



Naming the long-known: a new species of *Desmopsis* (Annonaceae) endemic to Mexico

Nombrando lo conocido: una nueva especie de *Desmopsis* (Annonaceae) endémica de México

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Abstract

Background and Aims: A frequently collected species of *Desmopsis* (Annonaceae) in Mexico has remained indeterminate for more than 30 years. Its floral characteristics are similar to those present in the Asian genus *Guamia* (now *Meiogyne*), and for many years it has been named “*Guamia mexicana*”, but not formally described. Recently, it was shown that “*Guamia mexicana*” is phylogenetically related to *Desmopsis* and *Stenanona* and not to *Guamia*. However, and despite being frequently collected, its taxonomic status has not been clarified. Here, the phylogenetic relationships and the morphological and ecological characteristics that distinguish “*Guamia mexicana*” from other species were studied. As a result, this new species is herein described.

Methods: The new species was recognized using the unique combination of features through comparisons with morphologically similar species and a literature review. Its pollen characteristics were analysed using scanning electron microscopy. Its phylogenetic relationships were determined based on previously published phylogenies. Lastly, its conservation status was tentatively assessed by calculating extent of occurrence (EOO) and area of occupancy (AOO) using the GeoCAT tool and applying the IUCN Red List categories and criteria.

Key results: A new species of Annonaceae endemic to Mexico, namely *Desmopsis ibarrarum*, is described and illustrated. It is distinguished from other *Desmopsis* species by the combination of long and cylindrical fruits with many seeds, with a hard and woody testa and densely covered by very small sericeous hairs (velvety), glabrous leaves with percurrent tertiary venation, the absence of leafy bracts on the pedicels, the morphological differentiation of internal and external petals, and the partial fusion of the sepals.

Conclusions: *Desmopsis ibarrarum* is only closely related to *Desmopsis dubia* and both species are here considered members of a particular lineage within the *Desmopsis-Stenanona* clade, the “*Desmopsis dubia* group”.

Key words: Chiapas, IUCN Red List, karst forests, Neotropical region, pollen grains, tribe Miliuseae.

Resumen

Antecedentes y Objetivos: Una especie de *Desmopsis* (Annonaceae) colectada frecuentemente en México ha permanecido indeterminada durante más de 30 años. Sus características florales son similares a las del género asiático *Guamia* (actualmente *Meiogyne*), y desde hace muchos años se le ha nombrado como “*Guamia mexicana*”, pero no ha sido descrita formalmente. Recientemente se demostró que “*Guamia mexicana*” está filogenéticamente emparentada con *Desmopsis* y *Stenanona* y no con *Guamia*. Sin embargo, y a pesar de ser colectada con frecuencia, no se ha aclarado su estatus taxonómico. En este artículo se estudiaron las relaciones filogenéticas y las características morfológicas y ecológicas que distinguen a “*Guamia mexicana*” de otras especies. Como resultado, esta especie nueva es aquí descrita.

Métodos: El reconocimiento de la especie nueva se basó en la correlación de varios caracteres morfológicos, a través de comparaciones con especies morfológicamente similares y de la revisión de literatura. Las características de su polen se analizaron mediante microscopía electrónica de barrido. Sus relaciones filogenéticas se determinaron con base en filogenias publicadas previamente. Finalmente, a partir de sus localidades conocidas se calculó extensión de ocurrencia (EOO) y área de ocupación (AOO) en GeoCAT, y aplicando las categorías y criterios de la Lista Roja de la UICN se determinó su estado de conservación.

Resultados clave: *Desmopsis ibarrarum*, una nueva especie de Annonaceae endémica de México, es descrita e ilustrada. Se distingue de otras especies de *Desmopsis* por la combinación de frutos largos y cilíndricos con muchas semillas, con una testa dura y leñosa y densamente cubierta por pelos seríceos muy pequeños (aterciopelados), por sus hojas glabras con venación terciaria percurrente, la ausencia de brácteas foliosas en los pedicelos, la diferenciación morfológica de los pétalos internos y externos, y por la fusión parcial de los sépalos.

Conclusiones: *Desmopsis ibarrarum* esta únicamente relacionada a *Desmopsis dubia* y las dos especies se consideran aquí miembros de un linaje particular dentro del clado *Desmopsis-Stenanona*, el “grupo *Desmopsis dubia*”.

Palabras clave: bosque kárstico, Chiapas, granos de polen, Lista Roja de la UICN, región neotropical, tribu Miliuseae.

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Introduction

The Annonaceae family, with around 108 genera and almost 2500 species of trees, shrubs and lianas, is among the most diverse lineages within the Magnoliidae clade (Canellales, Laurales, Magnoliales and Piperales) (Massoni et al., 2015; Guo et al., 2017). Most of the Annonaceae genera (except *Asimina* Adans., endemic to the United States of America) are distributed in tropical regions, where they contribute significantly to the floristic composition of lowland forests. In Mexico 12 genera and around 60 species are present. *Desmopsis* Saff., is one of the most species-rich genera in Mexico, where it is represented by 11 species, nine of which are endemic to this country (Espinosa-Jiménez and Ortiz-Rodríguez, 2020).

Desmopsis is a Neotropical genus endemic to Mesoamerica (from western Mexico to the Chocó-Darien region). Phylogenetic evidence shows that *Desmopsis* is part of the subtribe Sapranthinae, a clade composed of four Neotropical genera (*Desmopsis*, *Sapranthus* Seem., *Stenanona* Standl., and *Tridimeris* Baill.), embedded in the predominantly Asian tribe Miliuseae (Ortiz-Rodríguez et al., 2016a). Sapranthinae are composed of two main clades, one formed by the sister genera *Sapranthus* and *Tridimeris* and another with *Desmopsis* and *Stenanona* (Ortiz-Rodríguez et al., 2016a). It is now known that *Desmopsis* is not monophyletic and some of its species show a close phylogenetic relationship with species of *Stenanona* (Ortiz-Rodríguez et al., 2016a). The genus name *Desmopsis* has priority over that of *Stenanona*; however, the relationships between species are not clearly resolved, yet many species of both genera were not included in the phylogenetic analyses. Thus, a taxonomic decision based on currently available evidence is premature at this stage.

Under the traditional concept of the genus, *Desmopsis* species can be recognized by the combination of long-pedunculated inflorescences, often leafy peduncle bracts, trimerous flowers with free, yellow or greenish and somewhat rigid petals, disulcate globose pollen, and berry-like monocarps with discoid seeds (Safford, 1916; Schatz, 1987). Thus, 25 species of *Desmopsis* were accepted in the most recent revision of the genus (Schatz et al., 2018a). However, the knowledge of its diversity is still incomplete and as a result of recent botanical explorations

in the limestone karst forests of Mexico, new species have been recently described (Jiménez-Ramírez and González-Martínez, 2016; Schatz et al., 2018a; Espinosa-Jiménez and Ortiz-Rodríguez, 2020; Gómez-Domínguez and Ortiz-Rodríguez, 2020).

The species described here can be assigned to the non-monophyletic genus *Desmopsis* on the basis of its trimerous flowers with rigid and yellow petals, and by its pollen and seed characteristics. However, for more than 30 years, its long and cylindrical fruits with many seeds, its hard and woody testa densely covered by very small sericeous hairs (velvety), its leaves with percurrent tertiary venation, the absence of leafy bracts on the pedicels, and the morphological differentiation of internal and external petals and the partial fusion of its sepals, have precluded its inclusion in the genus *Desmopsis* as traditionally circumscribed (Schatz, 1987; Schatz et al., 2018a). Moreover, in 1987 as part of his Ph.D. thesis, George Schatz noted that the internal floral characteristics of this species resemble those of *Guamia mariannae* (Saff.) Merr., in the form and thickness of the petals and the presence of food bodies at the base of the inner ones, and it was tentatively named “*Guamia mexicana*” (Schatz, 1987), but not formally described. Several years later, it was shown that this species is phylogenetically related to *Desmopsis* and *Stenanona* and not to *Guamia mariannae* (= *Meiogyne cylindrocarpa* (Burck) Heusden) (Chaowasku et al., 2014)). However, and despite being frequently collected, its taxonomic status has not been clarified.

Therefore, the main objective of this study was to formally describe this new species of *Desmopsis*, as well as elucidate its phylogenetic relationships and the morphological and ecological characteristics that distinguish it from other species within the genus.

Material and Methods

Species differentiation

The new species was recognized using the unique combination of features criterion (Donoghue, 1985) through comparisons with morphologically similar species and literature review. I visited and reviewed the specimens of *Desmopsis* deposited in the scientific collections of the Instituto de Biología, Universidad Nacional Autónoma de



México (UNAM) and in those of the Instituto de Ecología, A.C. (INECOL) (MEXU and XAL herbaria, respectively, Thiers, 2022).

Pollen description

I analysed the pollen of the new species and three additional Mexican species of *Desmopsis* (*D. dubia* Ortiz-Rodr. & Espinosa-Jim., *D. duran* Gómez-Domínguez & Ortiz-Rodr., and *D. trunciflora* (Schltdl. & Cham.) G.E. Schatz) using the scanning electron microscope (SEM) at the Photography, Microscopy of the Biodiversity Lab 1, UNAM. The flowering material for SEM was rehydrated with hot water for two minutes and immersed in FAA (Formaldehyde-water-alcohol) for 24 h and then washed twice with distilled water. The material was dehydrated with gradual alcohols (ethanol) solutions at 10, 30, 50, 80, 96 and 100%, 10 min each. Then, the material was dried to critical point (EMITECH K850, London, England) using CO₂, placed on aluminium sample holders and covered with a layer of gold. Finally, specimens were observed under a scanning electron microscope (Hitachi-SU1510, Tokyo, Japan) at a voltage of 10 or 15 kw.

Phylogenetic relationships

Phylogenetic relationships of the new species (Fig. 1) are based on Ortiz-Rodríguez et al. (2016a). The phylogenetic inference used three different methodological approaches (parsimony, maximum likelihood, and Bayesian inference) on a dataset of six plastid regions (*ndhF*, *matK*, *psbA-trnH*, *rbcl*, *rps16-trnQ*, and *trnL-F*). In that study a sample of the new species was included and named as Annonaceae aff. *Guamia* (here as *Desmopsis ibarrarum*).

Climatic differentiation

Coordinates of occurrence data were assembled for the new species herein described and also for its closest relative, which were obtained from the information available on herbarium specimens (IBdata, 2022). Then climate layers were obtained at a 30 arc-sec (c. 1 km²) resolution from the WorldClim database (Hijmans et al., 2005) and for all occurrence records, I extracted data from 19 climatic variables using the *extract* function from the *raster-R*-package (Hijmans and van Etten, 2012). With these climatic data, I

performed a Non-metric multidimensional scaling (NMDS) analysis using a Gower distance matrix to explore patterns of climatic differentiation between species. The NMDS analyses was performed in R with the *metaMDS* function from the *vegan-R*-package v. 2.4-3 (Oksanen et al., 2017).

Conservation status

Based on all known localities for the new species, I assessed its conservation status by calculating its extent of occurrence (EOO) and its area of occupancy (AOO) using the GeoCAT tool (Bachman et al., 2011) and applying the IUCN Red List categories and criteria (IUCN, 2022).

Results

Taxonomy

Desmopsis ibarrarum G.E. Schatz ex Ortiz-Rodr., sp. nov., Figs. 1, 2, 3, 4.

TYPE. MEXICO. Veracruz, municipio San Andrés Tuxtla, Jardín Botánico de la Estación de Biología Tropical Los Tuxtlas, 18°35'05"N, 95°04'23"W, 150 m, 21.VII.2022 (fl, fr), *G. Ibarra Manríquez* and *S. Sinaca Colín* 7278 (holotype: MEXU!, isotypes: MO!, NY!, XAL!).

Similar to *Desmopsis dubia* in the leaves with percurrent tertiary venation, short-pedicellate flowers without leafy bracts at base of pedicels, food bodies at base of inner petals, the partially fused sepals, and the cylindrical fruits with hard, woody testa, but different in its glabrous leaves above and below, flowers with longer petals, and smaller fruits with fewer seeds.

Trees 4-10 m tall, 10-18 cm diameter, bark dark brown; twigs densely covered with very short, erect, golden brown hairs; leaves membranous, elliptic to elliptic-obovate or rarely lanceolate, alternate, phyllotaxy distichous, 8-17 cm long × 2.5-7 cm large, glabrous above and below, sparsely verruculose on both sides and sparsely covered with inconspicuous erect hairs along the primary vein, base cuneate to rounded, often asymmetrical, apex acute to acuminate, venation weakly brochidodromous, tertiary venation strongly percurrent, primary vein of-



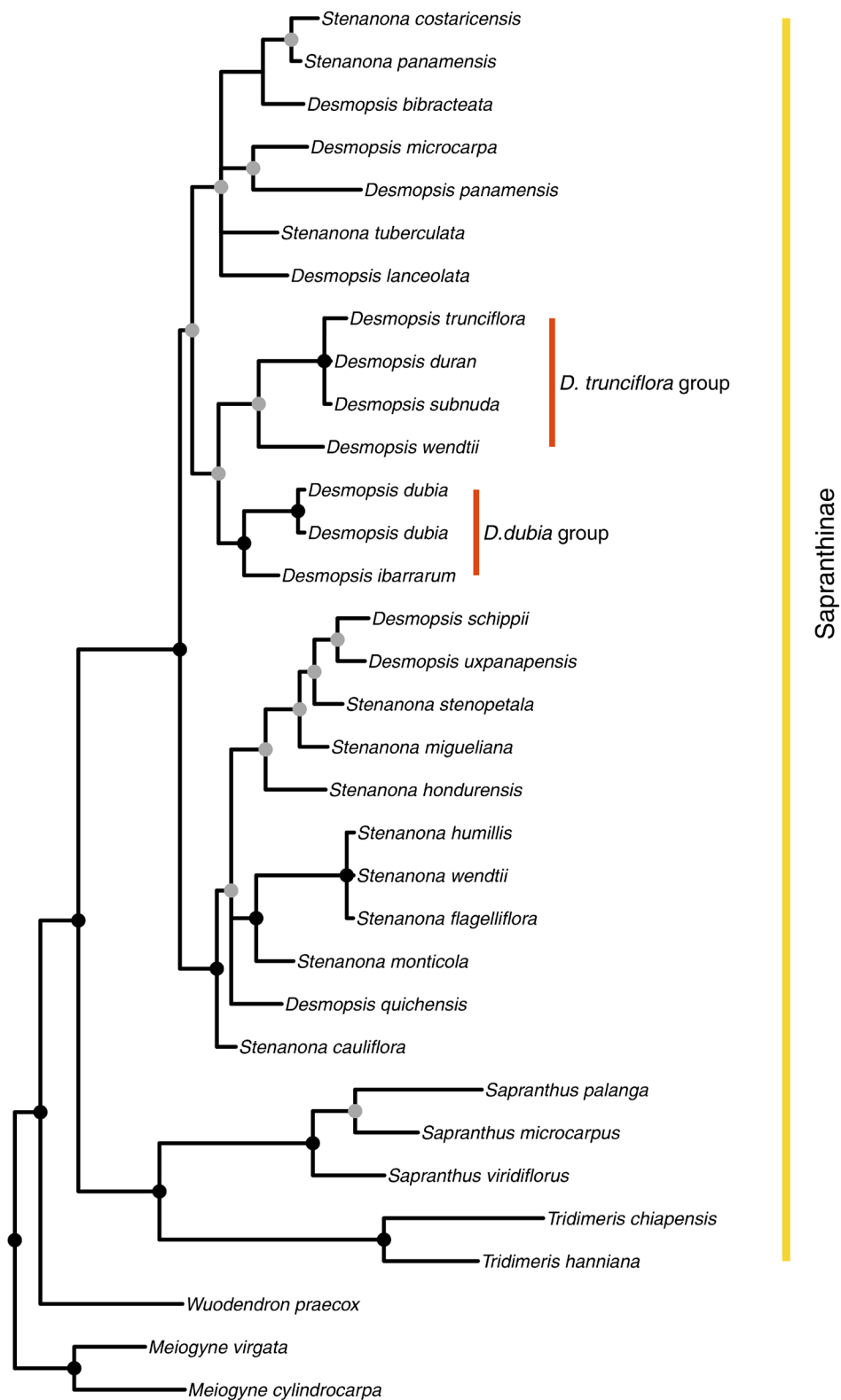


Figure 1: Phylogenetic relationships of the Neotropical clade of Miliuseae (subtribe Sapranthinae Ortiz-Rodr., Ruiz-Sanchez & Ornelas) based on six cpDNA markers (*ndhF*, *matK*, *psbA-trnH*, *rbcl*, *rps16-trnQ*, and *trnL-F*) and with emphasis on the species of *Stenanona* Standl. and *Desmopsis* Saff. (modified from Ortiz-Rodriguez et al., 2016a). Darker circles indicate strongly supported clades using three different methodological approaches (parsimony, maximum likelihood, and Bayesian inference). Lighter circles indicate that the clade was supported only in one of the methodological approaches. Posterior probability values greater than 0.95 and bootstrap values greater than 0.70 were considered to represent strong support.



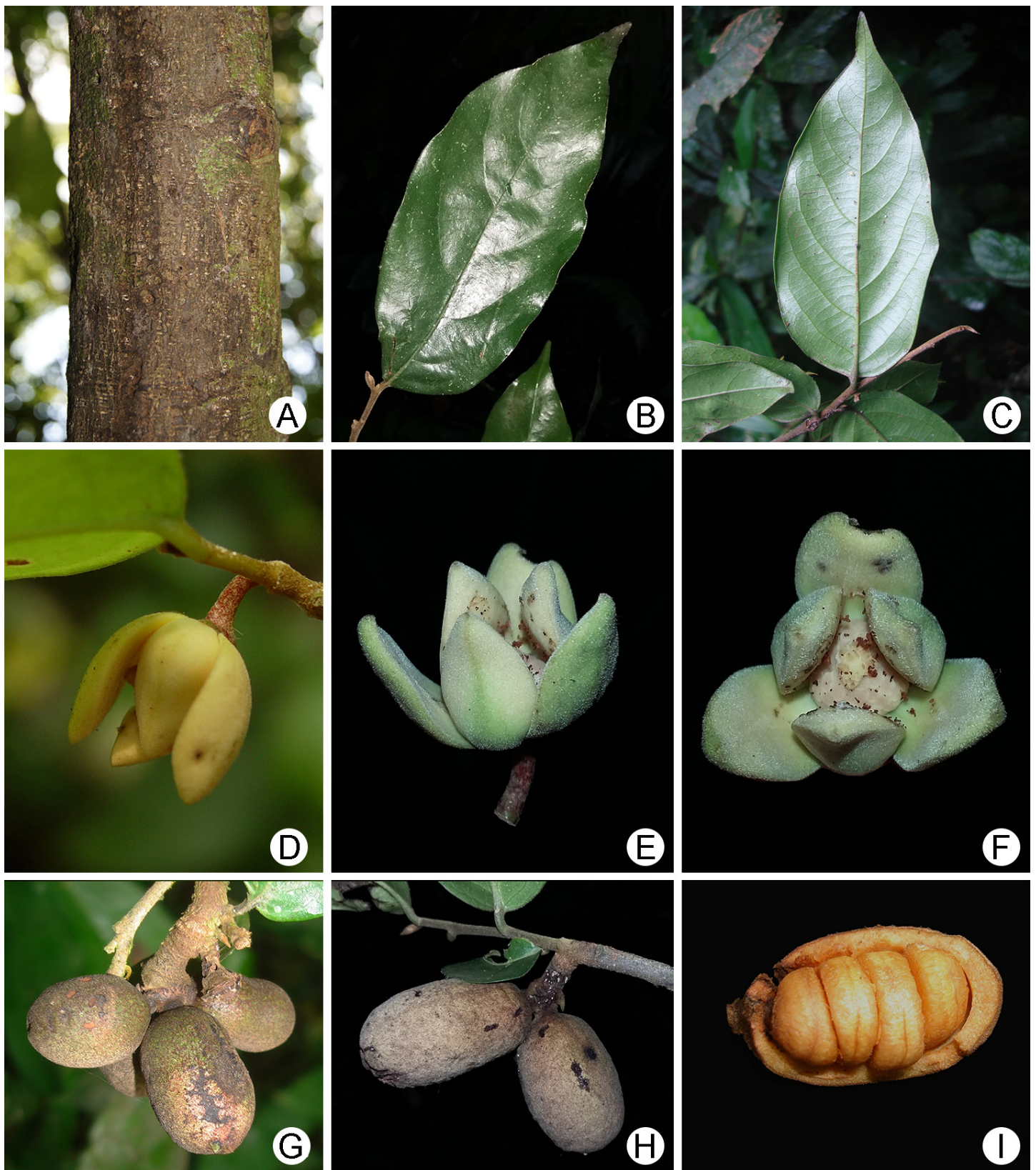


Figure 2: *Desmopsis ibarrarum* G.E. Schatz ex Ortiz-Rodr. (Annonaceae). A. main trunk bark; B. upper leaf surface; C. lower leaf surface; D. inflorescence with solitary, yellow flower; E. lateral view of the flower, the surface covered with sericeous hairs can be appreciated; F. front view of the flower, note the differentiation in the position and shape of the petals whorls; G. H. infructescences, the whitish or yellowish color of the fruits is due to the fact that they are densely covered by very small sericeous or golden, persistent hairs; I. open fruit, the thick and woody wall can be observed, as well as the numerous discoid seeds.

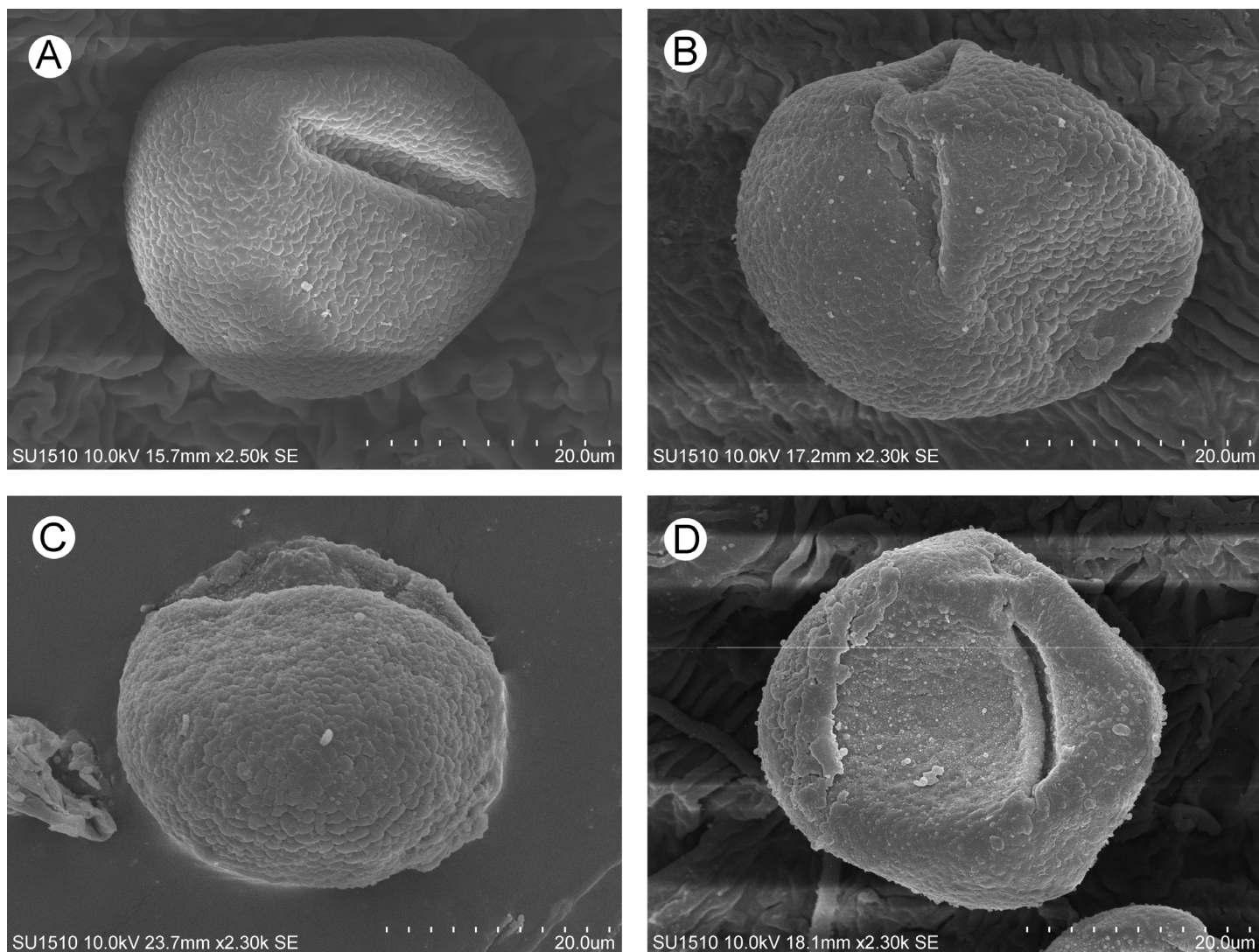


Figure 3: Scanning electron microscopy (SEM) image of pollen grain of A. *Desmopsis ibarrarum* G.E. Schatz ex Ortiz-Rodr.; B. *Desmopsis duran* Gómez-Domínguez & Ortiz-Rodr.; C. *Desmopsis dubia* Ortiz-Rodr. & Espinosa-Jim. and D. *Desmopsis trunciflora* (Schltdl. & Cham.) G.E. Schatz.

ten canaliculate above and prominent on the lower side, secondary veins 9-11 on either side; petiole swollen, densely covered with golden brown hairs, canaliculate, 2-8 mm long; inflorescences terminal, shifting to leaf-opposed, a 1-3-flowered rhipidium borne among the leaves or sometimes on the main trunk (cauliflorous); flowers pendulous, with a strong fragrance of ripe banana at anthesis, peduncle to 3 mm long, often inconspicuous, pedicels 5-10 mm long (up to 22 mm in fruit), bearing a minute narrowly lanceolate to ovate bract at the base to 2 mm above the base, apex acuminate, densely covered with very short, erect, golden hairs, pedicels and outer side of bracts densely covered with golden brown, erect to appressed hairs, sepals

three, connate at the base, broadly ovate, 4-5 mm long × 4-5 mm wide, base decurrent along the pedicel, apex acute, distal half thin, proximal half abruptly thickened, slightly keeled on outer surface, densely covered with very short, erect, golden hairs outside, glabrous inside, persistent during fruiting, petals six, free, in two whorls, fleshy and thick, densely covered with very short, erect white hairs outside, glabrous at the base to densely covered with very short, erect, white hairs at the apex inside: outer petals elliptic, 20-22 mm long × 12-13 mm wide, base obtuse to rounded, apex obtuse to acute, with a narrowly triangular ridge at the base inside corresponding to the opening where two inner petals meet, inner petals thicker than the

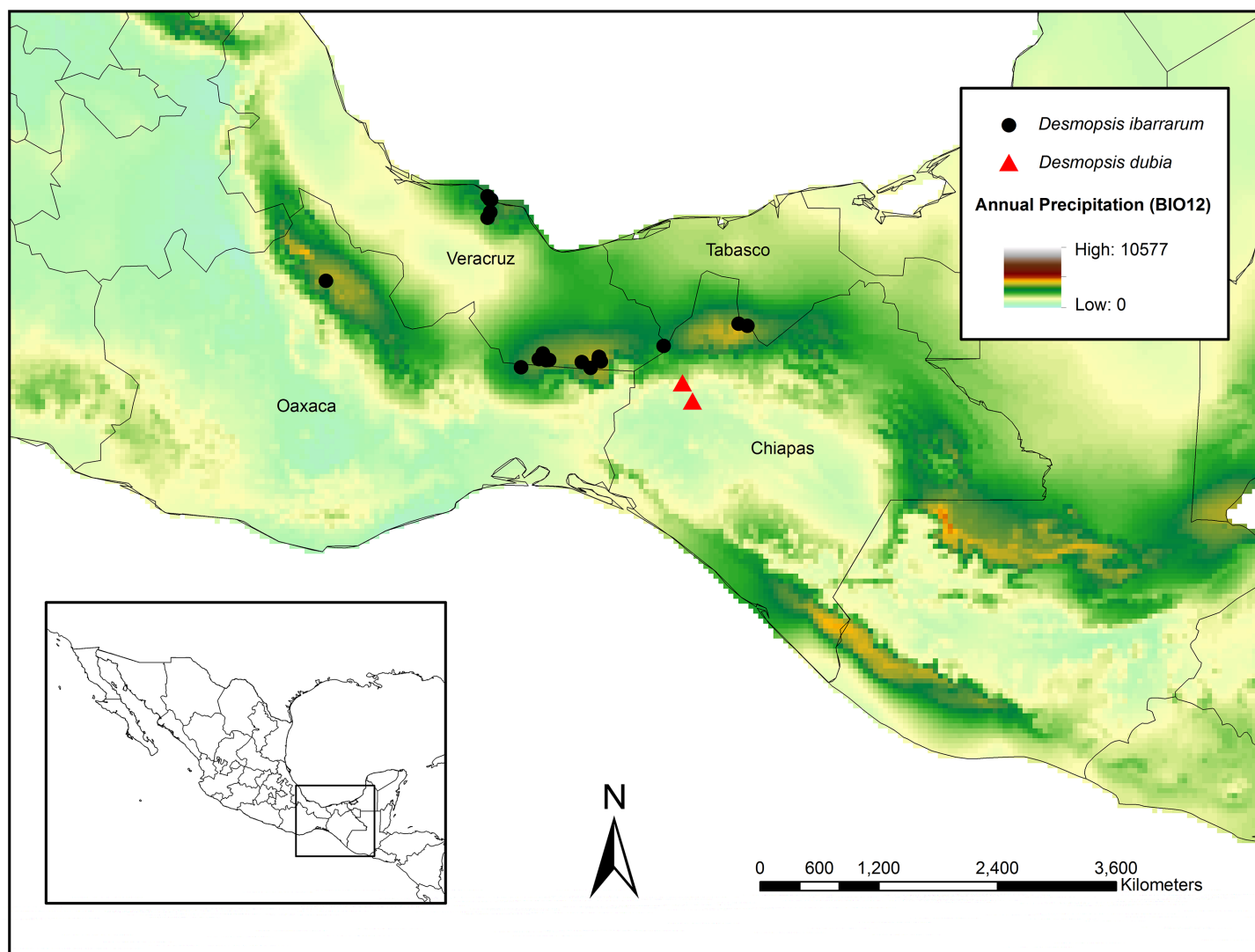


Figure 4: Localities and known distribution of *Desmopsis ibarrarum* G.E. Schatz ex Ortiz-Rodr. (black circles) and *Desmopsis dubia* Ortiz-Rodr. & Espinosa-Jim. (red triangles). In green and yellow the areas with the highest values of mean annual precipitation in Mexico.

outer petals, ovate, 19-21 mm long \times 11-13 mm wide, base cuneate, strongly concave and bent inward at 90° angle 4 mm from the base forming a cusp that fits tightly around the stamens, 2-3 mm broad and ca. 1 mm thick at point of attachment, with striations evident on the basal 4 mm inside, marking the impressions of stamens, with a triangular to rounded food body in the deepest portion of the cusp, margins revolute above the middle, apex acute, reflexed, faintly keeled outside, stamens 70-80, 2 mm long, filament 0.4 mm long, connective apex truncate discoid; carpels 8-14, stigma globose to napiform, 1 mm diameter, attached obliquely to ovary, ovaries densely covered with very short white hairs, ovules 4-6, lateral in one row, to-

rus densely setaceous at the base of ovaries and stamens; monocarps oval to cylindrical, 16-30 mm long \times 10-12 mm in diameter, rounded at both the base and apex, with a slightly elevated longitudinal ridge, densely covered (velvety) with very short, sericeous and golden hairs, wall (mesocarp) ca. 2 mm thick, somewhat woody, stipes 3-4 mm long, seeds 4-6, discoid or hemispherical if situated at the base or apex, 5-7 mm in diameter, ca. 3 mm thick, smooth, light reddish brown, endosperm ruminations spiniform to peg-shaped.

Distribution and habitat: known from the wet limestone karst forest in Oaxaca, Tabasco, and some regions of

Veracruz (Fig. 4). At the type locality, the species is found in tropical rain forest, on deep soils derived of volcanic ashes.

Phenology: the species flowers from March to May, and fruits between July and September. Nevertheless, it is possible some individuals flower and fruit outside of these months.

Etymology: the specific epithet honors Guillermo Ibarra Manríquez and his wife Guadalupe Cornejo Tenorio (“Los Ibarra”), two prolific Mexican botanists who for many years have contributed to the knowledge of the Mexican flora, in particular to the region of Los Tuxtlas in Veracruz.

Preliminary IUCN conservation status: according to criterion B established by the IUCN (2022), it is possible to determine tentatively that the species is Endangered (EN, B2ab (iii)). Its estimated area of occupancy (AOO) is 72 km² and extent of occurrence (EOO) is 30,395.476 km². The apparently wide distribution of the species (19 georeferenced collection sites) consists of three isolated patches, thus three locations sensu IUCN, of mostly limestone karst forest (the Uxpanapa and Los Tuxtlas forests in Veracruz, and the Teapa-Huimanguillo forest in Tabasco, Mexico). In recent years, many of those forest islands have been seriously fragmented, and only small remnants persist, which are surrounded by a matrix of crops, pastures and roads (Shaw et al., 2013; Hernández et al., 2014).

Pollen characteristics: the pollen of *Desmopsis ibarrarum* is globose to slightly ellipsoid, ~30 µm diameter, with a strongly rugulate to fossulate (-perforate) exine, with two depressed exine areas (weakly disulcate) (Fig. 3). Among Mexican species of *Desmopsis*, the barely developed depressed areas in the pollen grains of *D. ibarrarum* are similar to those of *Desmopsis duran* (from the *Desmopsis trunciflora* group, Fig. 1). These differ from the well-developed depressed areas present in the pollen grains of *Desmopsis dubia* or from the clearly disulcate grains of *D. trunciflora* (Fig. 3).

Common names: “Cascara Prieta”, “Icaco verde” (Tabasco), “Cuerillo”, “Palo de Bejuco”, “Matacahuite” (Veracruz).

Additional specimens examined: MEXICO. Oaxaca, municipio Matías Romero, ca. 22 km al S de Esmeralda, ca. 9 km al S del Aserradero La Floresta, lomas al S del Río Verde, 17°11'N, 94°49'W, 290 m, 25.III.1981(fl), *T. Wendt et al.* 3055 (CHAPA). Municipio San Felipe Usila, alrededores del poblado Nueva Santa Flora, 11 km en línea recta al NNE de San Felipe Usila, 17.9°N, 96.433°W, 600 m, 26.IX.1992 (fr), *G. Ibarra-Manríquez et al.* 3661 (MEXU). Tabasco, Huimanguillo, km 59 carretera Huimanguillo - Mal Paso (C-50-A), 23.VI.1962 (fr), *L. González L. et al.* 10921 (MEXU); loc. cit., 23.VI.1962, *L. González et al.* 11181 (MEXU); loc. cit., 23.VI.1962, *L. González et al.* 1280 (MEXU); ladera kárstica al S de Los Azufres, 14.II.1984 (fl, fr), *L. Rico and E. M. Martínez S.* 697 (MEXU). Veracruz, municipio San Andrés Tuxtla, Estación Biológica “Los Tuxtlas” (UNAM), ca. 25 km from Catemaco on the road to Montepio, 18°35'N, 95°04'W, 100-400 m, 17.IX.1973 (fr), *R. Cedillo* 305 (MEXU); loc. cit., 21.IV.1975 (fl), *M. Cházaro* 422 (MEXU, XAL); loc. cit., 30.V.1981 (fl), *A. Gentry et al.* 32470 (MEXU); loc. cit., 9.VI.1981 (fr), *D. H. Lorence and T. P. Ramamoorthy* 3462 (MEXU); loc. cit., 9.IV.1970 (st), *M. Rosas* 1768 (MEXU); loc. cit., 18.III.1971 (st), *S. Flores* 54 (MEXU); loc. cit., 6.IV.1973 (fl), *A. Villegas* 83 (XAL); “Basuras”, km 18 Catemaco - Las Palmas, 4.V.1960 (st), *L. González and V. Garza* 3195 (MEXU); km 18.5 de Catemaco camino “Las Palmas”, 7.V.1960 (st), *L. González and V. Garza* 3898 (MEXU), 6683 (MEXU), 6705 (MEXU); región de Los Tuxtlas, Sontecomapan, 60 m, 25.III.1967 (fl, fr), *M. Sousa* 3051 (MEXU); municipio Hidalgotitlán, del km 3 al km 5 del camino de Plan de Arroyos - Alvaro Obregon, 17°15'N, 94°40'W, 130-150 m, 2.IV.1974 (fl), *J. Dorantes et al.* 2725 (MEXU, XAL); 0-3 km camino a plan de arroyos Río Alegre, 17°15'N, 94°35'W, 140 m, 19.IV.1974 (fl), *J. Dorantes et al.* 2918 (XAL); km 0-3 del camino de Plan de Arroyos - Pancho Villa, 17°15'N, 94°40'W, 120 m, 9.VI.1974 (fl), *J. Dorantes et al.* 3145 (XAL); km 0-4 camino Hnos. Cedillo - Francisco Villa, 17°N, 94°40'W, 140 m, 9.IX.1974 (fr), *J. Dorantes et al.* 3517 (MEXU, XAL); camino viejo hacia Agustín Melgar, 140 m, 7.X.1974 (fr), *J. Dorantes et al.* 3602 (MEXU, XAL); La Escuadra, 17°18'N, 94°38'W, 152 m, 16.IX.1974 (fr), *R. Vásquez* 1056 (XAL). Municipio Jesús Carranza, 2 km al N de Poblado 2, 17°16'N, 94°40'W, 120 m, 13.IV.1984 (fl), *G. E. Schatz and T. Wendt* 979 (CHAPA). Municipio Minatitlán, Zona Uxpanapa, Loma Grande, 900 m, al S de Poblado 11,

ca. 27 km al E de La Laguna, 17°3'40"N, 94°18'30"W, 320 m, 14.IV.1984 (fl), *G. E. Schatz and T. Wendt 984* (CHAPA, MEXU, MO, XAL); 12 km al NE de Uxpanapa (Pob 12) sobre camino a Díaz Ordaz, loma al SO de Díaz Ordaz y NO de Pob 13, 17°16'15"N, 94°09'45"W, 200 m, 16.IV.1984 (fl, fr), *G. E. Schatz and T. Wendt 987* (CHAPA, MEXU, XAL), loc. cit., 13.V.1983 (fl), *T. Wendt et al. 4054* (CHAPA); 11.4 km al N de Uxpanapa sobre el camino a ejido Los Liberales, 17°15'N, 94°10'W, 200 m, 21.VII.1980 (fr), *T. Wendt et al. 2652* (CHAPA); Cerro Blanco, ca. 7 km al NE de Uxpanapa (Pob 12) en al camino a Pob 15, 17°14'N, 94°09'W, 200 m, 19.X.1983 (fr), *T. Wendt et al. 4226* (CHAPA); Lomas bajas 2-4 km al S de Uxpanapa (Pob 12) al E de Río Oaxaca, 17°11'N, 94°13'W, 120 m, 20.X.1983 (fr), *T. Wendt et al. 4232* (CHAPA).

Notes: As in many species of *Desmopsis* and *Stenanona* with yellow flowers, in *Desmopsis ibarrarum* the flowers release a strong, banana-like scent. Some observations in Mexican species (unpublished data) with flowers of a similar color and smell (banana-like) suggest that the flowers are visited by small beetles (Coleoptera: Nitidulidae) (unpublished data). The fruits of *Desmopsis ibarrarum* (and those of *D. dubia*) are probably attractive to small mammals (e.g., bats) as suggested by their short-stipitate indehiscent monocarps with a hard, dull-colored testa and with many small seeds (Onstein et al., 2019). Thus, fruits characteristics in *Desmopsis ibarrarum* and *D. dubia* are unique within the *Desmopsis* genus where most of their species have small, globose, long-stipitated monocarps, with a thin testa and brightly colored and with few seeds (one or two), suggesting a bird-dispersal syndrome (Onstein et al., 2019). However, direct observations in the field will be necessary to assess that.

Discussion

The *Desmopsis dubia* group

Desmopsis ibarrarum is only closely related to *Desmopsis dubia*, a recently described species endemic to Mexico (Espinosa-Jiménez and Ortiz-Rodríguez, 2020; Fig. 1). Although the trimerous flowers with subequal, rigid and yellow petals, as well as the discoid seeds of both species, are similar to those present in most species of *Desmopsis* (Schatz et al., 2018a), their long and cylindrical fruits with many seeds

and with thick and woody testa, their leaves with percurrent tertiary venation, the absence of leafy bracts on the pedicels, and the fused sepals, distinguish them from any other known species of *Desmopsis* (Schatz et al., 2018a; Espinosa-Jiménez and Ortiz-Rodríguez, 2020). However, these leaves, flowers and fruits characteristics of *D. ibarrarum* and *Desmopsis dubia* are shared with species of *Stenanona* (Espinosa-Jiménez and Ortiz-Rodríguez et al., 2020). Moreover, the presence of food bodies (or a similar structure) at the base of the inner petals of *Desmopsis ibarrarum* and *D. dubia*, is a feature shared only with other genera of Miliuseae such as *Sapranthus*, *Tridimeris* and *Meiogyne* Miq. (Ortiz-Rodríguez et al., 2016b; Schatz et al., 2018b; Johnson et al., 2019). Therefore, it is not surprising then that *Desmopsis ibarrarum* was considered a member of a different genus of Sapranthinae (Schatz, 1987). As a consequence, the two species are here considered members of a particular lineage within the *Desmopsis-Stenanona* clade, the "*Desmopsis dubia* group" (Fig. 1).

Phylogenetic analyses published so far (Ortiz-Rodríguez et al., 2016b, Ortiz-Rodríguez et al., 2018) suggest that *Desmopsis dubia* and *D. ibarrarum* are sister species and form a clade closely related to the *Desmopsis trunciflora* group (Gómez-Domínguez and Ortiz-Rodríguez, 2020; Fig. 1). Species of the *Desmopsis trunciflora* group have leafy bracts at the base of their long pedicels, ovate to lanceolate petals frequently with a red blush at the base inside, free sepals, and glabrescent, globose-elliptic fruits with thin skin, and one or two seeds (Schatz et al., 2018a). However, as mentioned these characteristics are completely absent in *Desmopsis dubia* and *D. ibarrarum*.

Members of the *Desmopsis dubia* group are restricted to the more humid forests of Mexico and are particularly frequent in the limestone karst forests of the region. It is well-known that many karstic areas in southern Mexico acted as refuges during periods of severe climatic oscillations which promoted several events of allopatric speciation (Wendt, 1989; Ortiz-Rodríguez et al., 2016b). Inferences of divergence times (Ortiz-Rodríguez et al., 2018) show that *Desmopsis ibarrarum* and *Desmopsis dubia* probably separated as lineages during the Pleistocene, so the strong climatic oscillations of that period could be precisely involved in their evolution. Currently, both species

are allopatrically distributed. *Desmopsis dubia* is endemic to central Chiapas, and *Desmopsis ibarrarum* is widely distributed in Veracruz, Oaxaca and Tabasco (Fig. 4, Table 1). Lastly, the two species do not inhabit forests with the same climatic conditions (Fig. 5). In general, *Desmopsis ibarrarum* inhabits wetter forests compared to *Desmopsis dubia* (Figs. 4, 5).

Species differentiation within the *Desmopsis dubia* group

Desmopsis dubia and *Desmopsis ibarrarum* can be easily separated based on their morphological characteristics, in particular leaf morphology (Table 1). The leaves of *Desmopsis dubia* are densely covered with golden hairs on the underside; this pubescence is evident to the naked eye.

Table 1: Morphological features of *Desmopsis ibarrarum* G.E. Schatz ex Ortiz-Rodr. compared to those of its close relative, *Desmopsis dubia* Ortiz-Rodr. & Espinosa-Jim.

Features	<i>Desmopsis ibarrarum</i> G.E. Schatz ex Ortiz-Rodr.	<i>Desmopsis dubia</i> Ortiz-Rodr. & Espinosa-Jim.
Lower leaf surface	Glabrous, except for midvein, hairs not discernible to the touch	Densely covered with erect and appressed hairs, clearly discernible to the touch
Inner petals	19-21 × 11-13 mm, 2-3 mm thick; as long as the outer ones	10.0-12.5 × 5.0-6.6 mm, 3 mm thick; distinctly smaller than outer ones
Monocarps	16-30 mm long	40-65 mm long
Seed number	4-6	3-10
Distribution	Veracruz, Oaxaca and Tabasco	Chiapas

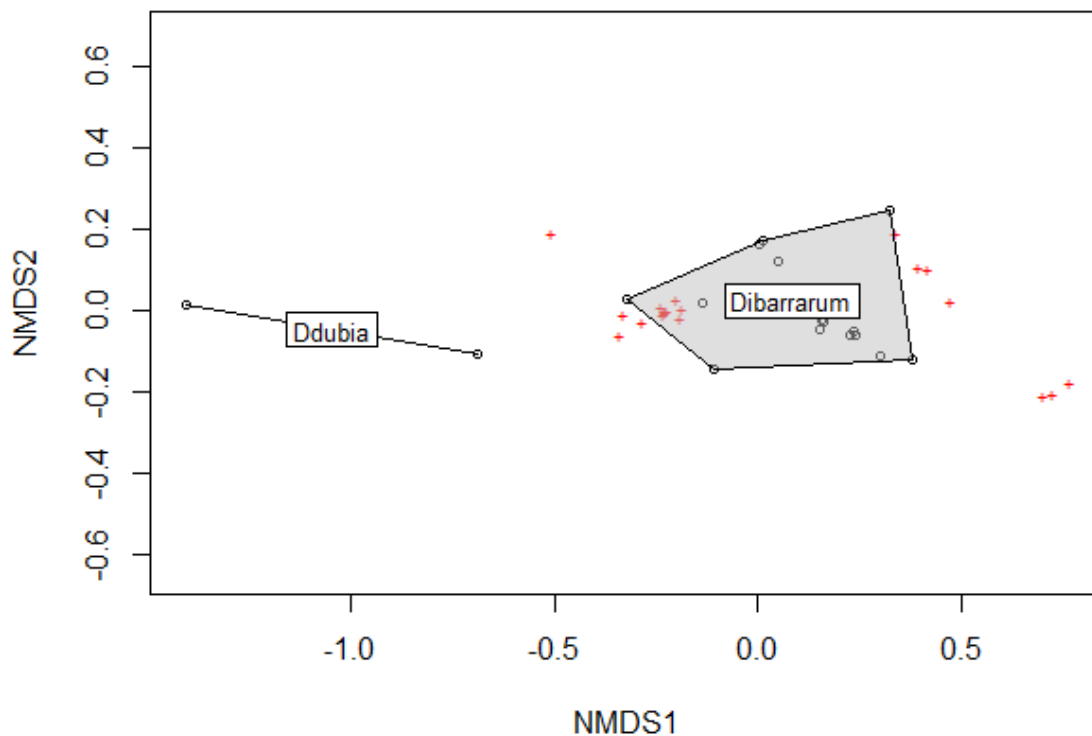


Figure 5: Non-metric multidimensional scaling (NMDS) plot based on bioclimatic variables. Based on this analysis, NMDS1 discriminates between *Desmopsis ibarrarum* G.E. Schatz ex Ortiz-Rodr. (Dibarrarum) and *Desmopsis dubia* Ortiz-Rodr. & Espinosa-Jim. (Ddubia). NMDS1 is correlated with precipitation variables, positively with Annual Precipitation, Precipitation of Driest Month, Precipitation of Wettest Quarter, Precipitation of Driest Quarter, and Precipitation of Coldest Quarter, and negatively with the Precipitation Seasonality.

Desmopsis ibarrarum has leaves that are glabrous below, except for the mid-vein, hairs along the mid-vein are indistinguishable to the eye or to the touch. Based on other characters (Table 1), the petals of *Desmopsis ibarrarum* are all similar in size but larger than those of *Desmopsis dubia* where; moreover, the inner petals are smaller than the external ones. Also, the fruits of *Desmopsis ibarrarum* are smaller and contain fewer seeds than those of *Desmopsis dubia* (Table 1).

Author contributions

AEOR conceived the idea of this study, carried out the analyses and wrote the manuscript.

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