Research article

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Reestablishment of *Zamia lawsoniana* (Zamiaceae, Cycadales), an endemic species of Mexico, with first description of the ovulate strobilus

Restablecimiento de *Zamia lawsoniana* (Zamiaceae, Cycadales), una especie endémica de México, con primera descripción del estróbilo ovulífero

Fernando Nicolalde-Morejón[1,5], Lilí Martínez-Domínguez[2], Marlon Aramis González-Aguilar[3], Dennis Wm. Stevenson[4]

Abstract:

Background and Aims: *Zamia*, with 86 species, is the most diverse Neotropical cycad genus. In Mexico, 18 species occur, of which 15 are endemics. These taxa are distributed from sea level to 1200 m a.s.l. Recently, the phenology of *Zamia* in wild populations from southern Veracruz and Tabasco was studied to evaluate the morphological patterns of reproductive structures. While these records have been considered as *Z. loddigesii*, a species with a wide distribution along the Gulf of Mexico, different populations do possess morphological differences. Based on these data, we reevaluated the synonymy of *Z. lawsoniana,* which was described in 1884 and synonymized with *Z. loddigesii* in 1995.

Methods: Botanical material was collected from three populations in Tabasco, ten in Veracruz and two in Oaxaca previously considered part of *Z. loddigesii*. Reproductive structures were measured at maturity in habitat. Populations were visited during 2022 and 2023 to record reproductive phenology. Herbarium specimens of *Zamia lawsoniana* and morphologically similar species (*Z. loddigesii*, *Z. spartea* and *Z. stenophyllidia*) were examined. A morphological description and an illustration for *Z. lawsoniana* were prepared. In addition, an identification key that included related species in terms of morphology, geography and phylogenetics was made.

Key results: *Zamia lawsoniana* is removed from synonymy and some taxonomic clarifications are made. In this context, we provide a complete description of pollen strobili, including the microsporophylls, range of vegetative morphological variation, and a botanical illustration. Additionally, the ovulate strobilus is described for the first time and a preliminary conservation status is proposed.

Conclusions: Based on morphological evidence of reproductive structures and vegetative characters, we propose the reestablishment of *Zamia lawsoniana* and its removal from synonymy with *Z. loddigesii*.

Key words: gymnosperms, Mesoamerica, Neotropics, taxonomy.

Resumen:

Antecedentes y Objetivos: *Zamia*, con 86 especies, es el género más diverso de cícadas neotropicales. En México se distribuyen 18 especies, de las cuales 15 son endémicas. Esos taxones se distribuyen desde el nivel del mar hasta 1200 m s.n.m. Recientemente, se estudió la fenología de poblaciones silvestres de *Zamia* en el sur de Veracruz y Tabasco para evaluar los patrones de variación morfológica de las estructuras reproductivas. Si bien estos registros han sido considerados como *Z. loddigesii*, especie de amplia distribución a lo largo del Golfo de México, poseen diferencias morfológicas. Basado en estos datos, reevaluamos la sinonimia de *Z. lawsoniana*, la cual es una especie descrita en 1884 y sinonimizada en 1995 con Z. *loddigesii*.

Métodos: Material botánico fue colectado en tres poblaciones en Tabasco, diez en Veracruz y dos en Oaxaca previamente consideradas parte de *Zamia loddigesii*. Se midieron estructuras reproductivas en madurez en hábitat. Las poblaciones fueron visitadas durante 2022 y 2023 para registrar la fenología reproductiva. Ejemplares de herbario de *Z. lawsoniana* y de las especies morfológicamente similares fueron examinados (*Z. loddigesii*, *Z. spartea* y *Z. stenophyllidia*). Se preparó la descripción morfológica y una ilustración para *Z. lawsoniana*. Además, se elaboró una clave de identificación que incluye a las especies relacionadas en términos morfológicos, geográficos y filogenéticos.

Resultados clave: *Zamia lawsoniana* es removida de sinonimia y se realizan algunas aclaraciones taxonómicas. En este contexto, proporcionamos una descripción completa de los estróbilos poliníferos, incluidas las microsporófilas, el rango de variación morfológica vegetativa y una ilustración botánica. Adicionalmente, se describe por primera vez el estróbilo ovulífero y se propone el estado de conservación preliminar.

Conclusiones: Basados en evidencia morfológica reproductiva y caracteres vegetativos, proponemos el reestablecimiento de *Zamia lawsoniana* y su remoción de la sinonimia con *Z. loddigesii*.

Palabras clave: gimnospermas, Mesoamerica, Neotrópico, taxonomía.

[1]Universidad Veracruzana, Instituto de Investigaciones Biológicas, Laboratorio de Taxonomía Integrativa, 91190 Xalapa, Veracruz, Mexico.
[2]Universidad Veracruzana, Facultad de Biología, Zona Universitaria, 91090 Xalapa, Veracruz, Mexico.
[3]Universidad Juárez Autónoma de Tabasco, División Académica de Ciencias Biológicas, 86150 Villahermosa, Tabasco, Mexico.
[4]The New York Botanical Garden, Bronx, 10458-5120 New York, USA.
[5]Autor para la correspondencia: f_nicolalde@yahoo.com

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Introduction

Cycadales, with 375 currently accepted species (Calonje et al., 2013-2024), is distributed throughout the tropical and subtropical areas of the world (Norstog and Nicholls, 1997). Zamiaceae includes four genera in the Neotropical region: *Ceratozamia* Brongn. (40 spp.), distributed in Mexico with some species in Guatemala, Belize and Honduras (Martínez-Domínguez et al., 2022); *Microcycas* (Miq.) A. DC., a monotypic genus endemic to Cuba; *Dioon* Lindl. (18 spp.), distributed in Mexico and Honduras, and *Zamia* L., the largest and morphologically and ecologically most diverse New World genus (Nicolalde-Morejón et al., 2009a, 2019; Calonje et al., 2019) with 86 species (Calonje et al., 2013-2024) from Florida through the Caribbean to southern Brazil and eastern Bolivia.

Mexico has the greatest cycad diversity in the Neotropics, with three genera and 73 species (Calonje et al., 2013-2024; Nicolalde-Morejón et al., 2014, 2019; Martínez-Domínguez et al., 2022). *Ceratozamia* is the most diverse of the three genera with 38 species and high endemism (95%), followed by *Dioon* with 17 endemic species (100%). Most of these species are distributed along the main mountain ranges of the Sierra Madre Oriental and Sierra Madre Occidental (Nicolalde-Morejón et al., 2009a, b, 2019; Martínez-Domínguez et al., 2022). *Zamia*, with 18 species in Mexico, has 15 endemics (84%) and three with a wide distribution that includes Belize, Guatemala and El Salvador. *Zamia* occurs in several vegetation types including coastal dunes, dry forest, oak forest, pine-oak forest and evergreen tropical forest (Nicolalde-Morejón et al., 2009a).

Most of the *Zamia* species that occur in Mexico have a restricted distribution, e.g., *Z. inermis* Vovides, J.D. Rees & Vázq. Torres, in the central region of Veracruz, and *Z. spartea* A. DC., in the Isthmus of Tehuantepec in Oaxaca (Nicolalde-Morejón et al., 2009a). Only three species have a wide distribution, i.e., *Z. paucijuga* Wieland along the Pacific coastal plain, and *Z. loddigesii* Miq. and *Z. prasina* W. Bull. along the coastal plain of the Gulf of Mexico and on the Yucatan Peninsula, respectively. These three species show conspicuous morphological similarities, which have led to erroneous taxonomic identifications when the herbarium specimens were infertile. Nevertheless, *Z. paucijuga* and *Z. prasina* do not have a long history of synonymy. In contrast, *Z. loddigesii* has a complex taxonomic history that includes 12 synonyms, one of which is *Z. lawsoniana* Dyer (Vovides et al., 1983; Stevenson et al., 1995; Nicolalde-Morejón et al., 2009a).

Historically, Mexican cycads have been widely collected and studied. Several advances in cycad taxonomy and ecology were presented at the end of the 20th century (Moretti et al., 1982; Vovides et al., 1983; Sabato and De Luca, 1985; Stevenson and Sabato, 1986; Vovides, 1990, 1991). Recently, some phylogenetic studies in *Dioon* provided support for newly described species (Gutiérrez-Ortega et al., 2018; 2020). In *Ceratozamia*, the efforts conducted during the last 30 years resulted in its first modern monograph and new phylogenies using genomic data (Martínez-Domínguez et al., 2022; Gutiérrez-Ortega et al., 2024).

New botanical explorations have resulted in an increase in the known diversity of *Zamia* mainly in Central and South America (e.g., Stevenson, 1993, 2001, 2004; Taylor Blake and Holzman, 2012; Segalla and Calonje, 2019). In line with this, some new records of populations resulted in new species descriptions, such as *Z. magnifica* Pérez-Farr., Gut. Ortega & Calonje that was recently discovered in the Sierra Norte of Oaxaca (Pérez-Farrera et al., 2023). Also, some new records have encouraged recircumscriptions of morphological patterns that have resulted in the description of new species, such as *Zamia grijalvensis* Pérez-Farr., Vovides & Mart.-Camilo described from a new population found in Chiapas (Pérez-Farrera et al., 2012), and *Z. stenophyllidia* Nic.-Mor., Mart.-Domínguez & D.W. Stev., described from populations previously considered to be part of *Z. paucijuga* (Nicolalde-Morejón et al., 2019).

Zamia loddigesii sensu lato has a wide distribution along the Gulf of Mexico, from Tamaulipas to southern Veracruz (Nicolalde-Morejón et al., 2009a). This species has high intra and inter-population vegetative morphological variation (Limón et al., 2016). The patterns of variation throughout populations of *Z. loddigesii* have not been evaluated because of a lack of detailed study of the ovulate and pollen strobili.

We conducted extensive fieldwork throughout the known distribution of *Zamia loddigesii*, studied herbarium specimens, and reevaluated the taxonomic

circumscription of the species. Reproductive characters of both pollen and ovulate strobili supported the taxonomic validity of *Z. lawsoniana* and resulted in the clarification of its morphology and geographical distribution. Thus, we present an amended description and new illustration for *Z. lawsoniana*, a taxonomic key, and a preliminary conservation status.

Materials and Methods

We reviewed specimens from the herbaria CHAPA, CHIP, CIB, ENCB, IEB, K, MEXU, NY, OXF, and XAL (acronyms of the herbaria follow Thiers (2023)). We conducted fieldwork throughout the known distribution of *Zamia loddigesii* in Tabasco, Oaxaca, and Veracruz (Table 1; Fig. 1). We sampled 10 to 20 adult specimens per population;

Table 1: Geographic distribution of *Zamia lawsoniana* Dyer and morphologically similar species in Mexico.

Species	State	Municipality	Locality	Elevation (m)	Herbarium voucher
Zamia lawsoniana Dyer	Tabasco	Huimanguillo	El Encinar	40	*M. González-Aguilar 178* (CIB)
Z. lawsoniana Dyer	Tabasco	Huimanguillo	Francisco Rueda	50	*M. González-Aguilar 180* (CIB)
Z. lawsoniana Dyer	Tabasco	Macuspana	Macuspana	25	*F. Nicolalde-Morejón et al. 4072* (CIB)
Zamia loddigesii Miq.	Veracruz	Cazones de Herrera	Ojo de Agua	15	*F. Nicolalde-Morejón et al. 3964* (CIB)
Z. loddigesii Miq.	Veracruz	Tihuatlán	5 de Mayo	130	*L. Martínez-Domínguez et al. 2763* (CIB)
Z. loddigesii Miq.	Veracruz	Papantla	Rodolfo Curti	110	*F. Nicolalde-Morejón et al. 4013* (CIB)
Z. loddigesii Miq.	Veracruz	Actopan	Pajaritos	100	*L. Martínez-Domínguez et al. 962* (CIB)
Z. loddigesii Miq.	Veracruz	Emiliano Zapata	Cerro Gordo	568	*F. Nicolalde-Morejón and L. Martínez-Domínguez 3798* (CIB)
Z. loddigesii Miq.	Veracruz	Coatepec	Vaquería	814	*F. Nicolalde-Morejón et al. 3885* (CIB)
Z. loddigesii Miq.	Veracruz	Teocelo	Llano Grande	850	*F. Nicolalde-Morejón et al. 3601* (CIB)
Z. loddigesii Miq.	Veracruz	Comapa	Dos Caminos	450	*L. Martínez-Domínguez et al. 2247* (CIB)
Z. loddigesii Miq.	Veracruz	Jalcomulco	Entre Vaquería y Monte Obscuro	731	*L. Martínez-Domínguez et al. 2383* (CIB)
Z. loddigesii Miq.	Veracruz	Coatepec	Cerca al rancho La Vega	780	*L. Martínez-Domínguez et al. 2180* (CIB)
Z. loddigesii Miq.	Oaxaca	Acatlán de Pérez Figueroa	2 km de Acatlán	130	*L. Martínez-Domínguez et al. 2151* (CIB)
Z. loddigesii Miq.	Oaxaca	San Felipe Usila	San Felipe Usila	150	*F. Nicolalde-Morejón et al. 4106* (CIB)
Z. spartea A.DC.	Oaxaca	Matías Romero Avendaño	La Princesa	220	*F. Nicolalde-Morejón and J. Torres 1505* (CIB)
Z. spartea A.DC.	Oaxaca	San Juan Guichicovi	Ocotal	240	*N. Antonio-Barrera 83b* (CIB)
Z. stenophyllidia Nic.-Mor., Mart.-Domínguez & D.W. Stev	Michoacán	Arteaga	El Guayabo	675	*F. Nicolalde-Morejón et al. 1539* (CIB)
Z. stenophyllidia Nic.-Mor., Mart.-Domínguez & D.W. Stev	Michoacán	Arteaga	Buena Vista	600	*F. Nicolalde-Morejón et al. 1571* (CIB)

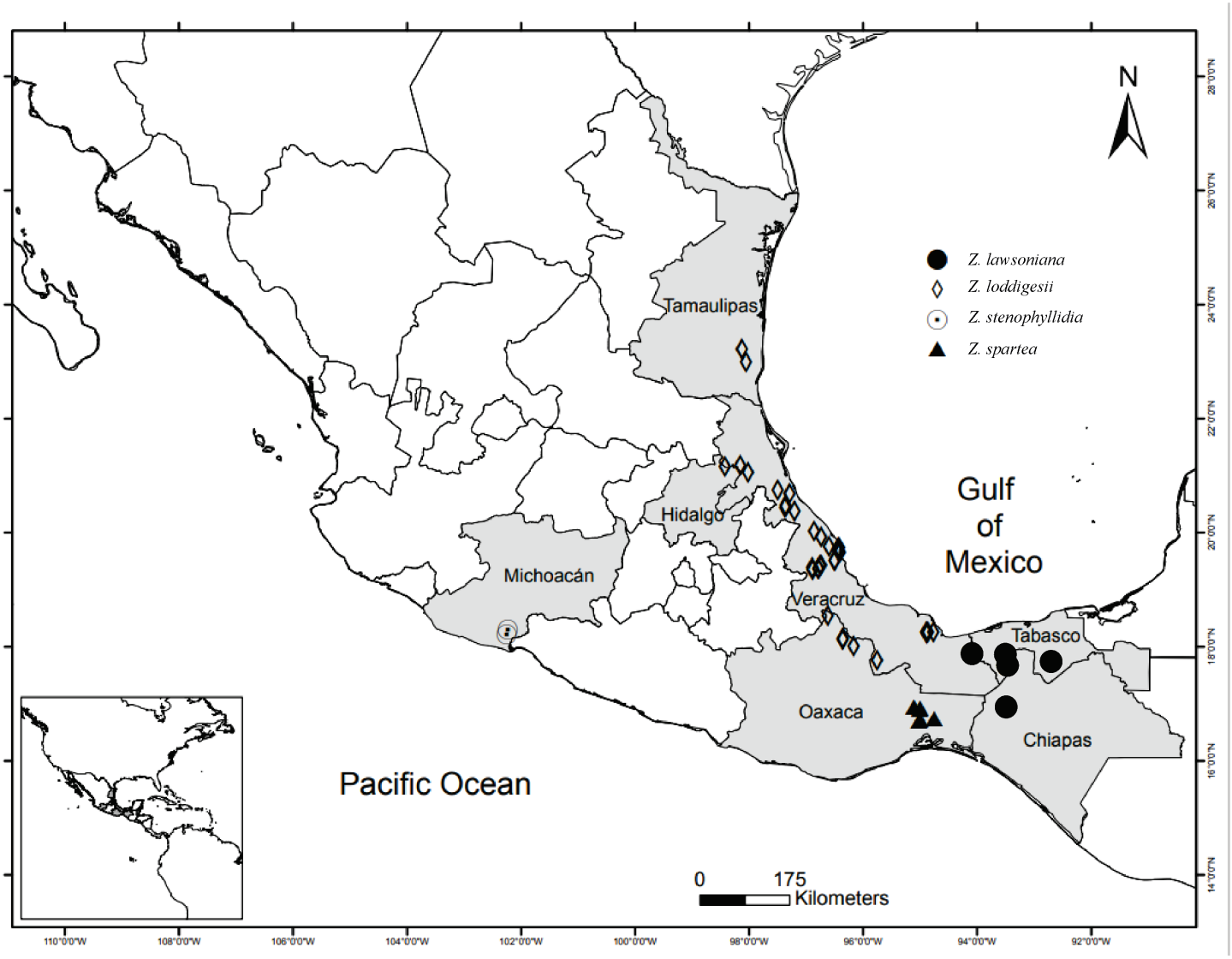

Figure 1: Geographic distribution of *Zamia lawsoniana* Dyer and morphologically similar species.

the collected specimens have been deposited in the herbarium CIB (Table 1). In addition, targeted sampling was conducted to record the developmental stages of pollen and ovulate strobili of some populations previously considered as *Z. loddigesii* from southeastern Veracruz and Tabasco. From the herbarium and field specimens, we evaluated a set of 11 qualitative and 17 quantitative morphological characters (Tables 2, 3). The reproductive characters were evaluated from a total of 153 and 103 ovulate and pollen strobili, respectively. Because *Z. spartea* and *Z. stenophyllidia* are species morphologically similar to *Z. loddigesii*, we added data from the specimens of those two species collected by our research group during 2014 and 2017. We constructed a matrix with qualitative characters to compare and analyze the morphological patterns by diagnosability (Table 2). We explored this matrix using searches for fixed character differences among populations. A total of 38 geographic coordinates from herbarium specimens that represent the range distribution of these species were registered using the ArcMap Geographic Information System v. 10.2 (Esri, Redlands, USA). The taxonomic key was elaborated with morphological data of *Z. inermis* by its geographical proximity to *Z. loddigesii* and all species included in the Mesoamerican Clade Furfuracea from the most recent *Zamia* phylogeny in which this species is included (Calonje et al., 2019).

Table 2: Comparison of qualitative morphological characters of *Zamia lawsoniana* Dyer and morphologically similar species.

Characters	*Zamia spartea* A. DC.	*Zamia stenophyllidia* Nic.-Mor., Mart.-Domínguez & D.W. Stev.	*Zamia loddigesii* Miq.	*Zamia lawsoniana* Dyer
Leaf position	Ascending	Ascending	Ascending to spreading	Ascending to spreading
Petiole disposition	Twisted	Straight	Straight	Slightly twisted
Rachis disposition	Slightly twisted	Straight	Straight	Slightly twisted
Prickles	Thin	Robust	Robust	Thin
Leaf emergent color	Reddish brown	Light green	Light green	Light green
Trichome color on petiole	Whitish gray	Reddish brown	Whitish gray	Whitish gray
Leaflet shape	Linear	Linear	Lanceolate	Linear
Leaflet texture	Coriaceous	Papyraceous	Coriaceous	Coriaceous
Ovulate strobilus shape	Cylindrical	Ovoid	Ellipsoid to cylindrical	Cylindrical
Ovulate strobilus color	Brown	Yellowish	Light brown	Light brown
Ovulate strobilus apex	Acute	Acuminate	Acute	Acute

Table 3: Comparison of quantitative morphological characters of *Zamia lawsoniana* Dyer and morphologically similar species. Values in parentheses show atypical data beyond the normal range that are uncommon. * Meristic characters.

Characters	*Zamia spartea* A. D.C.	*Zamia stenophyllidia* Nic.-Mor., Mart.-Domínguez & D.W. Stev.	*Zamia loddigesii* Miq.	*Zamia lawsoniana* Dyer
Number of leaves	2-5(8)	2-3	2-3(4)	2-5(14)
Length of leaves (cm)	35-60	48-88	45-95	66-163
Number of prickles on petiole	20-40	2-6	40-60	60-70
Width of leaves (cm)	30-52	37-71	30-41	60-75
Pairs of leaflets	15-27	28-34	12-23	16-32
Length of median leaflets (cm)	20-53	29-36	16-26	21.7-39
Width of median leaflets (cm)	0.3-0.6	0.6-0.8	1.8-3.1	0.65-1.46
Number of teeth on median leaflets	5-6	2-4	13-18	7-9
Number of pollen strobili per apex	2-3	2-3	1-6	1-3
Length of pollen strobilus (cm)	6.5-8.5	7.5-10.5	8-14	4.8-6
Diameter of pollen strobilus (cm)	1.4-1.9	2.3-2.8	1.8-3.5	1.4-1.7
Length of pollen strobilus peduncle (cm)	6-8	7.9-11.3	6-10	19-32
Synangia per lobe	10-14	12	10-18	8-12
Length of ovulate strobilus (cm)	9-12	6-7.1	12-16	5-14
Diameter of ovulate strobilus (cm)	4.2-4.8	5-6	4-6	3.5-5.6
Length of ovulate strobilus peduncle (cm)	3.4-3.8	3.8-4	5-10	10.2-24.6
Number of megasporophylls*	60-70	50-56	40-80	36-120

Results

Based on the revision of protologues, herbarium specimens and fieldwork *ex professo,* as well as comparative morphology, we found characters that support the populations from the border area in southeast Veracruz (near Oaxaca), northeast Chiapas and Tabasco to be identified consistently as *Zamia lawsoniana* (Tables 2, 3). *Zamia lawsoniana* was proposed based on a specimen collected in Oaxaca that was briefly described as having long-linear and coriaceous leaflets, the peduncle of pollen strobili two times longer than the fertile part, with all these characters clearly

corresponding to the holotype. The general habit of the holotype shows a twisted petiole and rachis and a very long peduncle of the pollen strobili; all of these are characters present in the aforementioned populations (Fig. 1). Also, character states of ovulate strobili collected from these populations exhibited differences in apex shape, shape and color of ovulate strobili when compared to other species (Table 2).

Despite the vegetative and geographic affinity of populations from Tabasco, southern Veracruz, and northern Chiapas with *Zamia loddigesii*, *Z. spartea* and *Z. stenophyllidia*, we found a combination of character states that distinguish *Z. lawsoniana* from these three species. Also, a complementary revision of the morphological characters of Mexican *Zamia* species based on revision of herbarium specimens shows that these populations correspond to this binomial. The most informative characters were (1) disposition of petiole and rachis, (2) number of prickles, (3) leaf emergent color, (4) length of pollen strobilus peduncle, and (5) length of ovulate strobilus peduncle (Tables 2, 3). After considering this evidence, we propose the reestablishment of *Z. lawsoniana* and its removal from synonymy with *Z. loddigesii*.

Taxonomic treatment

Zamia lawsoniana Dyer, Biologia Centrali-Americana, Botany 3(16): 195. 1884. Figs. 2, 3.

TYPE: MEXICO. Oaxaca, *Fielding 209* (holotype: OXF!, isotype: K!).

Stem hypogeous, branching dichotomously with age, to 60 cm long and 18 cm in diameter; cataphylls chartaceous, persistent, base triangular to 1.49 cm, apex long aristate to 8.4 cm, yellowish tomentose; ptyxis inflexed; leaves 2-5(-14), ascending, 66-163 cm long, light green when emerging, green when mature; petiole 18-52.3 cm long, slightly twisted (straight in juvenile), leaves green at emergence and maturity, subterete with abundant and thin prickles to 3.4 mm long; rachis 32-66.5 cm long, slightly twisted (straight in juvenile), subterete with prickles in the proximal third; leaflets 16-32 pairs, sessile, coriaceous, linear, canaliculate, opposite to subopposite, apex symmetrical and long acute, base attenuate, margins serrulate along distal third (up to 9 dentations per side), subrevolute, articulations 0.34-0.59 cm wide, median leaflets 21.7-39 × 0.65-1.46 cm; pollen strobili 1-3 per apex, erect, cylindrical, 4.8-6 cm long, 1.4-1.7 cm in diameter, light yellow tomentulose, apex acute; peduncle 19-32 cm long, 0.73-0.93 cm in diameter, light yellow tomentose; microsporophylls cuneiform, 0.71-0.92 × 0.7-1.22 cm, spirally arranged in 10-12 orthostichies with 10-22 sporophylls per orthostichy, distal face hexagonal truncate, 7-8 × 4-5 mm, two microsporangia per sorus, 8-12 microsporangia per abaxial side, proximal half free of microsporangia and 0.25-0.33 cm long; ovulate strobili 1-2 per apex, usually solitary, erect, cylindrical, 5-14 cm long, 3.5-5.6 cm in diameter, light brown tomentulose, with acute sterile apex 0.68-1.3 cm long; peduncle 10.2-24.6 cm long, 0.8-1.34 cm in diameter, brown tomentose; megasporophylls peltate, 1.4-1.67 × 0.6-1.02 cm, spirally arranged in 8-10 orthostichies with 6-13 sporophylls per orthostichy, distal face hexagonal truncate, 1.1 × 0.6 cm; seeds ovoid, sarcotesta pink when immature, red at maturity, sclerotesta smooth, up to 1.8 cm long, 1 cm in diameter.

Common name: Pozol agrio.

Distribution and habitat: *Zamia lawsoniana* is endemic to Mexico in Veracruz, northern Chiapas, Tabasco, and probably Oaxaca (Fig. 1). This species occurs between sea level and 840 m.a.s.l. It inhabits oak forest, disturbed areas (i.e., "acahuales") and secondary vegetation of evergreen tropical forest with *Bursera simaruba* Sarg., *Mimosa pigra* L., *Acoelorraphe wrightii* H.Wendl, *Ficus* sp., and *Pseudobombax ellipticum* (Kunth) Dugand.

Phenology: leaves are produced in groups of one to three. The receptivity of ovulate strobili has been recorded from June to August; the maturity phenophase occurs between November and December; the disintegration phenophase occurs during January to March. The open pollen shedding phase starts in April and continues to early October.

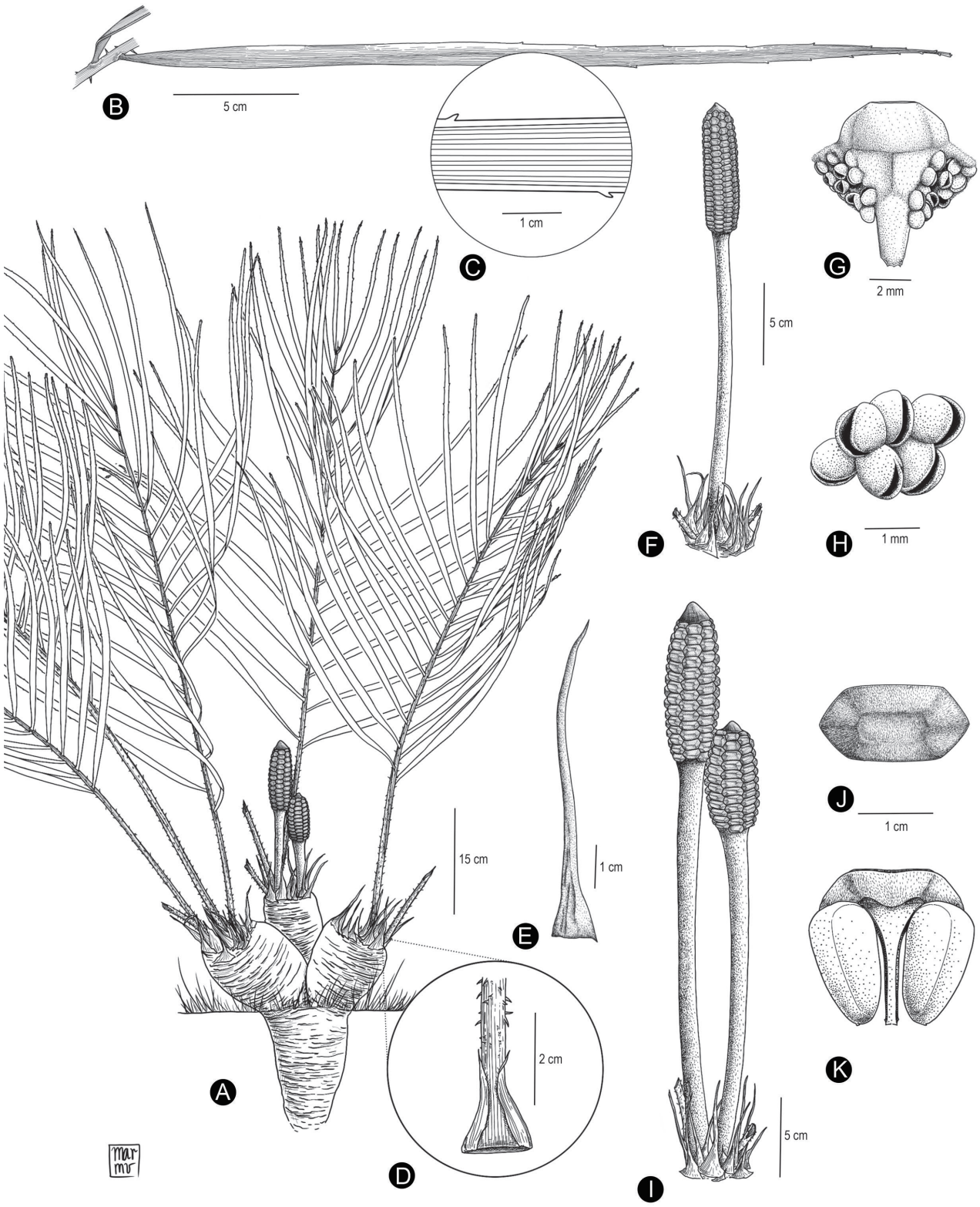

Figure 2: Illustration of *Zamia lawsoniana* Dyer. A. habit; B. leaflet; C. serrulate leaflet margins; D. base of petiole with stipules; E. cataphylls; F. pollen strobilus; G. abaxial view of microsporophyll; H. microsporangia; I. ovulate strobilus; J. megasporophyll with truncate hexagonal distal face; K. megasporophyll with two seeds. Illustration by Mariana Muñoz Velásquez based on *F. Nicolalde-Morejón et al. 4074* ♂ (CIB), *F. Nicolalde-Morejón et al. 4075* ♀ (CIB)

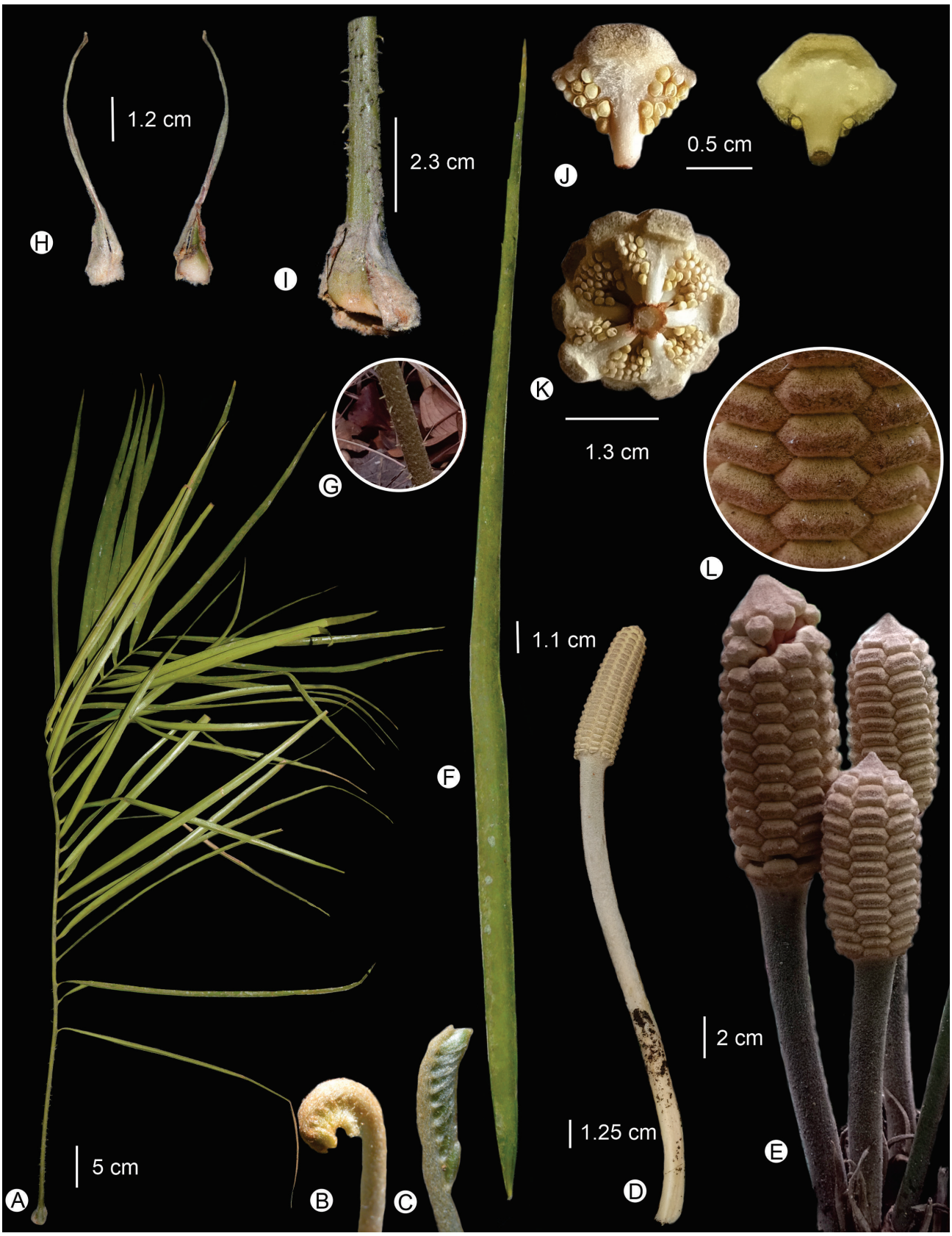

Figure 3: Reproductive and vegetative morphology of *Zamia lawsoniana* Dyer. A. leaf and leaflet arrangement; B. inflexed ptyxis; C. leaf elongation; D. pollen strobilus; E. receptive (left) and immature (right two) ovulate strobili; F. leaflet; G. prickles on the rachis; H. cataphylls; I. stipules; J. abaxial (left) and adaxial (right) side of microsporophylls; K. microsporophylls; L. megasporophylls.

Etymology: the specific epithet honors the naturalist John Lawson who collected several specimens of this species.

Diagnostic characters: *Zamia lawsoniana* is morphologically distinguished from other species by the unique combination of the following characters: ascending leaves with the petiole and rachis slightly twisted; linear and coriaceous leaflets with serrulate margins along distal third, 0.65-1.46 cm wide (Fig. 3); peduncles in ovulate strobili up to two times longer than the fertile portion (Fig. 4E); and peduncles in pollen strobili up to six times longer than the fertile portion (Fig. 4D).

Specimens examined: MEXICO. Chiapas, municipio Juárez, 120 m, 17.III.2000, *F. Hernández-Najarro et al. 340* (CHIP). Municipio Ocozocoautla, 840 m, 20.VIII.1994, *M. A. Pérez-Farrera 81* (CIB). Tabasco, municipio Huimanguillo, 9.V.2023, *M. González-Aguilar 178* (CIB), *179* (CIB); loc. cit., 28.VI.2023, *M. González-Aguilar 180* (CIB), *181* (CIB); loc. cit., 30.V.1962, *L. González and V. Garza 10695* (MEXU); loc. cit., 50 m, 28.V.2000, *S. D. Koch et al. 006* (CHAPA, IEB); loc. cit., 41 m, 6.III.2013, *F. Nicolalde-Morejón et al. 1743* (CIB), *1744* (CIB), *1745*(CIB), *1746* (CIB); loc. cit., 40 m, 8.VIII.2023, *F. Nicolalde-Morejón et al. 4076* (CIB); loc. cit., *A. P. Vovides et al. 1361* (XAL), *1365* (XAL). Municipio Macuspana, 22 m, 7.III.2013, *F. Nicolalde-Morejón et al. 1747* (CIB), *1748* (CIB), *1749* (CIB); loc. cit., 23 m, 9.VIII.2023, *F. Nicolalde-Morejón et al. 4071* (CIB), *4072* (CIB), *4073* (CIB), *4074* (CIB), *4075* (CIB); loc. cit., 9.VIII.2023, *L. Martínez-Domínguez et al. 2847* (CIB), *2848* (CIB), *2849* (CIB), *2850* (CIB), *2851* (CIB). Veracruz, municipio Las Choapas, 24.I.1970, *A. Lott 733* (MEXU); loc. cit., *A. P. Vovides et al. 1373* (XAL), *1374* (XAL), *1375* (XAL). Municipio Moloacán, 60 m, 18.XII.1974, *J. Rees 1656* (IEB).

Taxonomic notes: *Zamia lawsoniana* was described in 1884 by W.T. Thiselton Dyer (Thiselton-Dyer, 1884). In the original description, the author indicated only the characters of pollen strobili and mentioned Oaxaca state (Mexico) as the location without any further details. The morphological description has few and ambiguous vegetative morphological characters, and the ovulate strobili were not described in the protologue. Based on this information and lack of a detailed evaluation of the qualitative and quantitative variation of reproductive structures for populations of species with narrow leaflets similar to those of the holotype, the name was considered as a synonym of *Z. loddigesii* (Stevenson et al., 1995; Nicolalde-Morejón et al., 2009a). However, the holotype and isotype of *Z. lawsoniana* exhibit a slightly twisted distal end of the leaf similar to *Z. spartea*. The illustration and description provided by Thiselton-Dyer (1884) for *Z. lawsoniana* show a long pollen strobilus peduncle as a diagnostic character in contrast to *Z. spartea* that has short peduncles (Fig. 5). All morphological characters of the *Zamia* populations from northern Chiapas, Tabasco and southern Veracruz are very similar to the illustration, description and holotype of *Z. lawsoniana* (see Thiselton-Dyer, 1884 p. 10-11). Although no record of *Zamia* with these morphological characters has been found in southeastern Oaxaca, it is possible that *Z. lawsoniana* occurs there as well, though this area has been affected by high rates of deforestation, mainly due to cattle ranching (Dirzo and García, 1992).

Preliminary conservation status: *Zamia lawsoniana* inhabits evergreen tropical forest and oak forest; however, most populations occur in disturbed areas dedicated to extensive livestock. In particular, the evergreen tropical forest along the southern coastal plain of Veracruz and Tabasco has been highly deforested (Díaz-Gallegos et al., 2010). In the populations of Tabasco and Veracruz, we recorded scarce natural regeneration. The only population in good conservation status occurs in northern Chiapas. Currently, no records of *Z. lawsoniana* occur in natural protected areas. Given its distribution and relatively poor seedling establishment, this species should be considered as Endangered (EN) under criteria A1acd; B1ab(iii, iv), according to the IUCN Red List Categories and Criteria (IUCN, 2012).

Discussion

The reestablishment of *Zamia lawsoniana* is based on extensive fieldwork, monitoring of populations and review of specimens from several herbaria. In particular, the close examination of its reproductive morphology

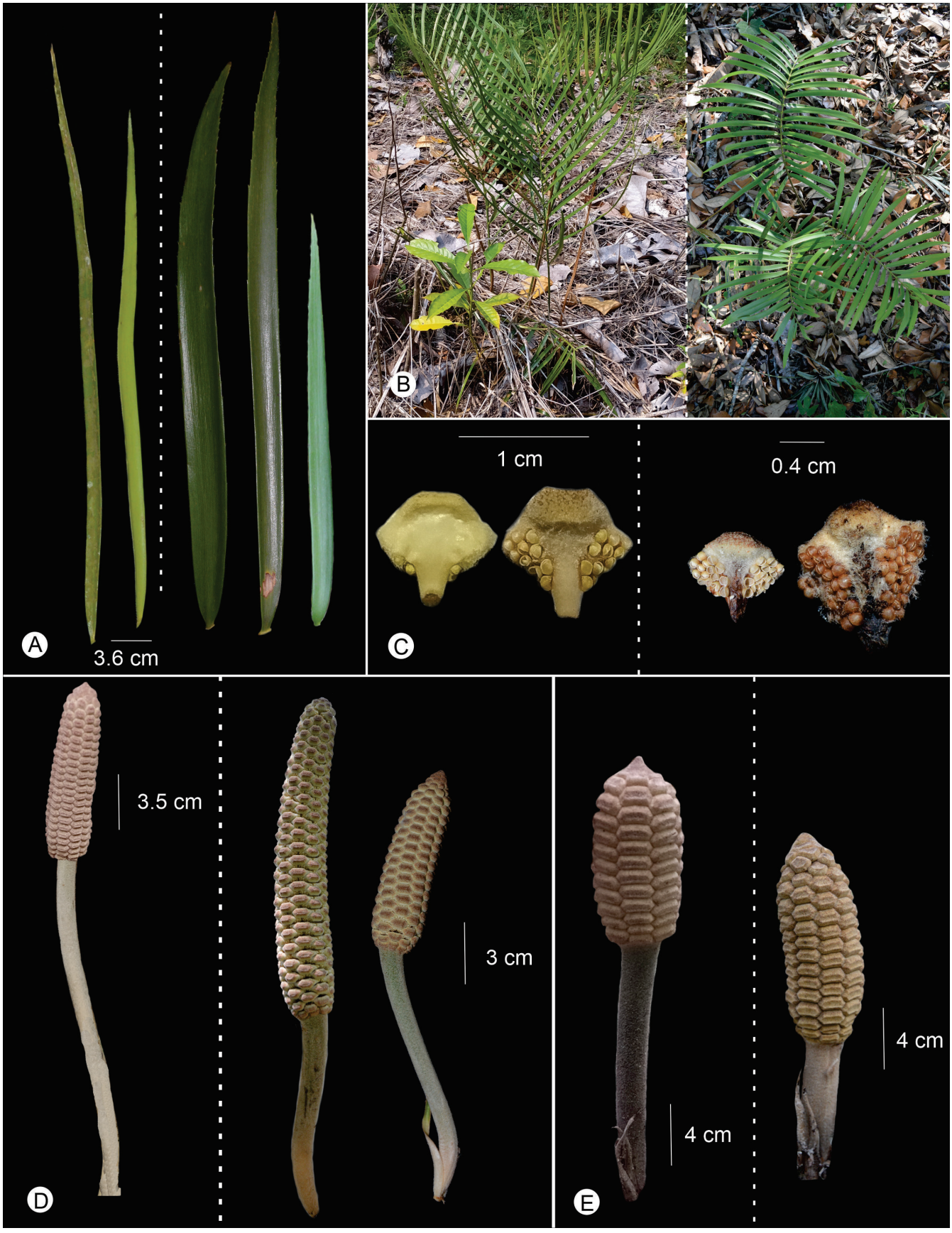

Figure 4: Comparison between *Zamia lawsoniana* Dyer (Left) and *Z. loddigesii* Miq. (Right). A. leaflet variation; B. leaves and habit; C. microsporophylls and microsporangia; D. pollen strobili; E. ovulate strobili.

Figure 5: *Zamia spartea* A. D.C. in the Jardín Botánico Francisco Javier Clavijero, Xalapa, Mexico. A. ovulate strobilus at late ovulate phenophase; B. pollen strobilus pre-open pollen (immature); C. habit with ovulate strobilus at the beginning of the disintegration phenophase.

has produced new evidence that the populations from southern Veracruz, northeastern Chiapas and northwestern Tabasco differ from the rest of the *Zamia* populations along the Gulf of Mexico and in the Isthmus of Tehuantepec and consequently represent a different species. After considering the brief description and illustrations of only a portion of a leaf and a single pollen strobilus with a long peduncle (Thiselton-Dyer, 1884), as well as examining the holotype and isotype of *Z. lawsoniana*, we propose that the populations presented above belong to this species. Currently, there are no records of *Z. lawsoniana* from Oaxaca; however, new explorations from southern Uxpanapa - Chimalapas could potentially result in the discovery of new populations of *Zamia*. This has recently occurred with some species of Mexican cycads where new records have been found in apparently well-explored areas (Martínez-Domínguez et al., 2020, 2022; Pérez-Farrera et al., 2023).

Zamia lawsoniana is most similar to *Z. spartea*, *Z. stenophyllidia* and *Z. loddigesii*, which are endemic to Mexico. *Zamia spartea* is more similar to *Z. lawsoniana* in its vegetative morphological characteristics (Table 2; Fig. 5C) but does have reddish-brown emergent leaves and fewer prickles on the petiole (20-40), whereas the leaves of *Z. lawsoniana* are light green at emergence and the petiole has 40-80 prickles. However, the main differences are in the reproductive structures, where *Z. spartea* has brown ovulate strobili and short peduncles in both pollen and ovulate strobili (Fig. 5A, B). In contrast, *Z. lawsoniana* has light brown ovulate strobili and long peduncles (Table 3; Figs. 3, 4). Additionally, *Z. spartea* is endemic to a small area in the Isthmus of Tehuantepec in Oaxaca between 200 and 400 m

a.s.l. and occurs in tropical deciduous forest (Fig. 1; Nicolalde-Morejón et al., 2009a), compared to *Z. lawsoniana* that occurs in oak forest, disturbed areas and secondary vegetation of evergreen tropical forest.

Zamia stenophyllidia is endemic to Michoacán and grows in oak forest at 450-600 m a.s.l. (Fig. 1). This species was circumscribed from populations previously considered *Z. paucijuga*, a species with high intra- and interspecific morphological variation. It is widely distributed throughout the Pacific coastal plain from Nayarit to Oaxaca in several habitats, including dry open woodlands to deciduous forest and pine oak forest (Nicolalde-Morejón et al., 2019). The vegetative morphological variation could be an effect of environmental heterogeneity as has recently been evaluated in *Z. prasina* W. Bull. (Limón et al., 2016). *Zamia stenophyllidia* bears ovoid and yellowish brown ovulate strobili and papyraceous leaflets, whereas *Z. lawsoniana* shows cylindrical and light brown ovulate strobili and coriaceous leaflets. Additionally, these species have quantitative vegetative characters that allow them to be distinguished from each other, such as the number of prickles on the petiole and the number of teeth on the median leaflets (Table 3).

A study of vegetative phenotypic and environmental variation of *Zamia loddigesii,* in which two populations from Tabasco were included, showed morphological and environmental differences among the populations of southern Tamaulipas to Veracruz and Tabasco (Limón et al., 2016). However, these morphological variations were attributed to environmental factors (Limón et al., 2016). Here, the characters of pollen and ovulate strobili were relevant to recognize these populations as a separate species because *Z. loddigesii* and *Z. lawsoniana* have clear differences in reproductive structures (Table 3; Fig. 4). Some populations of *Z. loddigesii,* mainly in disturbed areas, exhibit narrow leaflets that could be confused with *Z. lawsoniana* (Fig. 4); however, the rachis and petiole in those plants are not twisted.

In Tabasco, three other species of *Zamia* have been recorded (Nicolalde-Morejón et al., 2014): *Z. katzeriana* (Regel) E. Rettig, *Z. cremnophila* Vovides, Schutzman & Dehgan, and *Z. prasina*. These species have several morphological differences, both reproductive and vegetative, compared to *Z. lawsoniana*. The first is easily diagnosable by its oblong to oblanceolate leaflets that are reddish-pink lustrous at emergence, whereas *Z. cremnophila* has lanceolate leaflets and reddish-brown leaves at emergence (Nicolalde-Morejón et al., 2009a). *Zamia katzeriana* and *Z. cremnophila* occur on karstic rocks in evergreen tropical forest (Nicolalde-Morejón et al., 2009a). *Zamia prasina* differs from *Z. lawsoniana* by its oblong to oblanceolate leaflets more than 4 cm wide. *Zamia prasina* is widely distributed in subdeciduous tropical forests from sea level to 200 m.a.s.l. on clay and rocky soils with abundant organic matter in Belize, Guatemala and southeastern Mexico, including Campeche, Chiapas, Tabasco, Quintana Roo and Yucatán (Calonje and Meerman, 2009).

During the last decade, several new species of *Zamia* have been discovered (Segalla and Calonje, 2019; Segalla et al., 2023). However, the morphological and phenological patterns of the widely distributed species in *Zamia* has received limited attention. In this context, there have been some advances in *Zamia* species circumscriptions and/or clarifications, for example, as in *Z. paucijuga* and *Z. acuminata* Oerst. ex Dyer (Lindström et al., 2013; Nicolalde-Morejón et al., 2019). Finally, our work attempts to contribute to the study of the reproductive patterns in *Zamia* species and the clarification of the taxonomic identity of *Z. loddigesii* (Fig. 4).

Here we present an identification key to *Zamia lawsoniana* and morphologically similar species

1a. Leaflets papyraceous 2
1b. Leaflets coriaceous 4
2a. Leaflets elliptic, adaxial surface with yellow variegation ..... *Z. variegata* Warsz.
2b. Leaflets linear to lanceolate, adaxial surface without yellow variegation 3
3a. Leaflets linear, margins serrulate, apex long acuminate ..... *Z. stenophyllidia* Nic.-Mor., Mart.-Domínguez & D.W. Stev.
3b. Leaflets lanceolate, margins dentate, apex acute to acuminate ..... *Z. herrerae* Calderón & Standl.
4a. Leaflets obovate to oblanceolate, keeled adaxially ..... *Z. furfuracea* L.f.

4b. Leaflets linear to lanceolate, flat adaxially 5
5a. Leaflet margins entire .... *Z. inermis* Vovides, J.D. Rees & Vázq. Torres
5b. Leaflet margins serrulate 6
6a. Median leaflets lanceolate, ≥1.8 cm wide 7
6b. Median leaflets linear, up to 1.46 cm wide 8
7a. Ovulate strobili cream to yellowish, plants from the Gulf of Mexico coastal plain ..... *Z. loddigesii* Miq.
7b. Ovulate strobili brown, plants from the Yucatan Peninsula (Mexico, Belize and Guatemala) .... *Z. prasina* W. Bull
8a. Leaves light green at emergence; ≥60 prickles on the petiole; peduncle of ovulate strobili and pollen strobili up to 2-6 times longer than the fertile portion, respectively ..... *Z. lawsoniana* Dyer
8b. Leaves reddish brown at emergence; up to 40 prickles on the petiole; peduncle of ovulate and pollen strobili equal to or slightly longer than the fertile portion .... *Z. spartea* A. D.C.

Author contributions

FNM, LMD and DWS designed the study. MGA, FNM and LMD realized field work and monitored the populations. DWS, FNM and LMD reviewed the herbarium specimens. FNM and LMD wrote the manuscript. All authors reviewed and contributed to the final version of the manuscript.

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