

Taxonomy and systematics

***Tetramerium* (Acanthaceae) in the Depresión del Balsas Biogeographic Province of Mexico, two new species and a new combination**

***Tetramerium* (Acanthaceae) en la provincia biogeográfica Depresión del Balsas de México, dos especies nuevas y una combinación nueva**

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Abstract

A taxonomic account of *Tetramerium* in the Depresión del Balsas Biogeographic Province of western and central Mexico reveals 14 species there, with 2 of them, *T. cruzii* and *T. michoacanum*, described herein. A new combination, *T. barlerioides*, is proposed for the species previously known as *T. ochoterena*. This region of Mexico appears to be the center of both species richness and morphological diversity for this widely distributed American genus. A key to the 14 species is followed by geographic distribution ranges, ecological data within the region, and miscellaneous notes for each one that updates information from the last monograph of the genus. A verified voucher specimen is provided to document species occurrences in each state (or portion of a state) in the Depresión del Balsas. Occurrences of 2 species, *T. glandulosum* and *T. tenuissimum*, are newly reported from the Estado de México. A map of the region and floral photographs of 12 of the species are provided.

Keywords: Taxonomy; Floristics; Morphology; Distribution; Endemism; Pollen

Resumen

Un tratamiento taxonómico de *Tetramerium* en la provincia biogeográfica de la Depresión del Balsas en el oeste y centro de México revela la presencia de 14 especies; 2 de ellas, *T. cruzii* y *T. michoacanum*, descritas aquí. Se formaliza una nueva combinación, *T. barlerioides* para la especie anteriormente conocida como *T. ochoterena*. Esta región de México parece ser tanto el centro de riqueza de especies, como de diversidad morfológica de este género americano de amplia distribución. A la clave para las 14 especies le siguen rangos de distribución geográfica, datos ecológicos dentro de la región y notas diversas para cada una, que actualiza la información de la última monografía

del género. Se proporciona un espécimen para documentar la presencia de las especies en cada estado (o parte de un estado) en la Depresión del Balsas. Se reporta por primera vez la presencia de 2 especies, *T. glandulosum* y *T. tenuissimum* en el Estado de México. Se presenta un mapa de la región y fotografías florales de 12 de las especies.

Palabras clave: Taxonomía; Florística; Morfología; Distribución; Endemismo; Polen

Introduction

Tetramerium Nees is a genus of Acanthaceae in tribe Justiceae, subtribe Tetrameriinae that occurs in subtropical and tropical regions of the Western Hemisphere from the southern USA to southern Bolivia. Aspects of the morphology, cytology, phytogeography, reproductive biology and taxonomy of the genus were discussed by Daniel (1986), who recognized 28 species. Since then, 3 additional Mexican species have been described (Daniel, 2003; Daniel & Cruz-Durán, 2016; Daniel & Steinmann, 2016). Molecular phylogenetic data to date reveal the genus to be monophyletic and sister to a clade of numerous species of *Carlowrightia* (Daniel et al., 2008; McDade et al., 2018). Below, 2 new species are described and a new combination is proposed for another species restricted to the Depresión del Balsas Biogeographic Province in

Mexico. With these additions, 26 of the 33 species (79%) occur in Mexico, and 23 (70%) of them are endemic there.

In general, the Depresión del Balsas Biogeographic Province (DBBP henceforth) of western and central Mexico consists of most of the region between the Transmexican Volcanic Belt (Eje Neovolcánico or Faja Volcánica Transmexicana) to the north and the Sierra Madre del Sur to the south (Flores-Tolentino et al., 2023). Delimitation of the province differs among authors based on variables of biotic (e.g., biotic communities, taxa present) vs. abiotic (e.g., physiography, hydrology) components. For example, some interpretations include a small portion of Veracruz and/or much of Tlaxcala (e.g., Arreguín-Sánchez et al., 2002; Comisión Nacional de Agua, 2011; Wikipedia, 2023 [with qualifications]), whereas others exclude these regions (e.g., Flores-Tolentino et al., 2021, 2023). Boundaries for the region utilized here (Fig. 1) generally

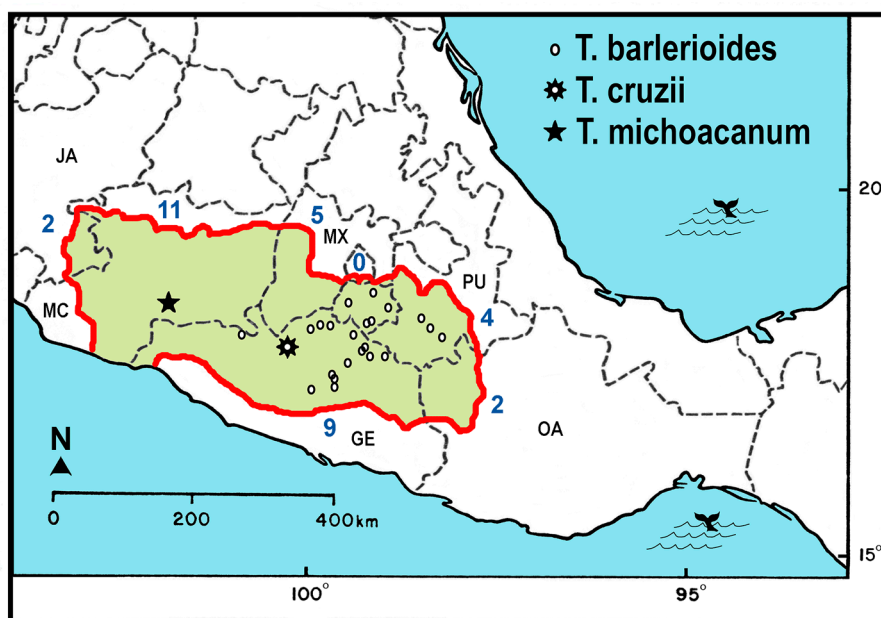


Figure 1. Map of central and southern Mexico showing generalized boundaries of the Depresión del Balsas Biogeographic Province (green outlined in red) and the distributions of *Tetramerium barlerioides*, *T. cruzii*, and *T. michoacanum*. Symbols for taxa may represent more than 1 occurrence. States or portions thereof comprising the province are abbreviated as: Guerrero (GE), Jalisco (JA), México (MX), Michoacán (MC), Oaxaca (OA), and Puebla (PU). The other 2 states, Ciudad de México and Morelos, are located respectively to the right and below MX. Numbers in blue indicate the number of species of *Tetramerium* that occur in regions of the DBBP in each state (except Morelos = 5, not shown).

follow the biogeographic delimitation of Flores-Tolentino et al. (2021, 2023). The DBBP of ca. 115,000 km² contains the state of Morelos and portions (sometimes very limited) of the following 7 Mexican states: Ciudad de México, Guerrero, Jalisco, Estado de México, Michoacán, Oaxaca, and Puebla. This largely seasonally dry region is drained by the Río Balsas (rivers Atoyac and Mezcala) system and contains several biotic communities, the most extensive being tropical deciduous forest (Rzedowski, 1978), which occurs at elevations from near sea level to ca. 1,600 meters (Flores-Tolentino et al., 2023; Rzedowski, 1978). Regions of thornscrub often at lower elevations, and oak forest and pine-oak forest at higher elevations, also occur in the DBBP.

Materials and methods

This study utilized specimens from the following herbaria: ARIZ, ASU, B, BM, CAS, CODAGEM, DES, DS, ENCB, F, FCME, GH, IEB, K, L, LL, LSU, MEXU, MICH, MO, MSC, NY, P, POM, PR, RSA, S, TEX, UC, US, and XAL, acronyms according to Thiers (2024). Geographic distributional information is noted for all species of *Tetramerium* occurring in the DBBP. Locality data provided (including longitude and latitude coordinates, when present) were taken from herbarium specimens. Voucher specimens with sufficient locality data, but lacking coordinates, were georeferenced using Google Earth Pro (2023) and the resulting approximate coordinates are provided in brackets. For the 5 species endemic there that are known from more than 2 collections, the Extent of Occurrence (EOO) and Area of Occupancy (AOO; grid cell area of 4 km²) were determined via calculations on GeoCAT (2024). Provisional conservation assessments based on IUCN (2022) guidelines are discussed, but no new ones are proposed due to insufficient knowledge of locations based on actual and/or potential threats. When available, specimens more recently collected than those previously cited by Daniel (1986) are listed to voucher occurrences by state. Unacetolyzed pollen (individual grains removed with insect pins from exposed anthers) from herbarium specimens that were not included in palynological studies of *Tetramerium* by Daniel (1986, 1998) was mounted on aluminum stubs, coated with gold-palladium, and observed at 15kV in the scanning electron microscopy laboratory of the California Academy of Sciences.

Results

The DBBP is rich in taxa of Acanthaceae and includes several endemics in diverse genera (e.g., *Holographis argyrea* (Leonard) T.F. Daniel, *Justicia mexiae* T.F.

Daniel, *Lepidagathis danielii* Cruz Durán & J. Jiménez Ram., *Ruellia foliosepala* T.F. Daniel). Fourteen of the 33 (42%) species of *Tetramerium* have been documented from the DBBP, including 8 that are endemic there. The numbers of species of the genus in portions of the DBBP by state are shown in Figure 1. The highest numbers of species occur in the states containing the largest areas of the biotic province, i.e., Michoacán (11) and Guerrero (9). Species of *Tetramerium* in the DBBP occur in most, if not all, of its major constituent biotic communities. All 14 occur in tropical deciduous forest, at least 3 also occur in thornscrub, 2 others also occur in tropical subdeciduous forest, 8 also occur in oak forest (and/or in the ecotone between tropical deciduous forest and oak forest), and 3 also occur in pine-oak forest at higher elevations in the DBBP. Flowering among the 14 species is known from September to July; however, most of the species flower between November and May. This generally corresponds to a dry season in the region of the DBBP. Fruiting and seed dispersal via explosive dehiscence tend to occur simultaneously with flowering periods, or sometimes begin in the month following the onset of flowering and/or extend into the month after the cessation of flowering.

The following account provides a brief description of *Tetramerium* in Mexico and Central America; a key to the 14 species in the DBBP; photographs of 12 species; descriptions and discussions of the new species; rationale for a new combination for the species previously named *T. ochoterena* (Miranda) T.F. Daniel; a catalog of each species with information updated from Daniel (1986); and a map of the region showing the number of species by states within the region and the distributions of *T. cruzii* T.F. Daniel, *T. michoacanum* T.F. Daniel, and *T. barlerioides* (Nees) T.F. Daniel.

Systematic account

Tetramerium Nees in Bentham, Bot. Voy. *Sulphur* 147. 1846, nom. cons., non *Tetramerium* Gaertner (1806). Type: *Tetramerium polystachyum* Nees, type conserv. (= *Tetramerium nervosum* Nees).

Perennial herbs or shrubs with cystoliths. Leaves opposite, subsessile to petiolate (distal leaves rarely sessile), petioles detaching a short distance from stems leaving petiolar stubs at nodes, blades usually entire. Inflorescences of terminal, conspicuously and usually densely bracteate, 4-sided, and unbranched dichasiate spikes. Bracts opposite, conspicuous, and larger than bracteoles. Calyces 4-5-lobed, lobes homomorphic (or if 5-lobed, 1 lobe sometimes reduced in size). Corollas white, cream, yellow, blue, or red, often with discolorous markings on upper lip, externally glabrous (excluding margins of lobes, which are sometimes pubescent),

tube subcylindric or gradually expanded distally, limb pseudopapilionaceous (i.e., with the lower-central lobe forward projecting, more or less conduplicate, and containing stamens and style; lateral lobes and upper lip spreading) to more or less pseudopapilionaceous or with all lobes linear and recurved, upper lip consisting of 2 fused lobes (sometimes apically emarginate), lower lip consisting of 3 mostly separate lobes. Stamens 2, exerted from mouth of corolla, anthers 2-theous, thecae equal to subequal in size, parallel to subsagittate, equally inserted on filament, dehiscing toward upper lip (i.e., flowers sternotribic). Pollen 3-colporate, 6-pseudocolpate, exine reticulate. Capsules stipitate, fertile head with 4 seeds (fewer by abortion), septa with attached retinacula separating slightly from inner wall of mature capsule at maturity. Seeds flattened, (0.8-) 1-2.5 (-3) mm long, lacking trichomes.

Remarks. The brief description above applies to Mexican and Central American species of the genus. *Tetramerium* is distinguished from its closest phylogenetic (e.g., McDade et al., 2018) and/or morphological relatives (Daniel, 1986) among subtribe Tetrameriinae (i.e., *Anisacanthus* Nees, *Carlowrightia* A. Gray, *Gypsacanthus* E.J. Lott, V. Jaram. & Rzedl., and *Henrya* Nees ex Benth.) by the combination of its conspicuous 4-ranked bracts that usually conceal the calyx; bracteoles smaller than bracts

with the pairs fused, if at all, only for a short distance at the base; capsules upon dehiscence with septa and retinacula separating slightly from inner capsule wall; and seeds usually 4 per capsule, small, and lacking trichomes. Of the 26 species of *Tetramerium* that occur in Mexico 14 (i.e., 54%, including the 2 new ones described below) are known from the DBBP.

Species or individual plants within a species exhibit morphological variation in habit (perennial herbs to shrubs); corolla size (9-60 mm long), color (white, yellow, red, and blue), stance (horizontal to vertical), and form (e.g., lower-central lobe flat, u-shaped, or v-shaped and either forward projecting or recurved); and capsule pubescence (present or absent). Some of the floral diversity among and within species in the DBBP is shown in Figure 2. Thus, the DBBP would appear to be the center of both richness and diversity for the genus.

For each species of *Tetramerium* known from the DBBP, the following key provides a means to identify them. A subsequent species catalog provides: a description (or reference to one), worldwide geographic distribution (by country and Mexican states), flowering period(s) by month(s) within the DBBP, and biotic community(ies) with elevational ranges within the DBBP. A verified voucher specimen for each occurrence by state within the DBBP is also cited.

Key to the species of *Tetramerium*

- 1a. Corollas purple with white discoloration streaked with dark purple on upper lip *T. glutinosum*
- 1b. Corollas white, cream, yellow, or red, often with discolorations on upper lip 2
- 2a. Calyces 4-lobed 3
- 2b. Calyces 5-lobed 4
- 3a. Ultimate branches often sharp-pointed at apex; spikes to 120 mm long, 4-7 mm wide near midpoint, rachis pubescent with erect to flexuose trichomes to 1.5 mm long (often floccose); bracts to 3 mm wide, more or less palmately 3-veined, apical portion not twisted and barely (if at all) recurved, margin ciliate with soft and mostly flexuose trichomes (often floccose)..... *T. butterwickianum*
- 3b. Ultimate branches not sharp-pointed at apex; spikes to 35 (-65) mm long, 8-18 mm wide near midpoint, rachis pubescent with mostly antrorse trichomes usually less than 1 mm long (not floccose); bracts to 7 mm wide, more or less palmately 3 or 5 (or 7)-veined, apical portion usually partially twisted and more or less recurved, margin ciliate with more or less stiff and straight to flexuose to distally curved trichomes (not floccose)..... *T. nervosum*
- 4a. Spikes with 4 or more dichasia bearing flowers, 9-12 mm wide (excluding flowers) near midspike, rachis more or less densely pubescent with soft, flexuose, and mostly interwoven eglandular trichomes to 1.5 mm long (appearing floccose and concealing surface of rachis); bracts with margins containing dense, flexuose, cotton-like eglandular trichomes to 2 mm long *T. michoacanum*
- 4b. Plants not with the above combination of characters 5
- 5a. Corollas (23-) 27-60 mm long, tube (14-) 18-28 mm long, (2.5-) 2.8-5.5 mm in diameter at mouth (measured flat), upper lip lacking discolorous markings 6
- 5b. Corollas (7-) 9-26 mm long, tube (2.5-) 3-12 mm long, (1-) 1.2-2.5 mm in diameter at mouth (measured flat), upper lip with discolorous markings (rarely inconspicuous in *T. glandulosum*)..... 8

- 6a. Flowers horizontal in stance; corollas yellow, 47-60 mm long, upper lip 27-35 mm long, lobes of lower lip homomorphic, strongly recurved (overlapping corolla tube), linear, 24-26 mm long, 2-3.3 mm wide, lower central lobe not conduplicate (not enclosing stamens); stamens 20-28 mm long, thecae 3.8-5.2 mm long; capsules 10-12 mm long. *T. barlerioides*
- 6b. Flowers usually vertical or nearly so in stance; corolla red or yellow, (23-) 27-42 mm long, upper lip (8.5-) 10-17 mm long, lobes of lower lip heteromorphic, lateral lobes laterally spreading (apically sometimes more or less recurved but not overlapping corolla tube), linear-elliptic to elliptic to oblanceolate-elliptic to obovate-elliptic, (7-) 9-15 mm long, (2.5-) 3.5-7.5 (-9.5) mm wide, lower-central lobe forward projecting, sub-conduplicate (U-shaped and usually partially enclosing stamens); stamens (10-) 11.5-16 mm long, thecae 2.5-3.6 mm long; capsules 7.5-10.5..... 7
- 7a. Bracteoles ovate-trullate to trullate, 2-5 mm wide; bracts foliose with distinct petioles; corollas red to orange-red *T. abditum*
- 7b. Bracteoles linear to linear-lanceolate to linear-elliptic to linear-oblanceolate, 0.8-2.3 mm wide; bracts (except lowermost, foliose ones) mostly sessile to subsessile; corollas red or yellow *T. rubrum*
- 8a. Capsules glabrous..... 9
- 8b. Capsules pubescent (at least distally or near apex)..... 12
- 9a. Shrubs to 3 m tall; corollas bright lemon yellow, upper lip with 2 reddish or maroon streaks (sometimes merged distally, often more or less diffuse, and/or rarely inconspicuous); bract linear to linear-elliptic to lance-ovate to oblanceolate to obovate, apically usually truncate to rounded..... *T. glandulosum*
- 9b. Perennial herbs or shrubs to 1 m tall; corollas white to cream to pale yellow, upper lip with purple and/or maroon markings outlining white to yellowish, pale maroon, or purplish patches; bracts lanceolate to ovate to deltate to subcircular, apically usually acute to acuminate to attenuate 10
- 10a. Bracts lanceolate to lance-elliptic, 16-19 mm long, length:width = 7.4-10, attenuate at apex; bracteoles 9-14 mm long; calyx 6.5-8.5 mm long..... *T. vargasiae*
- 10b. Bracts deltate to ovate to elliptic to subcircular, 6-16 mm long, length:width = 0.9-3.5, acute to acuminate at apex; bracteoles 0.8-10 mm long; calyx 1.8-5.5 mm long 11
- 11a. Bracts abaxially glabrous, apical portion erect and straight (not twisted); corolla 24-26 mm long, margin of lower-central lobe conspicuously ciliate with trichomes to 0.7 mm long; rare in southeastern Michoacán..... *T. emilyanum*
- 11b. Bracts abaxially pubescent with eglandular (and sometimes also glandular) trichomes, apical portion usually more or less recurved and partially twisted; corolla 10-23 mm long, margin of lower-central lobe ciliolate with trichomes to 0.2 mm long; common throughout the DBBP..... *T. nervosum*
- 12a. Spikes to 12 mm long; dichasia with flowers 1 or 2 per spike; bracts 0.7-1.2 mm wide, length:width = 6-8.6, only midvein evident; lower-central lobe of corolla more or less flat or only slightly cupped and distally inrolled exposing stamens and style..... *T. pauciflorum*
- 12b. Spikes to 180 mm long; dichasia with flowers 4 or more per spike; bracts 2-10 mm wide, length:width = 0.9-4.5 (-6.5), 3 or 5 (or 7) more or less palmate veins evident (sometimes obscure in *T. tenuissimum*; rarely midvein only evident in *T. cruzii*); lower-central lobe of corolla conduplicate (keel-like, U-shaped or V-shaped), partially enclosing stamens and style, distally not inrolled 13
- 13a. Seeds prominently concavo-convex, covered with low, rounded ridges or subconic projections on convex side and with deep valleys outlined by conspicuous, irregular ridges on concave side *T. langlassei*
- 13b. Seeds plano-convex, both surfaces covered with low, rounded tubercles or subconic projections 14
- 14a. Spikes 4-7 (-11) mm wide (excluding corollas) near midspike; bract margins with trichomes to 0.5 mm long..... *T. tenuissimum*
- 14b. Spikes (7-) 10-19 (-23) mm wide (excluding corollas) near midspike; bract margins with at least some (usually most) trichomes longer than 0.5 mm 15
- 15a. Bracts distally tapered from or below midpoint, apical portion erect and straight (not twisted), margin ciliate with trichomes to 1 mm long; capsules 6-7.5 mm long; local endemic in north-central Guerrero *T. cruzii*
- 15b. Bracts usually distally tapered from or above midpoint, apical portion usually recurved and partially twisted, margin ciliate with trichomes to 3.5 mm long; capsules 4-6.5 mm long; common throughout DBBP *T. nervosum*

1. *Tetramerium abditum* (Brandege) T.F. Daniel

Description. Daniel (1986).

Distribution. Endemic to western Mexico (Chihuahua, Durango, Michoacán, Nayarit, Sinaloa, Sonora). In the DBBP, plants occur in central Michoacán.

Flowering in DBBP. January.

Biotic community in DBBP. Tropical deciduous forest at 600-700 m elevation.

Voucher by state. Michoacán: Municipio de Gabriel Zamora, 15 km S de Tarétan, autopista Morelia-Lázaro Cárdenas (19°14'20" N, 101°53'00" W), E. Carranza & V. Steinmann 6318 (CAS).

Remarks. This species is known from the DBBP only by the single collection cited above. It is morphologically similar to *Tetramerium rubrum* (see below), but occurs more frequently farther northward in western Mexico. Unlike *T. rubrum*, which has both red- and yellow-flowered populations, *T. abditum* is only known to have red to orange-red corollas. The corollas of both species appear to differ from other Mexican *Tetramerium* by their usually vertical (i.e., appearing subsalverform) or nearly vertical (i.e., appearing upside-down or oriented sideways with the 2 lateral lobes of the lower lip uppermost and lowermost respectively) stance. In other species of Mexican *Tetramerium*, flowers are horizontal in stance (i.e., oriented with the upper lip uppermost and the lower lip lowermost; Fig. 2). Flowers of both species appear to be adapted for pollination by hummingbirds. Visitation to flowers of *T. abditum* by hummingbirds and butterflies was reported by Daniel (1986).

2. *Tetramerium barlerioides* (Nees) T.F. Daniel, comb. nov. *Jacobinia barlerioides* Nees in Alph. de Candolle, Prodr. 11: 332. 1947. Type: Mexico: Guerrero: "Canada de Supilote" [Cañón del Zopilote; ca. 17°48'09.70" N, 99°33'46.38" W], A. von Humboldt s.n. (holotype: B, barcode-B-W 00315-010-image!; F-image!). *Justicia straminea* Humb. & Bonpl. ex Schult., Mant. 1 (Schultes) 1: 146. 1822, nomen nudum. (Fig. 3)

Anisacanthus ochoterena Miranda, Anales Inst. Biol. Univ. Nac. México 12: 606. 1941. Type: Mexico: Morelos: en terrenos rocosos de la ladera occidental de Cerro de Sta. Clara, cerca de Jonacatepec, [ca. 18°39'43.69" N, 98°48'3.37" W], 5 Mar 1941, F. Miranda 1327 (holotype: MEXU, T00030062!; isotypes: F, 1113415!, MEXU, T00030063!, MEXU T00069084!). *Tetramerium ochoterena* (Miranda) T.F. Daniel, Syst. Bot. Monogr. 12: 109. 1986.

Description. Daniel (1986, as *T. ochoterena*).

Distribution. Endemic to the DBBP in Mexico (Guerrero, Morelos, Puebla). Plants in the DBBP occur

from northwestern Guerrero through central and northern Guerrero and Morelos to central and southern Puebla.

Flowering in DBBP. January-May.

Biotic communities in DBBP. Tropical deciduous forest and tropical deciduous forest/oak forest ecotone at 600-1,600 m elevation.

Voucher by state. Guerrero: Municipio de Zumpango del Río [= Eduardo Neri], Cañón del Zopilote, MEX 95, 3.3 km N de la desviación a Xochipala (17°49'31" N, 099°33'48" W), V. Steinmann & J. Porter 4921 (CAS, MEXU). Morelos: 6 km al NW de Jonacatepec, [ca. 18°50'54.96" N, 098°59'44.57" W], L. González Q. 3631 (DS, ENCB, MICH, MSC). Puebla: along Hwy. 190 between Oaxaca and Izúcar de Matamoros, NW of Tehuiztzingo, 11 mi NW of Río Atoyac (18°27'N, 98°22'W), T. Croat & D. Hannon 65721 (CAS, MEXU).

Remarks. This species was known to Daniel (1986) from only 6 collections. Recent collecting has resulted in at least 31 total collections (Fig. 1), but the species remains known only from the DBBP. Updated information on phenology, habitat, and elevation is indicated above. The total distribution of the species (EOO) is 21,037.792 km² and the AOO is 116 km². If sufficient information concerning actual or potential threats (and locations) to this species were known, it could potentially be assessed as Endangered (EN) based on the AOO.

Nees (1847) indicated that *Jacobinia barlerioides* Nees was collected by Alexander von Humboldt "ad Canade de Supulote in districtu Quitensi." As a result, the locality of Humboldt's type collection has been attributed to Ecuador in various sources (e.g., IPNI, 2024; JSTOR, 2024). However, the species does not occur there, and no such locality is noted by Sandwith (1926) among Humboldt's Ecuadorian collecting sites. However, "Cañada de Sopilote" and "Valle de Sopilote" are specifically listed among Humboldt and Bonpland's Mexican collection localities by Sprague (1924). Indeed, the species has been collected numerous times in and near the Cañón del Zopilote in the DBBP of central Guerrero between Zumpango del Río and Mezcala. The canyon lies along the route between Chilpancingo and Taxco that Humboldt followed on his journey from Acapulco to Mexico City. He would have passed through the canyon in early April of 1803 (Stevens-Middleton, 1956).

Humboldt's type specimen in the Willdenow Herbarium at B (Fig. 3) contains several annotations: "Barleria aff.," "Jacobinia barlerioides" in Nees' handwriting, and "J. straminea" (an unpublished name written on the sheet and cited in Nees' protologue). In the protologue of *Jacobinia barlerioides*, Nees (1847) noted numerous characteristics that match those of Mexican



Figure 2. Floral diversity among 11 of the species of *Tetramerium* occurring in the Depresión del Balsas Biogeographic Province. A, *T. butterwickianum*; B, *T. emilyanum*; C, *T. langlassei*; D, *T. glandulosum*; E, *T. glutinosum*; F, *T. pauciflorum*; G, *T. tenuissimum*; H, *T. abditum*; I, *T. rubrum*; J, *T. rubrum* (yellow form); K, *T. nervosum*; L, *T. nervosum*; M, *T. barlerioides*. *Tetramerium michoacanum* is shown in Figure 4; images were not available for *T. cruzii*, and *T. vargasiae*. Photos by T. Daniel, except E, G, K by Dale Denham (used with permission), F by Victor Steinmann (used with permission), and M by José Javier Barrios Flores (CC BY NC 4.0 DEED, cropped, from iNaturalistMX, <https://creativecommons.org/licenses/by-nc/4.0/>).

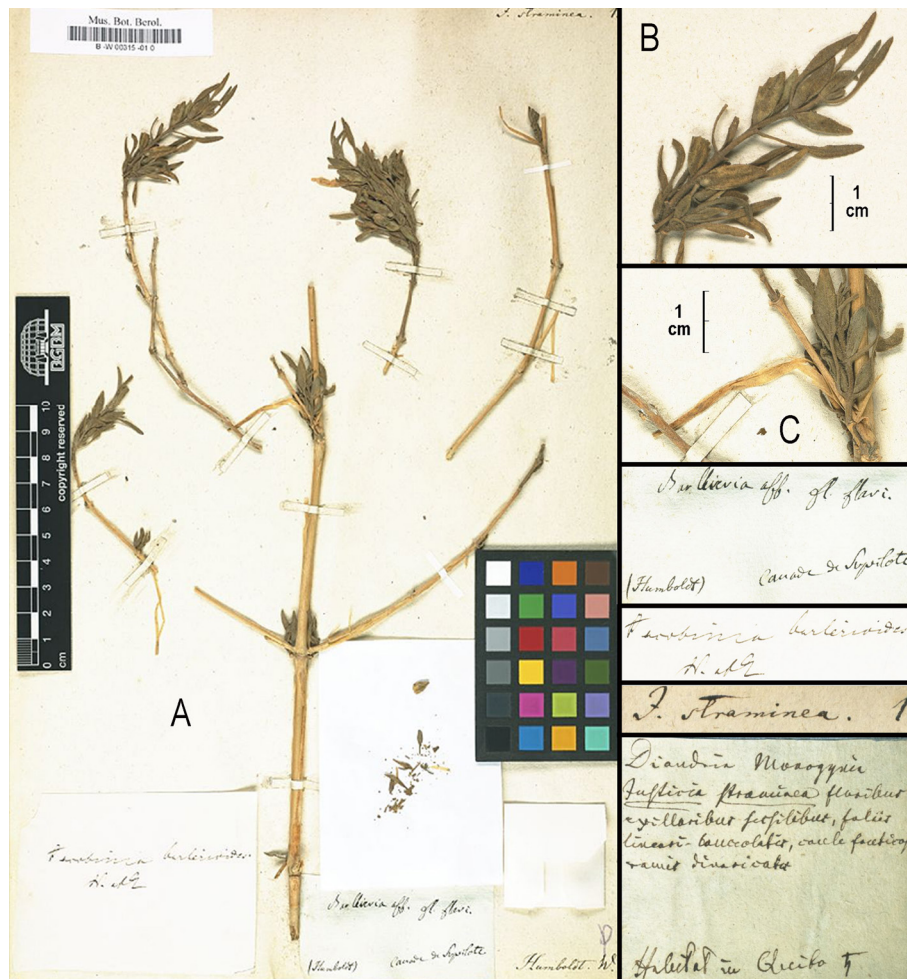


Figure 3. *Tetramerium barlerioides*, holotype (A. von Humboldt s.n.). A, Specimen at B-W; Curators Herbarium B (2000+); B, close-up of terminal foliose spike; C, partially folded corolla. Annotations noting (from top): affinities with *Barleria*, yellow flowers, collector (Humboldt), and collection locality (“Canada de Supilote”); Nees’ annotation (*Jacobinia barlerioides*); a subsequent determination (*Justicia straminea*); and on the backside, a brief description of the plant as *J. straminea* noting “Habitat in Quito.”

plants treated as *Tetramerium ochoterena* for the past ca. 4 decades (e.g., yellow corollas). However, he provided measurements of the corolla (“3/4 poll. longa” = ca. 25 mm) and capsule (“4 lin. longa” = ca. 8.4 mm) that would suggest instead the yellow-flowered form of the similar species, *T. rubrum*. Measurements made from a high-resolution color image of the type specimen reveal: the single intact corolla appears to be ca. 50 mm long, lobes of the lower lip of the corolla are linear and ca. 1.3 mm wide, and a capsule is ca. 11 mm long. These updated measurements and the geographic locality all conform to data for *T. ochoterena* rather than *T. rubrum* (Daniel,

1986; see key to species above). Miranda (1941) described this species from Mexico as *Anisacanthus ochoterena*. It was transferred to *Tetramerium* by Daniel (1986), who noted its morphological affinities with that genus, despite having elongate corollas with recurved, linear lobes and prominently protruding stamens and style (Fig. 2M) that more closely resemble flowers of *Anisacanthus*. Subsequent molecular phylogenetic data confirmed its generic status in *Tetramerium* (Daniel et al., 2008; McDade et al., 2018). Resemblance of flowers between species of *Anisacanthus* and this sole species of *Tetramerium* likely results from adaptations to similar hummingbird pollinators.

3. *Tetramerium butterwickianum* T.F. Daniel

Description. Daniel (1986).

Distribution. Endemic to the DBBP in Mexico. Plants occur in south-central to southeastern Michoacán.

Flowering in DBBP. November-March.

Biotic communities in DBBP. Thornscrub and tropical deciduous forest at 225-500 m elevation.

Voucher by state. Michoacán: Municipio de La Huacana, 1.5 km NE de Los Ranchos, ladera NW de Cerro El Barril (18°42'40" N, 102°00'15" W), *V. Steinmann 4196* (CAS, IEB, MEXU).

Remarks. This species, previously known only from the type (Daniel, 1986), is now known from at least 6 collections. Conspicuous variation in the presence and/or densities of glandular trichomes on young stems, leaves, and inflorescence rachises are evident among them. The species total distribution (EOO) is 249.120 km² and the AOO is 24 km². If sufficient information concerning actual or potential threats (and locations) to this species were known, it could potentially be assessed as Endangered (EN) based on either the EOO or the AOO.

4. *Tetramerium cruzii* T.F. Daniel, sp. nov. Type. Mexico. Guerrero: Municipio de Arcelia, Campo Morado, Campamento Minero, 4.57 km W (18°11'45" N, 100°10'48" W), 1,177 m, bosque tropical caducifolio, 30-IV-2010 (flr, frt), *R. Cruz 8344* (holotype: FCME 129144) (Fig. 4).

This species is distinctive in the genus by the combination of its elongate spikes 12-14 mm wide near midpoint; bracts that taper distally from or below the midpoint, have the apical portion neither twisted nor reflexed, and bear marginal trichomes to 1 mm long; white and pseudopapilionaceous corollas 15 mm long; and pubescent capsules.

Perennial herbs to 5 dm tall. Young stems subterete to subquadrate, 2-fariously pubescent with mostly retrorse eglandular trichomes to 0.1 mm long and often with erect stipitate glandular trichomes near distal nodes, older stems with epidermis exfoliating in strips. Leaves not seen. Inflorescences of terminal, sessile to pedunculate dichasiate spikes to 100 mm long (including peduncle, if present), 12-14 mm wide (excluding flowers) near midspike, spikes more or less dense (median internodes 4-5 mm long), peduncles (if present) to 12 mm long, peduncles and rachis evenly pubescent with erect subglandular, eglandular, and glandular trichomes < 0.1-0.2 mm long, dichasia opposite, decussate, sessile, 1-2 (or more?)-flowered. Bracts lance-ovate to ovate to elliptic, 9-12 mm long, (2-) 2.2-4 mm wide, 2.9-4.1 (-4.5) times longer than wide, proximally tapered, distally acuminate to attenuate, erect, not twisted, apically mucronate, mucro

to 1 mm long, abaxial surface prominently (1 or) 3-veined, pubescent like rachis, margin ciliate with erect to flexuose eglandular trichomes to 1 mm long and erect to flexuose stipitate glandular trichomes 0.1-0.3 mm long. Bracteoles fused at base for ca. 0.5 mm, lance-linear to lanceolate, 7-9.5 mm long, 0.6-1.1 mm wide, abaxially pubescent with mostly erect eglandular trichomes 0.05-0.2 mm long and scattered stipitate glandular trichomes to 0.2 mm long, distally attenuate, apically subspinose, margin ciliate with flexuose eglandular trichomes to 0.7 mm long; secondary bracteoles (if present) smaller than bracteoles. Flowers sessile. Calyces 5-lobed, 2.5-3.5 mm long, tube 0.5 mm long, lobes subulate, 2-3 mm long, 0.2-0.3 mm wide, abaxially and marginally puberulent with a mixture of subglandular, stipitate glandular, and eglandular trichomes 0.01-0.1 mm long. Corollas pseudopapilionaceous, white with purplish markings on upper lip, 15 mm long, externally glabrous, tube 5 mm long, 1.8 mm in diam. at apex, narrow proximal portion 2.5 mm long, expanded throat 2.5 mm long, upper lip spatulate, 9 mm long, 4 mm wide, lower lip 10 mm long, lateral lobes obovate, 9 mm long, 5 mm wide, lower-central lobe conduplicate, ca. 6.5-7 mm long, 4.5 mm wide (spread open). Stamens ca. 7-7.5 mm long, thecae dark purple-maroon, 1.5 mm long. Pollen not observed. Styles 11 mm long, glabrous, stigmas 0.1 mm long, lobes not evident. Capsules 6-7.5 mm long, externally pubescent with erect to downward pointing eglandular trichomes to 0.1 mm long, stipe 1.8-2.5 mm long, head ovoid to ellipsoid, 4-5 mm long. Seeds 4, more or less plano-convex, 1.6-1.7 mm long, 1.5-1.7 mm wide, surfaces and margin minutely papillose and covered with more or less broad conical projections.

Distribution. Endemic to the DBBP in Mexico. Plants are known only from north-central Guerrero.

Flowering in DBBP. April.

Biotic community in DBBP. Tropical deciduous forest at 1177 meters elevation.

Conservation. Because the species is known solely by the type collection with no information on its current status or possible threats, a preliminary conservation assessment of Data Deficient (DD) concurs with IUCN (2022) guidelines.

Remarks. This species is named for Ramiro Cruz Durán, botanist at FCME, collector of the type and many other taxa from Guerrero, and helpful colleague. Guerrero is the second richest Mexican state for species of *Tetramerium*, with 10 species currently known to occur there (those listed herein plus *T. guerrerense* T.F. Daniel, which occurs in west-central Guerrero on the southwestern escarpment of the Sierra Madre del Sur and the adjacent coastal plain; Daniel 1986).

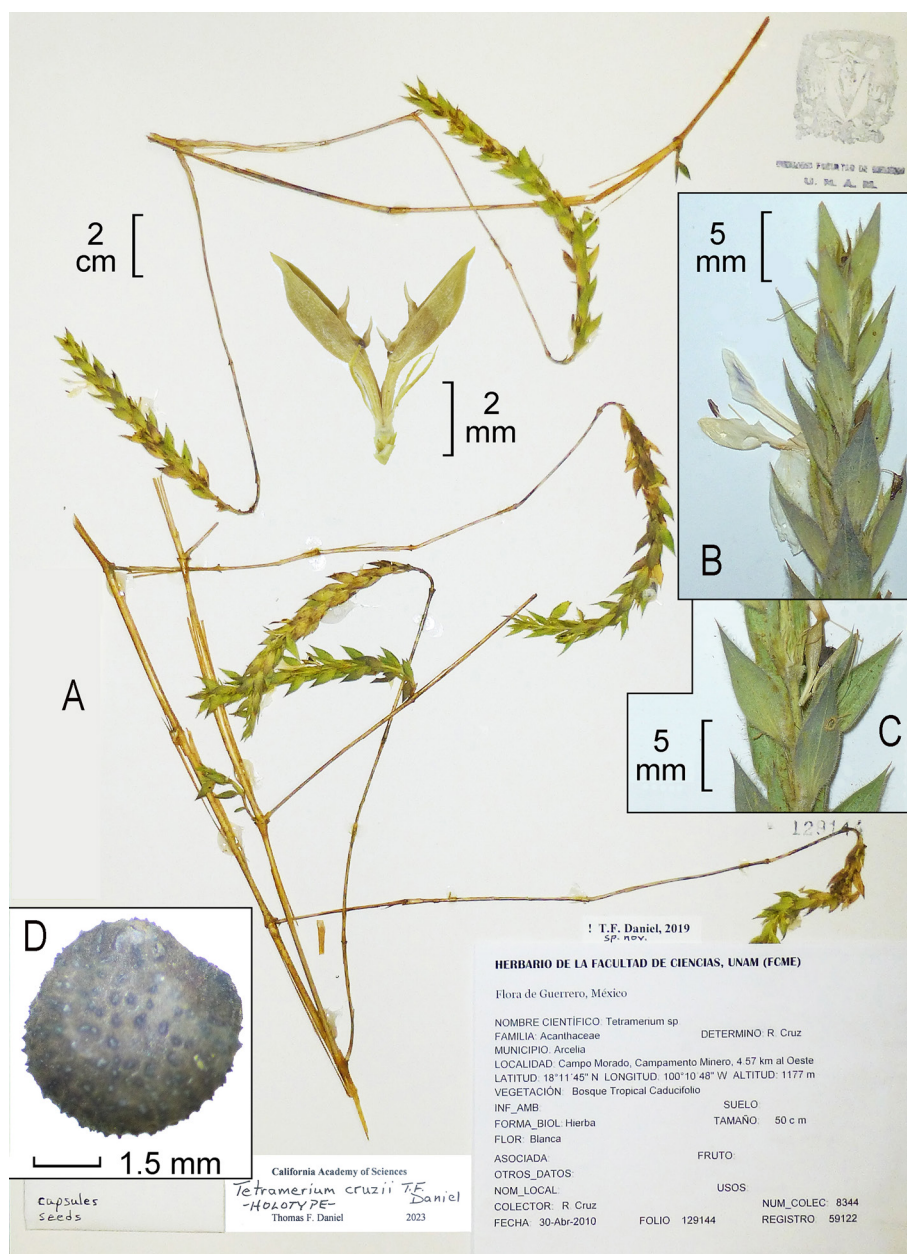


Figure 4. *Tetramerium cruzii*, holotype (Cruz 8344). A, Specimen at FCME; B, close-up of inflorescence with flower; C, close-up of inflorescence with capsule; D, close-up of seed.

5. *Tetramerium emilyanum* T.F. Daniel

Description. Daniel (1986).

Distribution. Endemic to the DBBP in Mexico. Plants occur in southeastern Michoacán.

Flowering in DBBP. November-December, March.

Biotic communities in DBBP. Tropical deciduous forest, tropical subdeciduous forest, and lower limit of oak zone at 550-630 m elevation.

Voucher by state. Michoacán: Municipio de Lázaro Cárdenas, carr. Nueva Italia-Playa Azul, 34 km S de Arteaga, [ca. 18°10'39.74" N, 102°16'30.71" W], J. Soto Núñez & S. Aureoles C. 7780 (IEB).

Remarks. This species is known definitively from only 2 collections from the same region of Michoacán. Plants intermediate between *T. emilyanum* and *T. nervosum*, potentially representing hybrids, were discussed by

Daniel (1986). Additional recent collections intermediate between these species from the same region of southeastern Michoacán include *Daniel 5316* (CAS) and *Steinmann & Carranza 2165* (CAS).

6. *Tetramerium glandulosum* Oerst.

Description. Daniel (1986).

Distribution. Endemic to western and southern Mexico (Baja California Sur, Chihuahua, Colima, Durango, Guerrero, Jalisco, México, Michoacán, Morelos, Oaxaca, Puebla, Sinaloa, Sonora, Zacatecas). Plants in the DBBP occur from southwestern to northeastern Michoacán eastward through southern México, the northern half of Guerrero, and Morelos to central and southern Puebla and northwestern Oaxaca.

Flowering in DBBP. November-April

Biotic communities in DBBP. Thornscrub, tropical deciduous forest, tropical subdeciduous forest, and oak forest at 700-2,100 m elevation.

Voucher by state. Guerrero: 15.9 mi N of Zumpango del Río in Cañón del Zopilote, [ca. 17°49'46.30" N, 099°33'50.02" W], *W. Anderson & C. Laskowski 4321* (MICH). México: Municipio de Ixtapan de la Sal, near Hwy. 55 between El Salitre and Ixtapan de la Sal (18°49'58.83" N, 099°40'2.96" W), *D. Denham 3210* (CODAGEM). Michoacán: Municipio de Churumuco, El Limón, Ejido Llano Ojo de Agua (18°43'51" N, 101°40'23" W), *M. Rojas 779* (MEXU). Morelos: Municipio de Puente de Ixtla, 6 km SE de Tilzapotla, camino a El Salto o 7 km de El Salto camino a Tilzapotla (18°28'06" N, 099°16'18" W), *R. Ramírez et al. 2995* (MEXU). Oaxaca: La Reforma, 20 km NW de Tamazulapan (17°44'N, 097°44'W), *A. García M. et al. 2058* (MEXU). Puebla: Municipio de Acatlán de Osorio, Barranca El Terrero, llegando por La Trinidad (18°12'41.30" N, 098° 0'46.91" W), *C. Rojas-Martínez et al. 45* (MEXU).

Remarks. *Tetramerium glandulosum* is known from many collections throughout the DBBP. The collection cited above from the State of México represents the first report of the species in that state. It is the only species of *Tetramerium* in the DBBP with relatively large and pseudopapilionaceous corollas that are yellow (more intensely yellow and/or larger than in any of the cream to yellowish forms of *T. nervosum* or *T. tenuissimum*), and usually with 2 elongate reddish bands on the upper lip. It also differs from other species with white or cream to yellowish pseudopapilionaceous corollas by its habit (fragrant and viscid shrub to 3 m tall vs. non-fragrant perennial herbs to shrubs to 1 m tall).

7. *Tetramerium glutinosum* Lindau

Description. Daniel (1986).

Distribution. Endemic to the DBBP in Mexico. Plants occur from eastern Michoacán and southwestern México through Morelos and the northern half of Guerrero to western and south-central Puebla.

Flowering in DBBP. December-July.

Biotic communities in DBBP. Thornscrub, tropical deciduous forest, and ecotone between tropical deciduous and oak forests at 280-1,680 m elevation.

Voucher by state. Guerrero: Municipio de General Canuto Neri (Acapetlahuaya), ca. 4 km NE de El Crustel y 19 km NE de Arcelia, carr. Cd. Altamirano-Iguala (18°23'09.5" N, 100°07'43.5" W), *J. Soto N. 21320* (IEB, MEXU). México: 25 km S de Amatepec, terracería Amatepec-Arcelia, [ca. 18°31'38.28" N, 100°13'37.39" W], *G. Flores F. & L. Terpán A. 745* (MEXU). Michoacán: Municipio de Huetamo, sobre Mex. 51, 7 km S de Huetamo (18°34'22" N, 100°51'51" W), *V. Steinmann et al. 4116* (CAS, IEB, MEXU, XAL). Morelos: Municipio de Yautepec, Cañón de Lobos, 12-14 km E de Cuernavaca, carretera (libre) Cuernavaca-Cuautla, [ca. 18°51'31.93" N, 099°07'01.89" W], *S. Koch & J. García P. 7649* (MEXU). Puebla: 5 mi W of Matamoros, [ca. 18°34'07.62" N, 098°32'53.22" W], *D. Dunn & D. Dunn 18755* (ENCB, MSC, NY).

Remarks. Daniel (1986) cited 11 collections of this species. At least 47 collections are now known from throughout its total geographic range in the DBBP. The total geographic distribution of the species (EOO) is 34,092.476 km² and the AOO is 164 km². If sufficient information concerning actual or potential threats (and locations) to this species were known, it could potentially be assessed as Endangered (EN) based on the AOO.

Tetramerium glutinosum is a fragrant and more or less viscid perennial herb to shrub to 1 m tall. It is the only species of the genus in the DBBP with purple flowers. The conspicuous mucro at the bracteal apex is often conspicuously curved, bent, or coiled. Floral visits by a megachilid bee (*Dianthidium* sp.) were noted by Daniel (1986).

8. *Tetramerium langlassei* G.B. Happ

Description. Daniel (1986).

Distribution. Southern Mexico (Guerrero, Jalisco, Michoacán, Veracruz). In the DBBP, plants occur from western to eastern Michoacán and southward into western Guerrero.

Flowering in DBBP. November-February, May

Biotic communities in DBBP. Tropical deciduous forest and ecotone between tropical deciduous forest and oak forest at 302-1,450 meters elevation.

Voucher by state. Guerrero: Municipio de Coahuayutla de Guerrero, 1.5 km N de La Vainilla (18°14'53.5" N,

101°30'30.4" W), *J. Calónico Soto 13457* (MEXU). Michoacán: Municipio de La Huacana, E foothills of Sierra Las Cruces, 3.5 km (air) SW of Los Ranchos, trail to La Verdura (ca. 18°41'00" N, 102°02'45" W), *V. Steinmann 3180* (CAS, IEB).

Remarks. Daniel (1986) cited 11 collections of this species; at least 20 collections are currently known.

9. *Tetramerium michoacatum* T.F. Daniel, sp. nov. Type. Mexico. Michoacán: Municipio de Churumuco, La Barranca, Ejido Llano Ojo de Agua (18°42'11" N, 101°40'20" W), 365 m, bosque tropical caducifolio, 24-IV-2016 (flr), *M. Rojas 735* (holotype: MEXU, accession 1499906!). (Fig. 5).

Tetramerium michoacatum differs from *T. nervosum* by its inflorescence rachis and bracteal margins with more or less densely floccose (vs. neither dense nor floccose) trichomes, distally apically attenuate (vs. rounded to acute to acuminate) bracts, longer (10-13 vs. 1.5-10 mm) bracteoles, generally longer (23-29 vs. 10-23 mm) corollas, and longer (2-3 vs. 0.9-1.7 mm) anther thecae.

Perennial herbs or shrub to 1 m tall. Young stems subquadrate to 2-sulcate, 2-fariously pubescent with retrorse (to flexuose, especially at nodes) eglandular trichomes 0.2-0.7 mm long, older stems with epidermis exfoliating in strips. Leaves petiolate, petioles 3-21 mm long, pubescent with straight to flexuose eglandular trichomes, blades lance-ovate, to ovate, 18-83 mm long, 5-29 mm wide, 2.3-5.5 (-8.3) times longer than wide, acuminate to attenuate at apex, rounded to acute to subattenuate at base, adaxial surface pubescent with erect to antrorse to antrorsely appressed eglandular trichomes 0.05-0.3 mm long, abaxial surface more or less evenly pubescent with flexuose to retrorse to antrorse eglandular trichomes 0.1-0.3 mm long, margin ciliate with mostly antrorse eglandular trichomes to 0.5 mm long. Inflorescences of terminal, sessile to short-pedunculate dichasiate spikes to 75 mm long (including peduncle) and 9-12 mm wide (excluding flowers) near midspike, spikes more or less dense (median internodes 4-6 mm long), peduncles (if present) to 2 mm long, densely and evenly pubescent with flexuose to mostly straight and downward pointing eglandular trichomes to 0.8 mm long, rachis more or less densely and more or less 2-fariously pubescent with flexuose and largely interwoven eglandular trichomes to 1.5 mm long (appearing more or less floccose), dichasia opposite, decussate, sessile, 1-2 (or more?)-flowered. Bracts lance-ovate to narrowly ovate-elliptic, 11-16 mm long, 3-5 mm wide, 2.8-4.7 times longer than wide, proximally slightly tapered and truncate at base, distally attenuate, erect to slightly recurved, straight or slightly twisted, apically mucronate, mucro 0.1-0.3 mm long,

abaxial surface prominently 3-veined, proximal bracts abaxially pubescent with an understory of subglandular and stipitate glandular trichomes 0.02-0.2 mm long and an overstory of more or less interwoven eglandular trichomes to 0.5 mm long, distal bracts less densely pubescent with a similar understory and an overstory of flexuose eglandular trichomes to 1 mm long (especially along veins), margin of bracts ciliate with subglandular and glandular trichomes to 0.5 mm long and flexuose eglandular trichomes to 2 mm long, eglandular marginal trichomes becoming cotton-like and so dense as to obscure rachis, bracteoles, and calyces. Bracteoles linear-lanceolate, 10-13.5 mm long, 0.8-1.5 mm wide, abaxially pubescent with flexuose trichomes to 2.5 mm long, apically acute, emucronate, margin ciliate like bracts but with trichomes sparser. Flowers sessile. Calyces 5-lobed, 4.5-6.5 mm long, tube 0.5-1 mm long, lobes subulate, subequal in size, 3.5-6 mm long, 0.3-0.4 mm wide, abaxially and marginally pubescent with an understory of erect eglandular and subglandular to glandular trichomes 0.01-0.02 (-0.05) mm long and an overstory of sparse flexuose eglandular trichomes to 1 mm long. Corollas pseudopapilionaceous, white with upper lip cream bearing a purplish chevron outlined with maroon, (21-) 23-29 mm long, externally glabrous, tube subcylindric, 12-16 mm long, 1.7-2.2 mm in diam. at apex, narrow proximal portion 8-11 mm long, more or less expanded throat 2-5 mm long, upper lip obovate to subspatulate, 11-14.6 mm long, 3.5-4 mm wide, lower lip 13.5-15 mm long, lateral lobes elliptic to obovate-elliptic, 12-13 mm long, 6.5-10 mm wide, lower-central lobe conduplicate, 8-12 mm long, 4.4-6 mm wide (spread open). Stamens 7.5-13 mm long, thecae 2-3 mm long. Pollen euprolate, polar diameter (P) 46-53 μm , equatorial diameter (E) 28-33 μm , P:E = 1.4-1.8. Styles 19-20 mm long, glabrous distally and sometimes with a few eglandular trichomes proximally, stigmas 0.2-0.3 mm long, lobes not evident, ovary glabrous. Capsules and seeds not seen.

Distribution. Endemic to the DBBP in Mexico. Plants occur in the northern watershed of the Río Atoyac in the Cerro Conchitero region of southeastern Michoacán.

Flowering in DBBP. November-December, April.

Biotic communities in DBBP. Tropical deciduous forest at 365-664 meters elevation.

Conservation. The species is known only from 3 collections. The known distribution of *T. michoacatum* consists of an EOO of 46.592 km² and the AOO is 12 km². Additional information on actual or potential threats (and locations) would be useful to make a potential conservation assessment.

Paratypes. Mexico. Michoacán: Municipio de Churumuco, Cerro El Zipimo, ca. 3.7 km (línea recta)

NW del Ejido Llano de Ojo de Agua (18°42'22" N, 101°40'18" W), 530 m, 15-IX-2023 (flr), *G. Ibarra Manríquez et al.* 7326 (IEB, MEXU); Municipio de Churumuco, Las Higueras, Ejido Llano Ojo de Agua (18°43'36" N, 101°39'58" W), 664 m, 13-XI-2014 (flr), *M. Rojas* 283 (MEXU). Additional duplicate specimens to be distributed.

Remarks. The species is named for the Mexican state from which all plants of it known to date have originated. Michoacán is the richest Mexican state for species of *Tetramerium*, with 13 species currently known to occur there (those listed herein plus *T. diffusum* Rose and *T. rzedowskii* T.F. Daniel, both of which occur just to the west and northwest of the DBBP). Capsules and seeds were not available for measurements for *T. michoacanum*. The presence or absence of eglandular trichomes on capsules in species of *Tetramerium* is a diagnostic character for all species except *T. nervosum*, in which both states occur. It is possible that capsules of *T. michoacanum* are glabrous because ovaries seen lack trichomes. However, some species with pubescent capsules (e.g., *T. tenuissimum* and perhaps others) have the younger ovaries glabrous and the older ones pubescent. Thus, capsule pubescence of *T. michoacanum* remains to be determined. The euprolate pollen of *T. michoacanum* is typical for the genus (e.g., Daniel, 1986, 1998) and shows harmomegathic variation that affect its shape (Fig. 6).

The distinctions noted in the key above distinguish *T. michoacanum* from morphologically similar and/or geographically close congeners. It also shares some morphological traits (e.g., dense and elongate trichomes in the inflorescence, especially along the bracteal margins) with *T. tetramerioides* (Lindau) T.F. Daniel from a region of tropical deciduous forest in southeastern Oaxaca. *Tetramerium tetramerioides* differs from *T. michoacanum* by: young stems with an understory of glandular trichomes 0.05-0.2 mm long; spikes 3-7 mm wide near midpoint; bracts linear-lanceolate to lanceolate-elliptic, 7-10 × 1-2.5 mm, and usually with only the midvein evident; bracteoles 6-8 × 0.5-0.8 mm; calyces 3.2-4 mm long; and corollas 14-15 mm long. Although duplicates are noted on the specimen labels of all 3 known collections cited above, the destinations of most of those duplicates remain unconfirmed at present.

10. *Tetramerium nervosum* Nees

Description. Daniel (1986).

Distribution. USA, Mexico (Aguascalientes, Baja California Sur, Campeche, Chiapas, Chihuahua, Coahuila, Colima, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, Quintana Roo,

San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Veracruz, Yucatán, Zacatecas), Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Ecuador, and Peru. Plants occur throughout most of the DBBP (from southeastern Jalisco through Michoacán, southern México, northern and central Guerrero, and Morelos to south-central Puebla and northwestern Oaxaca). It has not been recorded from portions of the states of Ciudad de México, Tlaxcala, and Veracruz that are sometimes included in delimitations of the DBBP.

Flowering in DBBP. September-May.

Biotic communities in DBBP. Thornscrub, tropical deciduous forest, tropical deciduous forest-oak forest ecotone, oak forest, tropical deciduous forest-pine-oak ecotone, pine-oak forest at 200-1,940 meters elevation.

Voucher by state. Guerrero: Municipio de Teloloapan, Tehuixtla (18°18'16.8" N, 099°55'34.3" W), *D. Tejero-Díez & A. Torres* 6466 (MEXU). Jalisco: Municipio de Jilotlán de los Dolores, 7 km SE de Huapala, camino a Jilotlán, [ca. 19°20'33.93" N, 103°05'08.41" W], *A. Mendoza et al.* 3700 (MEXU). México: Municipio de Tejuzilco, ca. 2 km NO del centro de Tejuzilco, camino a San José de La Laguna, en la col. Vista Bella (18°54'46.1" N, 100°09'26.5" W), *J. Soto N.* 21287 (MEXU). Michoacán: Municipio de Carácuaro, camino de La Eréndira a El Puerto del Salitrillo, ca. 2 km E del entronque con la carr. La Eréndira-Caracuáro (18°50'29.50" N, 100°55'37.19" W), *J. Soto N. & B. Gómez Rosales* 17372 (MEXU). Morelos: Municipio de Tepalcingo, 4 km SW de El Limón (18°30'00" N, 098°57'28" W), *A. Ramírez Guadarrama et al.* 789 (MEXU). Oaxaca: Dto. Huajuapán, Cañada Cuasá, 3 km (línea recta) N de San Juan Bautista Suchitepec (17°59'57.3" N, 097°39'10.5" W), *R. Redonda Martínez et al.* 460 (MEXU). Puebla: Municipio de Acatlán de Osorio, Barranca La Macahuite (18°12'41.32" N, 098°00'46.91" W), *C. Rojas-Martínez et al.* 49 (MEXU).

Remarks. This is the most widely distributed and morphologically diverse species in the genus (Daniel 1986). It is distributed from the southwestern USA to northwestern Peru. Plants in the DBBP show morphological variation in calyx lobe number (4 or 5), bract shape (lance-ovate to ovate to elliptic to subcircular), corolla color (white to pale yellow), pubescence (length, form, and glandular vs. eglandular trichomes), and patterning of discolorations on the upper lip (Fig. 2K, L). Daniel (1986) noted visitation to flowers of *T. nervosum* by several genera of bombyliid flies and a genus of hesperiid butterflies.

11. *Tetramerium pauciflorum* T.F. Daniel & V.W. Steinm.

Description. Daniel and Steinmann (2016).

Distribution. Endemic to the DBBP in Mexico. The species has a restricted distribution in southeastern

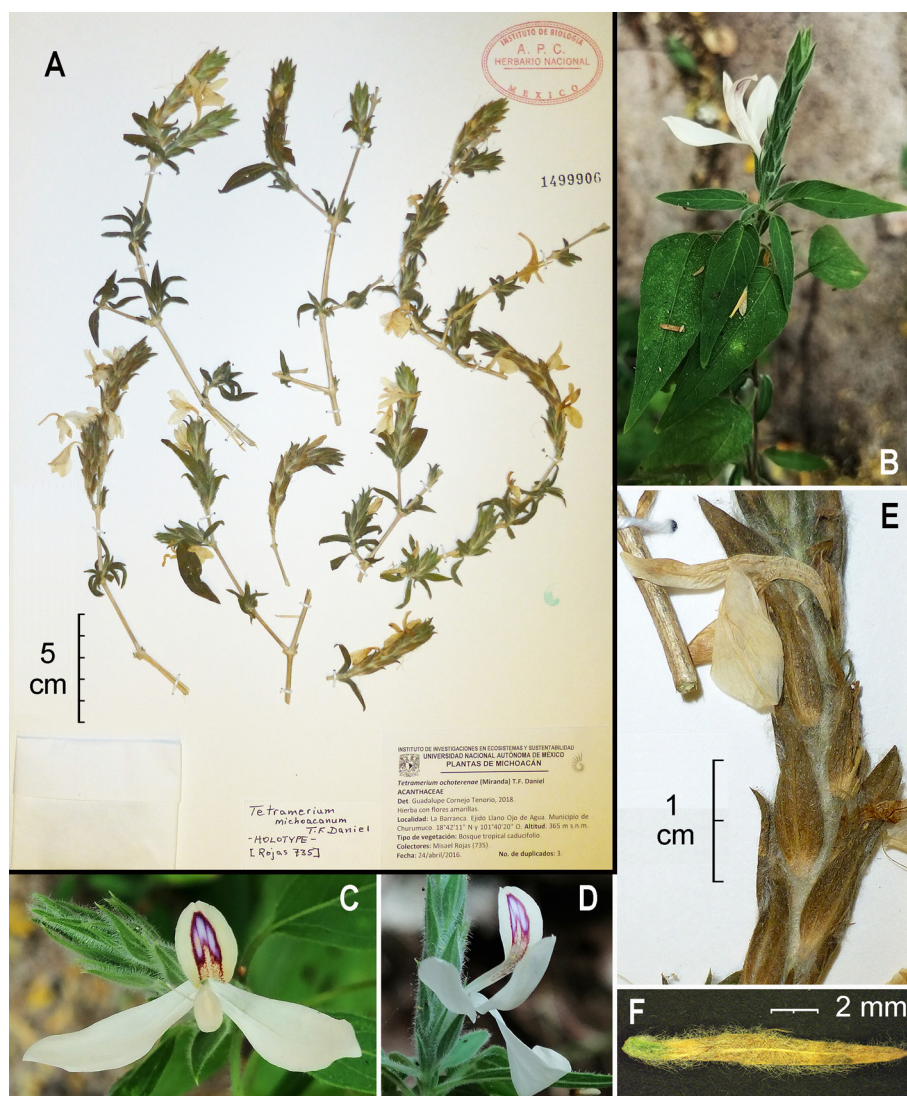


Figure 5. *Tetramerium michoacanum*. A, Holotype at MEXU (Rojas 735); B, live plant with leaves and flowering inflorescence (Ibarra Manríquez et al. 7326); C, live flower (frontal view; Ibarra Manríquez et al. 7326); D, live flower (side view; Ibarra Manríquez et al. 7326); E, portion of inflorescence with flower showing dense, floccose pubescence concealing rachis (from holotype); F, bracteole (from holotype). Photos B-D by G. Ibarra-Manríquez.

Michoacán. Daniel and Steinmann (2016) noted that it is known from 2 regions ca. 30 km apart, the valleys of the Río Marqués to the north and the Río Tepalcatepec to the south.

Flowering in DBBP. November, February, May.

Biotic community in DBBP. Tropical deciduous forest at 250–400 meters elevation.

Conservation. The 5 known collections from 4 localities reveal an extent of occurrence (EOO) of ca. 3 km² and an area of occupancy (AOO) of 8 km². Despite the limited

distribution, Daniel and Steinmann (2016) provided a rationale for a provisional conservation assessment of Least Concern (LC) for this species. Additional information on actual or potential threats (and locations) would be useful to make a potential conservation assessment.

Voucher by state. Michoacán: Municipio de Múgica, 5.5 km NE de la salida a Nueva Italia sobre la autopista Morelia-Lázaro Cárdenas (19°01'57" N, 102°03'12" W), V. Steinmann & Y. Ramírez-Amezcuca 8089 (CAS, MEXU, RSA).

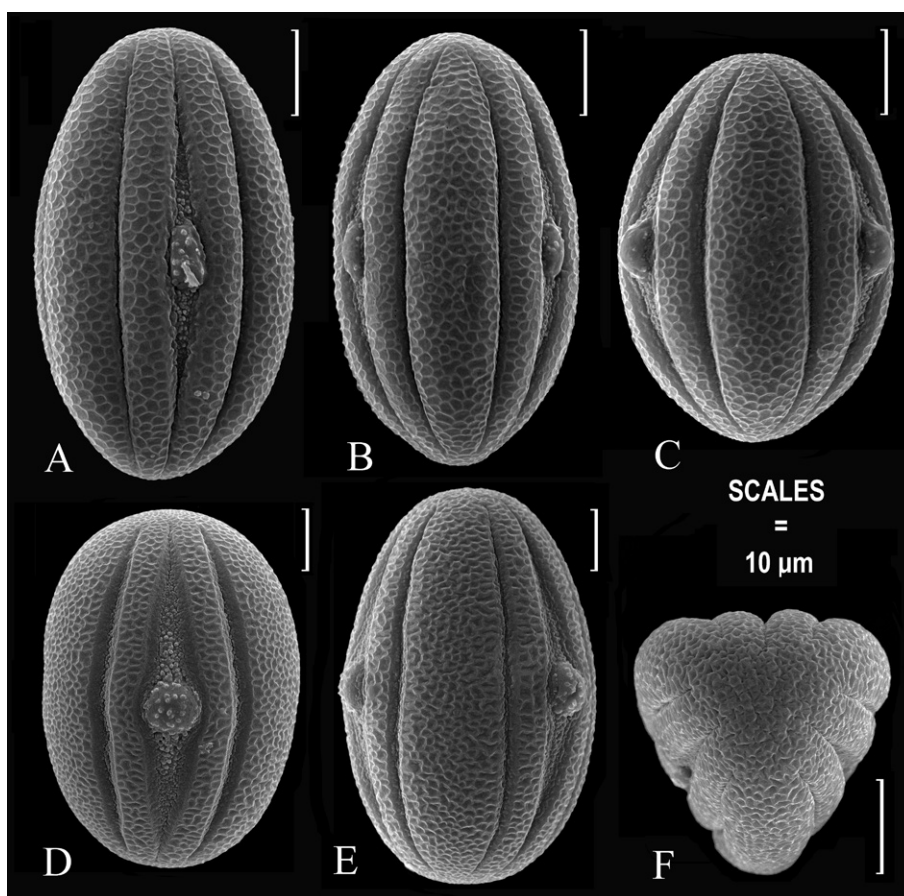


Figure 6. Pollen of *Tetramerium michoacanum* (Rojas 735, A-C) and *T. barlerioides* (D-F). A, Apertural view; B, interapertural view; C, interapertural view (showing harmomegathic variation); D, apertural view (Steinmann & Porter 4921); E, interapertural view (Steinmann & Porter 4921); F, polar view (Grimes et al. 2612).

12. *Tetramerium rubrum* G.B. Happ

Description. Daniel (1986).

Distribution. Endemic to west-central Mexico (Guerrero, Jalisco, México, Michoacán, Nayarit). Plants occur throughout much of the DBBP: western Jalisco, southern and northeastern Michoacán, western Guerrero, western México, and southwestern Puebla. It appears to be most abundant in Michoacán and western México. No collections have been seen from Morelos, central and eastern Guerrero, or Oaxaca.

Flowering in DBBP. November-June.

Biotic communities in DBBP. Tropical deciduous forest, oak forest, and pine-oak forest at 200-1,700 meters elevation.

Voucher by state. Guerrero: Municipio de La Unión, MEX 134, ca. 31 km NE de Vallecitos y 3 km E de Puerto del Bálsamo (17°58'49" N, 101°12'16" W), *V. Steinmann*

& *J. Porter* 4932 (CAS, MEXU). Jalisco: Municipio de de Jilotlán de los Dolores, 5 km al N de Tepalcatepec, [ca. 19°13'33.74" N, 102°52'04.83" W], *J. Rzedowski* 16639 (ENCB). Mexico: Municipio de Santo Tomás de los Plátanos, valley just N of (below) Nuevo Santo Tomás (19°11'05.37" N, 100°15'55.93" W), *T. Daniel et al.* 12323 (CAS). Michoacán: Municipio de Buenavista Tomatlán, ca. 3 km SW de El Terrero, [ca. 19°02'34.91" N, 102°40'24.62" W], *J. Soto Núñez et al.* 8045 (CAS, MEXU).

Remarks. The very similar species *T. abditum* and *T. rubrum* both occur in Nayarit and Michoacán (and likely Jalisco, but *T. abditum* has not been recorded from that state, which lies between the other 2), and maintain their distinctions as noted in the key. Plants of *T. rubrum* with yellow corollas appear almost as frequently as those with red flowers. Collections with yellow corollas are known

from Guerrero (*Campos R. 360*, MEXU; *Moreno Gtz. & Alberto Monroy 742*, MEXU) and Michoacán (*Daniel & Butterwick 3270*, ASU, CAS, ENCB, MEXU, MICH, NY; *Rojas 704* and *780*, MEXU; *Roman de Soto N. et al. 8045*, CAS; *Steinmann 5065*, CAS; *Steinmann et al. 3997*, CAS).

13. *Tetramerium tenuissimum* Rose

Description. Daniel (1986).

Distribution. Western and southern Mexico (Campeche, Chiapas, Chihuahua, Colima, Guanajuato, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Sinaloa, Sonora, Veracruz, Yucatán, Zacatecas), Guatemala, and El Salvador. In the DBBP this species is widespread, occurring from eastern Michoacán and western México through northern and central Guerrero and Morelos to the borders of Puebla and Oaxaca. It likely occurs within the latter 2 states as well, but no collections from them have been seen.

Flowering in DBBP. October–April.

Biotic communities in DBBP. Tropical deciduous forest and oak forest at 280–1,500 meters elevation.

Voucher by state. Guerrero: Municipio de Taxco, 4 km SW del cruceo Cacahuamilpa-Toluca, camino a Taxco, [ca. 18°34'20.01" N, 099°34'5.89" W], *E. Martínez S. & E. Cabrera 73* (MEXU). México: Municipio de Santo Tomás de los Plátanos, valley just N of (below) Nuevo Santo Tomás (19°11'05.37" N, 100°15'55.93" W), *T. Daniel et al. 12328* (CAS). Michoacán: Municipio de Huetamo, MEX 51, 7 km S de Huetamo (18°34'22" N, 100°51'51" W), *V. Steinmann et al. 4117* (CAS, MEXU). Morelos: Municipio de Jonacatepec, 2 km S de Tlayca, [ca. 18°41'28.43" N, 098°51'54.72" W], *E. Cabrera C. et al. 12137* (MEXU).

Remarks. *Tetramerium tenuissimum* is newly documented from the state of México. Daniel (1986) noted visitation to flowers of this species by bombyliid flies. Plants are sometimes confused with *T. nervosum*. These species can be distinguished by the characters in the following couplet:

- 1a. Bracts with margins conspicuously and more or less densely ciliate with trichomes to 3.5 mm long, at least some (usually most) of the trichomes \geq 1 mm long, abaxially more or less palmately and prominently 3 or 5 (or 7)-veined, apically usually more or less recurved and partially twisted; corolla tube 5–12 mm long *T. nervosum*
- 1b. Bracts with margins inconspicuously and more or less sparsely ciliate with trichomes to 0.5 mm long, abaxially more or less palmately and often obscurely (1 or) 3-veined, apically erect and not twisted; corolla tube (2.5-) 3–5 mm long *T. tenuissimum*

14. *Tetramerium vargasiae* T.F. Daniel & R. Cruz Durán
Description. Daniel and Cruz Durán (2016).

Distribution. Endemic to the DBBP in Mexico. Plants occur in north-central Guerrero.

Flowering in DBBP. March.

Biotic community in DBBP. Tropical deciduous forest at 650 meters elevation.

Conservation. Because the species is known solely by the type collection with no information on its current status or possible threats, a preliminary conservation assessment of Data Deficient (DD) concurs with IUCN (2022) guidelines.

Voucher by state. Guerrero: Municipio de Huitzucó de los Figueroa, 0.7 km NE de San Francisco Ozomatlán [ca. 17°56'0.63" N, 099°19'37.41" W], *A. Vargas P. 288* (FCME).

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