León, Tamaulipas, northeastern Zacatecas, and San Luis Potosí.

The specific epithet is derived from the proper noun, but it is not known to whom the plant was dedicated by Lemaire.

Representative specimens. UNITED STATES: TEXAS: Presidio County: E of Shafter, *Warnock s.n.* (SRSC); S of Shafter, *Boke s.n.* (POM), *Anderson 925, 2308* (POM). Brewster County: Chilicotal Mt., Big Bend National Park, *Warnock 18498* (SRSC). Val Verde County:

mouth of the Pecos River, *W. M. Lloyd s.n.* (US). Webb County: Laredo, *Weinberg 25477* (NY), *Shiner s.n.* (US), *MacKensee s.n.* (US). Starr County: N of Rio Grande City, *Clover 1879* (DS), *Albert s.n.* (POM), *Anderson 1127* (POM); E of Rio Grande City, *Rose 24374* (US), *Anderson 1129* (POM); N of Escobares, *Anderson 947, 1126* (POM). Jim Hogg County: S of Mirando City, *Anderson 948, 1123, 2307* (POM). MEXICO: TAMAULIPAS: S of Reynosa, *Anderson 1134* (POM); W of La Perdida, *Anderson 2275* (POM); W of Miquihuana, *Anderson 1726* (POM). COAHUILA: N of Saltillo, *Anderson 1063, 2306* (POM); W of Saltillo, *Anderson 1238, 2305* (POM); E of Saltillo, *Anderson 1250, 2304* (POM); Cerro del Zapatero, *Purpus s.n.* (US); SW of Parras, *Anderson 1248* (POM). NUEVO LEÓN: N of Matehuala, *Anderson 1228, 2303* (POM). SAN LUIS POTOSÍ: oeste de Nuñez, *Rzedowski 5796* (ZDSLP); entronque carreteras 57 y 80, *A. Gomez G. 55* (ZDSLP); El Huizache junction, *Anderson 1079* (GH, K, MO, NY, POM, US), *961, 1256, 1757, 2282* (POM); W of El Huizache junction, *Anderson 1211* (POM); E of El Huizache, *Bratz s.n.* (POM), *Anderson 1215* (POM); near Las Tablas, *Anderson 1752* (POM); W of Ciudad del Maíz, *Anderson 1182, 1615, 2280* (POM). ZACATECAS: northern Zacatecas [without precise locality], *F. E. Lloyd 52* (NY, US).

DISCUSSION OF SYNONYMS

Echinocactus williamsii Lemaire ex Salm-Dyck in Otto & Dietr., Allgem. Gartenzeit. **13**: 385. 1845.

Anhalonium williamsii Rümpler in Förster, Handb. Cact. ed. 2. 233. 1886.

Mamillaria williamsii Coulter, Contr. U. S. Nat. Herb. **2**: 129. 1891.

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Lophophora williamsii Coulter, Contr. U. S. Nat. Herb. **3**: 131. 1894.

The original epithet was attributed to Lemaire by Salm-Dyck, who stated that the original name appeared in Cels Catalog in 1845 without a description. Salm-Dyck presented a Latin description but did not mention the origin of the plant nor its type locality. No illustration accompanied Salm-Dyck's description; apparently the first illustration of this plant appeared as a color plate in Curtis' Bot. Mag. (*pl.* 4296) two years later. As no plant was designated as the type specimen and apparently there are no specimens preserved in Europe by Lemaire or Salm-Dyck, the following specimen is designated as a neotype: "On the flat lands northeast of the junction of federal highways 57 and 80 near El Huizache, San Luis Potosí," *Edward F. Anderson 1079*, 3 Jul 1958. (NEOTYPE: POM 298103.)

Anhalonium lewinii Hennings, Gartenflora **37**: 410. 1888.

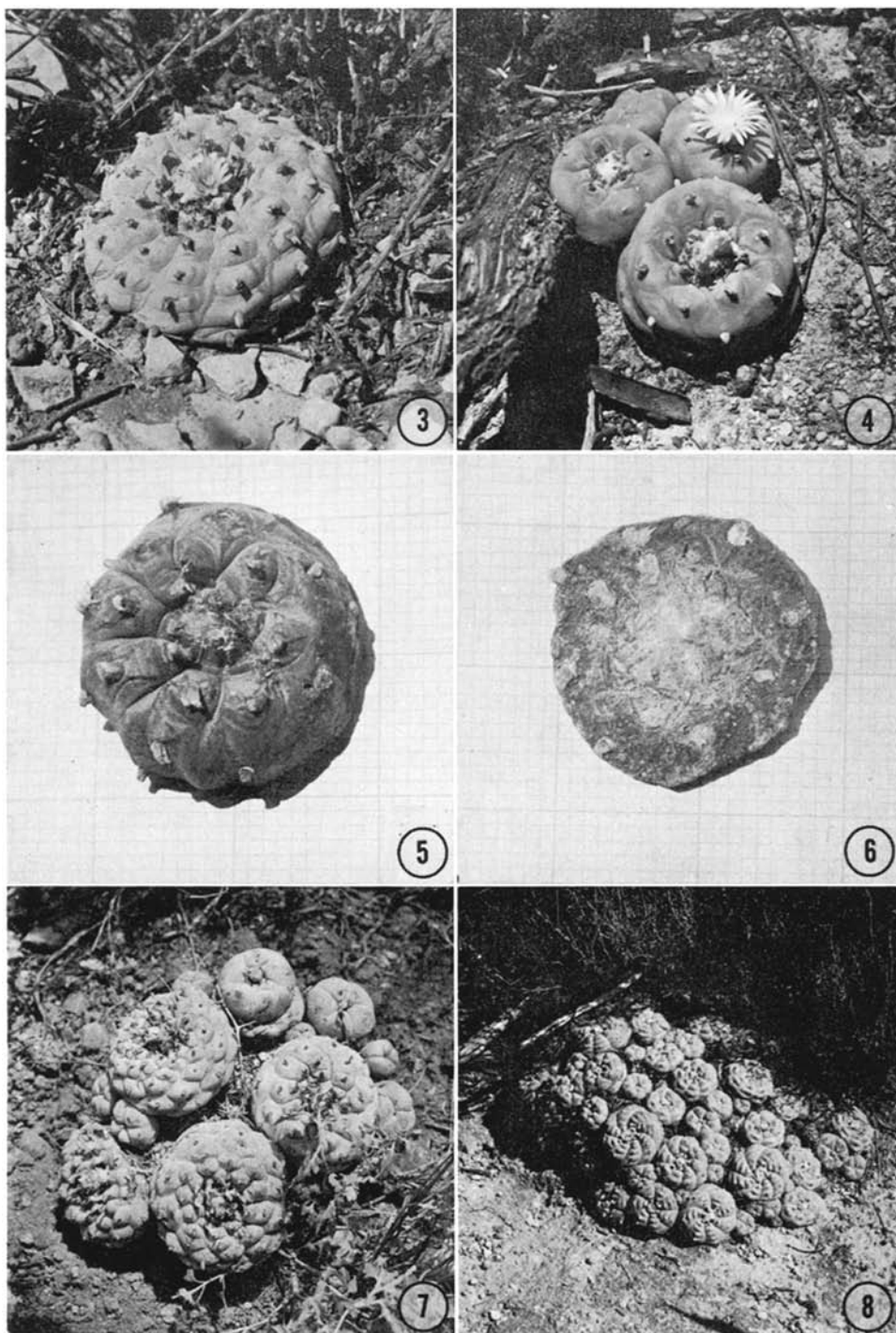
Echinocactus lewinii K. Schumann, Nat. Pflanzenfam. **3**. Abt. 6a: 173. 1894.

Lophophora williamsii var. *lewinii* Coulter, Contr. U. S. Nat. Herb. **3**: 131. 1894.

Lophophora lewinii Rusby, Bull. Pharmacy **8**: 306. 1894.

Mamillaria lewinii Karsten, Flora Deutsch. ed. 2. **2**: 457. 1895.

This epithet, proposed by Hennings, was based on body form and the characteristics of the tufts of hair at each areole. He stated that the hairs of the Salm-Dyck species were whiter, silkier, and longer than those of *A. lewinii*. The latter species was also said to possess a larger hairy pad in the center of the plant and had some differences in flower parts. Henning's description and illustration were based on dried plant material received in Germany under the designation "mescal buttons" by Dr. L. Lewin in 1887 from Park, Davis, & Co. in the United States. From the same materials Lewin (1888a, 1888b, 1894) extracted alkaloids and studied their physiological effects. It was Lewin's belief that only *A. lewinii* possessed the alkaloids, but current studies by J. S. Todd (oral communication) show all peyote plants to contain them. Another illustration of *A. lewinii* was later published (Arendt, 1891). This showed that the body was not as flat and had more trichomes than did the Salm-Dyck species. Body shape and quantity of trichomes are highly variable in *Lophophora*, and it would be impractical to base a species on these characters alone, especially when the original description and illustration are based on dried rather than living



FIGS. 3-8. FIG. 3. *Lophophora williamsii* ($\times \frac{1}{2}$). FIG. 4. *Lophophora diffusa* ($\times \frac{1}{2}$). FIG. 5. Freshly cut top of *L. williamsii* ($\times \frac{3}{4}$). FIG. 6. Same top after drying. Note the greater proportion of trichomes to other tissue ($\times \frac{3}{4}$). FIG. 7. Clump of *L. williamsii* showing both ribbed and non-ribbed heads. FIG. 8. Large caespitose clump of *L. williamsii* at El Huizache, S.L.P.

cactus material. Specimens of peyote are soft and succulent, and there is little cork or woody tissue of any kind. A dried specimen has a different shape, and the relative amount of surface covered by trichomes is altered, because the trichomes maintain the same volume while the body decreases in size through loss of water. Consequently, a dried specimen has a more woolly apical area than has a living specimen (Figs. 5, 6). More recently Ochoterena (1922) distinguished *A. lewinii* on the basis of its flower color and lack of definite ribs. Ochoterena (1922) reported the flowers of *A. lewinii* to be yellow, but Henning's original description clearly states that the flowers were pink. Hennings made no mention of the rib condition. Absence of or number of ribs has also been a commonly used diagnostic feature by more recent students of the cacti, but field studies show that single clones have both ribbed and non-ribbed branches (Fig. 7). Probably the plants originally described by Hennings and later called *Lophophora lewinii* were just one form of the highly variable species *L. williamsii*. It is not possible to find single populations that correspond to the characters attributed to Henning's *Anhalonium lewinii* and that are clearly distinct from *L. williamsii*.

Echinocactus williamsii var. *lutea* Rouhier, Trav. Labouret Mat. Med. Pharm. Galén 17 (pt. 5): 65. 1926.

Lophophora echinata var. *lutea* Croizat, Desert Plant Life 16: 44. 1944.

Lophophora williamsii var. *lutea* Soulaire, Cactus et Médecine 121. 1947.

Lophophora lutea Backeberg, Die Cactaceae 5: 2901. 1961.

These names were all based on the observation by Rouhier that the appearance of the tubercles varied somewhat from that of the "typical" peyote and that the flowers supposedly were yellow. Rouhier did not designate a type specimen, nor have yellow flowers been observed in any distinct population of peyote.

Lophophora echinata Croizat, Desert Plant Life 16: 43. 1944.

Lophophora williamsii var. *echinata* H. Bravo, Cact. Sucul. Mex. 12(1): 12. 1967.

These combinations were based on a photograph by Schultes in Cact. Succ. Jour. 12: 180. fig. 3. 1940. Croizat's criterion for establishing the new species was that "*L. williamsii* can hardly be made to cover, indeed, the peculiar form with loose tubercles. . . . The tubercles that are flattened out and run into definite ribs in *L. williamsii* are here endowed with distinct individuality." A relatively minor rib variation is insufficient to establish a separate species or variety, because plants in single clones and populations vary too widely.

Lophophora williamsii var. *decipiens* Croizat, Desert Plant Life 16: 44. 1944, was based on an illustration in Britton & Rose, The Cactaceae 3: pl. 10, fig. 4. 1923. Croizat stated that the vegetative body of this variety was basally tubercled, having distinct podaria rather than ribs, and that the flower extended out of the top of the plant to a greater extent. He designated the type to be the illustration cited above. I do not believe these characters are consistent enough in occurrence to justify separate taxonomic status.

Lophophora williamsii var. *pentagona* Croizat, Desert Plant Life 16: 44. 1944, was based on a photograph by Y. Wright in Cact. Succ. Jour. 3: 55. 1931, titled "Anhalonium sp. undetermined." It is an illustration of a young 5-ribbed plant that commonly occurs in populations having plants with branches bearing 7–14 ribs. Rib number alone is an insufficient basis for establishing a separate taxon.

Lophophora williamsii var. *pluricostata* Croizat, Desert Plant Life 16: 9. 1944, was proposed because Croizat believed specimens of peyote having 13 ribs and form-

ing clusters were worthy of separate taxonomic rank. He offered as a type an illustration by Schultes in *Cact. Succ. Jour.* **12**: 178. fig. 1. 1940. As stated earlier, rib number is highly variable, depending on the age and health of the plant. Moreover, clusters of heads are also common, especially if the plants have been injured.

2. *L. DIFFUSA* (Croizat) Bravo H., *Cact. Sucul. Mex.* **12**: 13. 1967.

TYPE: Fig. 201 in Bravo, *Las Cactaceas de México* 378. 1937. Bravo, when elevating the epithet to the specific level, stated that the plant in the photograph was collected in 1935 by Carolina Schmoll near Vizarrón, Querétaro.

Plants soft, yellow-green, often somewhat globular in shape, 2–7 cm high, 5–12 cm in diam; ribs usually absent, podaria rarely elevated but broad and flat; areoles 1–2 cm apart, 2–3 mm in diam; flower 1.3–2.2 cm in diam, 1.3–2.4 cm long; outer perianth segments 1–2 mm broad; inner perianth segments 2–2.5 mm broad, usually white or faintly pink but sometimes appearing yellowish white; pollen 0–6 colpate, 26.1–48.5 μ in diam (Fig. 4).

Occurring in Mexico within a fairly restricted range near Vizarrón in the state of Querétaro.

Representative specimens. MEXICO: QUERÉTARO: N of Cadereyta, *Anderson 1656, 1659, 2300* (POM); without precise locality, *Altamirano s.n.* (US), *Willi Wagner s.n.* (POM).

Lophophora echinata var. *diffusa* Croizat, *Desert Plant Life* **16**: 44. 1944, and *Lophophora diffusa* Bravo H., *Cact. Sucul. Mex.* **12**: 13. 1967, are both based on the Schmoll photograph of a plant collected near Vizarrón, Querétaro. The Querétaro population is isolated and self-perpetuating, and has several distinct characteristics as just described. It is deserving of recognition as a separate taxon; therefore, the illustration designated as a type by Croizat must serve as the type.

EXCLUDED NAMES AND TAXA OF UNCERTAIN STATUS

Anhalonium rungei Hildmann ex Arendt in *Monatssch. Kakteenk.* **3**: 68. 1893, is a *nomen nudum*, although it was applied occasionally to peyote by horticulturists. The name is not used in the trade today. *Anhalonium subnodosum* Hildmann ex Arendt in *Monatssch. Kakteenk.* **3**: 68. 1893 should be treated in the same way.

Anhalonium jourdanianum Lewin, *Ber. Deutsch. Bot. Ges.* **12**: 289. 1894, nom. nud., as well as *Echinocactus jourdanianus* Rebut ex Maass, *Monatssch. Kakteenk.* **15**: 122. 1905, and *Lophophora jourdaniana* Kreuz., *Verzeichnis* 9. 1935, probably referred to a form of *L. williamsii* having a somewhat different arrangement of ribs. However, the lack of an original illustration or description makes this conclusion speculative at best.

Echinocactus williamsii, "Hylaeid," β *anhaloninica* (= *E. lewinii*) K. Schumann, *Bot. Jahrb.* **24**: 567. 1898, nom. provisorum, and *Echinocactus williamsii* var. *anhaloninica* Rouhier, *Trav. Labouret Mat. Med. & Pharm. Galén* **17** (pt. 5): 70. 1926, were both based on chemical studies by European chemists. Schumann apparently meant this epithet to be nothing more than a synonym of *E. lewinii*.

Echinocactus williamsii "Hylaeid," α *pellotinica* (= *E. williamsii*, Type) K. Schumann, *Bot. Jahrb.* **24**: 567. 1898, nom. provisorum, and *Echinocactus williamsii* var. *pellotinica* Rouhier, *Trav. Labouret Mat. Med. & Pharm. Galén* **17** (pt. 5): 70. 1926, should be considered as nothing more than synonyms of *E. williamsii*.

A. D. Houghton proposed the varietal epithet *cristata* (under *Lophophora williamsii*) in *Cact. Succ. Jour.* **2**: 490. 1931. From time to time abnormal plants appear within natural populations. These cristate specimens are prized by horticulturists and are often in collections, but they are aberrant forms of the typical plant and do not deserve formal taxonomic status.

Lophophora caespitosa Frič ex Roeder, Kakteenkunde **1937**: 190, nom. nud., and *Lophophora williamsii* var. *caespitosa* Y. Ito, Cacti 96. 1952, are epithets which apparently refer to forms of *Lophophora* with several branches arising from the same root, a common phenomenon in natural populations (Fig. 8).

Lophophora texana Frič ex Roeder, Kakteenkunde **1937**: 190, nom. nud., and *Lophophora williamsii* var. *texana* Kreuz. ex Backeberg, Die Cactaceae **5**: 2895. 1961, are without description or illustration. The epithet probably was proposed by European horticulturists for peyote plants arriving from Texas. Apparently their main source of plants was Mexico, and this may have been to differentiate the two geographical groups. Backeberg stated that Kreuzinger had used the epithet on the varietal level in his *Verzeichnis*. However, in actuality he used it on the specific level.

Lophophora ziegleri Werdermann ex Borg, Cacti 210. 1937, *Lophophora ziegleriana* Soulaire, Cact. et Med. 121. 1947, as syn., and *Lophophora tiegleri* Soulaire, Cact. et Med. 121. 1947, as syn., commonly have been known in the cactus trade as peyote plants having quite distinct, deep ribs with well pronounced tufts of trichomes. However, Borg described them as having less depressed stems, low tubercles, smaller tufts of wool, and pale yellow flowers. None of the names were published with illustrations or descriptions, and they probably refer to varying forms of *L. williamsii* reaching European markets.

Lophophora albilanata Schmoll, Katalog 2, 1947, nom. nud. and *Lophophora ziegleri* var. *albilanata* Soulaire, Cactus et Médecine 121. 1947, nom. nud. apparently were epithets applied to some horticultural forms having very white trichomes.

Lophophora ziegleri var. *diagonalis* Schmoll, Katalog 2. 1947, nom. nud., possibly was proposed to describe the shape or arrangement of tubercles and ribs.

Lophophora flavilanata Schmoll, Katalog 2. 1947, nom. nud. and *Lophophora ziegleri* var. *flavinata* Soulaire, Cactus et Médecine 121. 1947, nom. nud., may have been epithets referring to forms of peyote having golden-yellow flowers or trichomes.

Lophophora ziegleri var. *mammillaris* Schmoll, Katalog 2. 1947, nom. nud. probably was proposed because certain plants had protuberant podaria.

Rouhier (1927), in his extensive treatment of peyote, presented some nomenclatural combinations that have led to considerable confusion among taxonomists. One epithet, "*pseudo-Lewinii hortulorum*," appeared on p. 61, while on p. 62 he referred to "*Echinocactus pseudo-Lewinii Thompsonii*." Although his discussion is unclear, it appears that he probably did not intend to create any new varieties or binomials; rather, he simply reverted to Latin in referring to certain descriptive phrases when dealing with various forms often recognized in the horticultural trade. Should these have to be accepted as legitimate epithets, they would be referred to the synonymy of *L. williamsii*.

The binomial *Anhalonium visnagra* K. Schumann, Monatssch. Kakteenk. **6**: 174. 1896, nom. nud., occasionally has been referred to *Lophophora*. However, Schumann made reference to this plant as a new species in the trade along with *Echinocactus williamsii* and *E. lewinii*. There is no indication that he thought they were related.

Mammillaria cirrhifera Mart., Nov. Act. Physico-med. Acad. **16**: pars 1. 1832, has also been mentioned in *Lophophora* synonymy. Martius' description obviously is not that of *Lophophora*, and presently the epithet is considered to be a synonym of *M. compressa*.

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