

Article

Ceratozamia chinantlensis (Zamiaceae): A New Cycad Species from La Chinantla, Oaxaca, Mexico [†]

Miguel Angel Pérez-Farrera ^{1,*} , Steven M. Ramirez-Oviedo ¹ , Mauricio Gerónimo Martínez-Martínez ¹, Gaspar Moreno Mendez ¹ , Ana Guadalupe Rocha Loredo ¹  and José Said Gutiérrez-Ortega ² 

¹ Herbario Eizi Matuda, Laboratorio de Ecología Evolutiva, Instituto de Ciencias Biológicas, Universidad de Ciencias y Artes de Chiapas, Tuxtla Gutiérrez 29039, Mexico; cafecontesis@gmail.com (S.M.R.-O.); mauriciog.mtzmzt@gmail.com (M.G.M.-M.); gasparmoreno0524@gmail.com (G.M.M.); ana.rocha@unicach.mx (A.G.R.L.)

² RIKEN Interdisciplinary Theoretical and Mathematical Sciences Program, Wako 351-0198, Japan; jose.go@riken.jp

* Correspondence: miguel.perez@unicach.mx

[†] urn:lsid:ipni.org:names:77350072-1.

Abstract: *Ceratozamia chinantlensis* sp. nov., a new cliff-dwelling cycad species from Sierra de La Chinantla, Oaxaca, Mexico, is described and compared with its congeners. The species is morphologically similar to *Ceratozamia zoquorum* and *Ceratozamia santillanii*, two geographically distant species, yet it is effortlessly distinguishable from its most proximally geographic congeners. *Ceratozamia chinantlensis* can be recognized based on several qualitative traits, such as its very coriaceous, long, linear to oblanceolate leaflets. Also, it has bronze-colored emerging leaves and mature leaves with articulations of a light copper color. Compared with *C. zoquorum* and *C. santillanii*, *C. chinantlensis* has significantly longer and wider leaflets. *C. chinantlensis* should be considered a critically threatened species due to its limited number of populations and individuals. Habitat destruction—historically through the extraction of *Dioscorea mexicana* and *Vanilla planifolia*, along with ongoing coffee and corn plantations—is an ongoing threat that narrows its distribution range.

Keywords: endangered species; karst landscape; relict species; Sierra Norte de Oaxaca; tropical rainforest



Citation: Pérez-Farrera, M.A.; Ramirez-Oviedo, S.M.; Martínez-Martínez, M.G.; Moreno Mendez, G.; Rocha Loredo, A.G.; Gutiérrez-Ortega, J.S. *Ceratozamia chinantlensis* (Zamiaceae): A New Cycad Species from La Chinantla, Oaxaca, Mexico. *Taxonomy* **2024**, *4*, 733–747. <https://doi.org/10.3390/taxonomy4040039>

Academic Editor: Francisco Lara

Received: 11 September 2024

Revised: 4 October 2024

Accepted: 9 October 2024

Published: 14 October 2024



Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Ceratozamia (Zamiaceae) is one of the most studied cycad genera in recent years. Several published studies have used morphometric [1–3], molecular [4,5], or anatomical [2,6] methods to delimit species and infer their evolutionary relationships. Such studies have led to the discovery of new species. As currently circumscribed, the genus comprises 41 species, with 39 of them occurring in Mexico [7]. Notably, since 2007, the number of valid *Ceratozamia* taxa has grown from 21 to 41. That same rate of described species was achieved over the previous 161 years, after the description of the genus by Brongniart [8]. Even so, it is possible that the number of species will increase when further explorations can be carried out, especially in the cycad-rich areas of Chiapas, Oaxaca, and Veracruz in Mexico.

The La Chinantla region, located in the mountains of northern Oaxaca, is one of the most important biodiversity hotspots in Mexico. It is one of the largest tropical rainforests in the country and is home to more than 1000 plant species [9–11]. La Chinantla comprises an area of 459,489 hectares along the foothills of Sierra Juárez, between La Cañada, Palapalan, and Sierra Norte, a region that shelters a high diversity of floristic biomes [9,10]. La Chinantla can be considered a hyper-humid region, with an annual precipitation ranging 3600–5800 mm. It also has a steep elevation gradient, 60–3000 m a.s.l. [12]. The area is characterized by rugged terrain, with slopes between 6° and 45° in 80% of the territory [12], which makes it difficult for exploration. Indeed, large areas of well-conserved

forest—including tropical montane cloud forests and tropical rainforests (typical habitats of this region [12])—have not been inventoried from a botanical perspective. Thus, it is possible that a high number of undiscovered taxa still exist in La Chinantla. For example, the recently discovered cliff-dwelling species *Zamia magnifica* Pérez-Farr., Gut.-Ortega, & Calonje [13], a relict cycad species, tells us about the importance of La Chinantla as a center of micro-endemism in southern Mexico.

In early 2024, while conducting explorations to monitor and attempt to locate new populations of *Zamia magnifica*, we found a group of cliff-dwelling plants that turned out to be an unknown *Ceratozamia* species. In parallel, the second author of this manuscript discovered this same population in mid-2023, while exploring La Chinantla in a botanical excursion. After sharing information and material, we collectively determined that this population represents a new species that we shall call *Ceratozamia chinantlensis*.

2. Materials and Methods

In total, we have found and visited four populations of *C. chinantlensis* six times since mid-2023, exploring the region over a total of 29 days in the field. With the permission of the local people, we have observed the plants in their habitat and evaluated their habits and qualitative trait characteristics. Based on those observations, we determined that *C. chinantlensis* is morphologically very different from the three *Ceratozamia* species living nearby (Figure 1): *C. aurantiaca* Pérez-Farr., Gut. Ortega, J.L. Haynes & Vovides [1], *C. miqueliana* H.Wendl [14], and *C. whitelockiana* Chemnick & T.J. Greg. [15] (see discussion). It is more similar to *C. santillanii* Pérez-Farr. & Vovides [16] and *C. zoquorum* Pérez-Farr., Vovides & Iglesias [17], which were also used for comparison (Table 1).

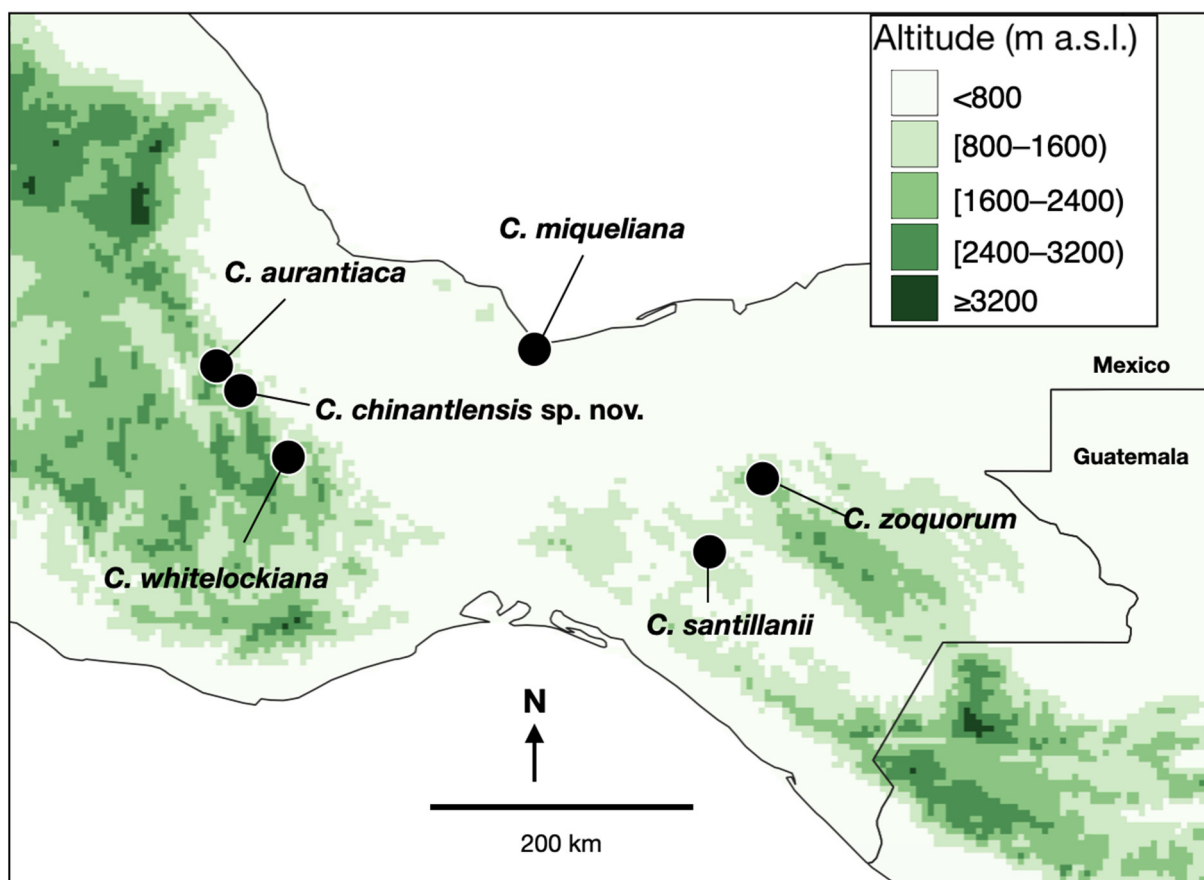


Figure 1. Geographic distribution of the species discussed in this manuscript. *Ceratozamia chinantlensis* sp. nov. is compared with its most geographically proximal congeners and the two species with which it has the highest morphological resemblance, *C. santillanii* and *C. zoquorum*.

Table 1. Morphological qualitative trait variation of *Ceratozamia chinantlensis* and comparison with other species that may be confused with *C. chinantlensis*.

Species	<i>C. chinantlensis</i> <i>sp. nov.</i>	<i>C. santillanii</i>	<i>C. zoquorum</i>	<i>C. whitelockiana</i>	<i>C. aurantiaca</i>	<i>C. miqueliana</i>
Trunk	Long and thick	Thin, cylindrical and elongated	Thin and elongated	Semihypogeous, moderately short and thin	Aerial, robust, thick, elongated	Robust, thick
Emerging leaf color	Dark beige to bronze	Olive-green	Light green	Light green	Orange	Light green
Vernation	Circinate	Circinate	Circinate	Circinate	Inflexed	Circinate
Leaf position when mature	Descendant	Descendant to decumbent	Ascending to decumbent	Ascending	Erect	Ascending
Petiole	Armed with short, thick prickles	Armed to unarmed; when armed, few slightly erect prickles	Unarmed	Sparsely armed with simple spines	Densely armed with thick prickles	Abundant thick prickles
Leaflet shape	Long, linear to oblanceolate	Linear, oblong to oblanceolate	Linear, long and lanceolate	Linear lanceolate to falcate	Linear to subfalcate, occasionally sigmoid	Oblong
Articulation color	Light green to yellowish when young; light copper when maturing	Yellow to orange-green	Yellow	Green	Brownish to green	Green
Leaflet texture	Very Coriaceous	Coriaceous	Coriaceous	Papyraceous	Coriaceous	Papyraceous
Vein in abaxial part of leaflets	Visible	Not visible	Visible	Visible	Not visible	Not visible
Megastrobilus disposition	Erect	Erect	Decumbent	Erect	Erect	Erect
Megastrobilus apex shape	Acuminate	Acute	Acuminate	Apiculate	Mucronate	Mucronate

To make a morphometric comparison, we collected leaves from a total of 22 adult plants of *C. chinantlensis*. This sampling number was decided and agreed to with the permission of the local people, who supervised our fieldwork. The morphometric variation was compared with that of 19 individuals of *C. santillanii* and 19 of *C. zoquorum* collected from their type populations in Chiapas (Table 2). A total of 11 vegetative morphometric traits commonly used as diagnostic characters in *Ceratozamia* [1,2] were measured and evaluated to quantitatively test the delimitation among species (Table 3, Figure 2). Morphometric variables were analyzed using Past v4.04 [18]. To evaluate pairwise differentiation between species for each character separately, we estimated the pairwise Tukey's Q values and their statistical significance. From the 11 vegetative variables, a linear discriminant analysis (LDA) was performed, producing a confusion matrix to assess whether the individuals fell within the overall delimitation of the four a priori species. Also, the quadratic distances of Mahalanobis were calculated.

Table 2. The three species analyzed in this study are *C. zoquorum*, *C. santillanii*, and the new species *C. chinantlensis*. *n* = number of individuals analyzed in morphometric analyses.

Species	Locality	Elevation m a.s.l.	<i>n</i>
<i>C. chinantlensis</i>	La Chinantla, Oaxaca (type population)	100–700	22
<i>C. santillanii</i>	Berriozábal, Chiapas (type population)	840	19
<i>C. zoquorum</i>	Solosuchiapa, Chiapas (type population)	580	19

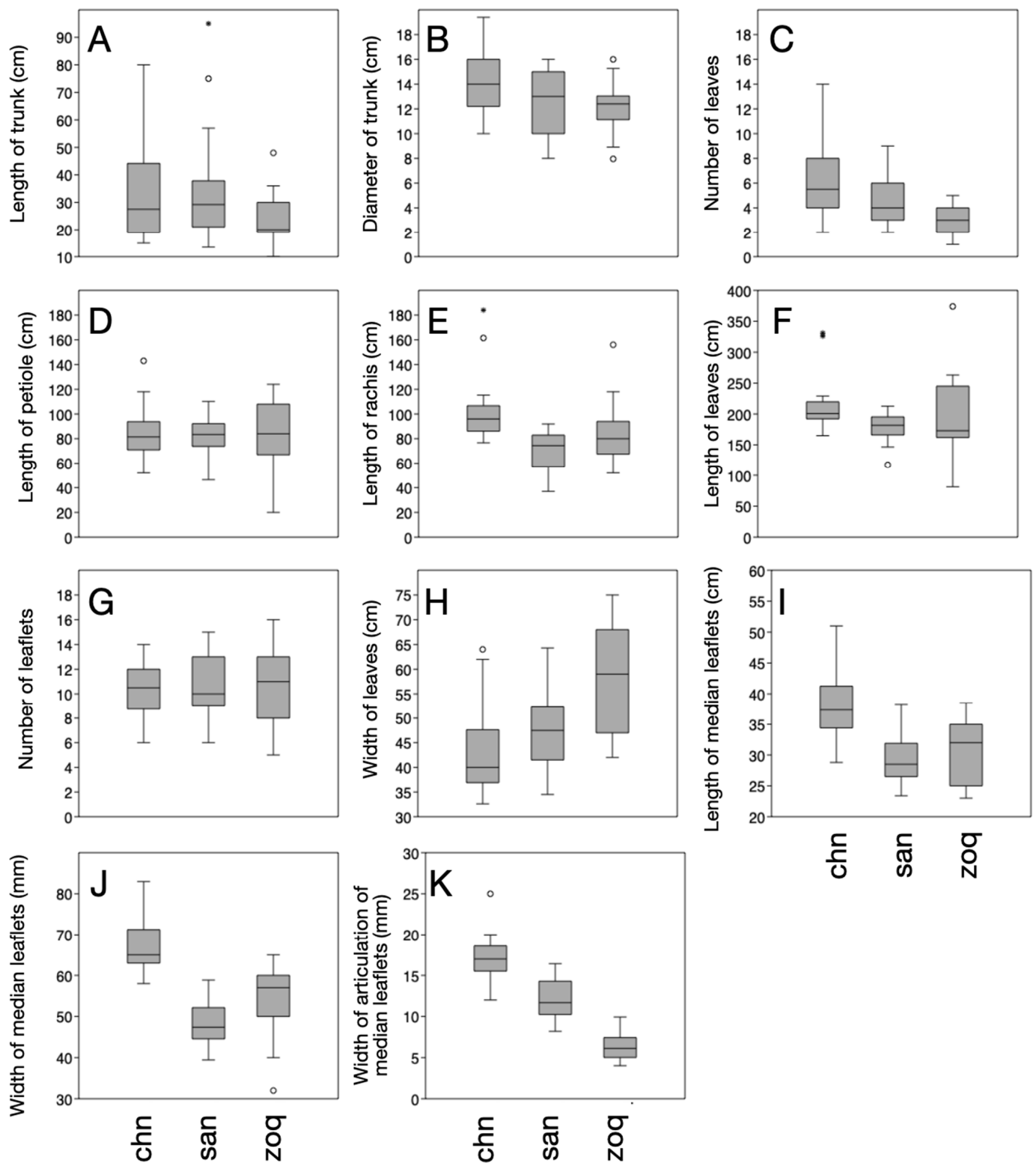


Figure 2. Morphological vegetative trait variation in the three *Ceratozamia* species examined. Traits (A–K) correspond to those listed in Table 3. Abbreviations: chn = *C. chinantlensis*, san = *C. santillanii*, zoq = *C. zoquorum*. Dots and open dots above or below the boxplots indicate outliers.

Table 3. Vegetative morphometric traits evaluated in statistical analyses. Tukey's Q values for the pairwise comparison of traits A–K among the three evaluated species are annotated. Also, loading scores for the two axes in the linear discriminant analysis are annotated. Abbreviations: chn = *C. chinantlensis*; san = *C. santillanii*; zoq = *C. zoquorum*. *: $p < 0.05$; ***: $p < 0.0001$.

Key	Trait	chn vs. san	chn vs. zoq	san vs. zoq	Axis 1 Loading	Axis 2 Loading
A	Length of trunk	0.2039	2.856	2.942	0.0075547	0.011907
B	Diameter of trunk	2.775	3.717 *	0.8916	−0.13445	−0.10241
C	Number of leaves	3.489 *	6.19 ***	2.607	0.24086	0.1106
D	Length of petiole (cm)	0.2858	0.7092	0.4087	−0.012669	0.0089196
E	Length of rachis (cm)	6.436 ***	3.733 *	2.609	0.006532	−0.033606
F	Length of leaves (cm)	3.108	1.964	1.197	−0.00068717	0.0086227
G	Number of leaflets	0.5664	0.469	0.09397	−0.0041128	0.061243
H	Width of leaves (cm)	2.085	7.573 ***	5.356 *	−0.081051	0.031637
I	Length of median leaflets (cm)	7.913 ***	6.522 ***	1.343	0.070033	−0.0585
J	Width of median leaflets (mm)	12.17 ***	8.09 ***	3.942 *	0.051623	−0.12233
K	Width of articulation of median leaflets (mm)	9.918 ***	20.9 ***	10.61 ***	0.35023	0.28479

3. Results

3.1. Observations of Qualitative Morphological Traits

Based on qualitative traits, *Ceratozamia chinantlensis* can be differentiated from the other two compared species by several characteristics. The leaves of *Ceratozamia chinantlensis* emerge as bronze to dark beige coloration, while *C. santillanii* and *C. zoquorum* emerge as green, with all species having circinate vernation. The trunk of *C. chinantlensis* is long and thick, while *C. santillanii* and *C. zoquorum* are thin and elongated, with all three species being rupicolous. The color of the articulations in the leaflets is light copper, while those of *C. santillanii* and *C. zoquorum* are yellow. The petiole in *C. chinantlensis* is armed with short, thick prickles, while *C. santillanii* may be armed or unarmed; when armed, it has a few slightly erect, spaced prickles. The leaflets of *C. chinantlensis* are very coriaceous in texture and are thicker than those of *C. santillanii* and *C. zoquorum*. The veins are visible in the abaxial part of the leaflets in *C. chinantlensis* and *C. zoquorum*, and unlike *C. santillanii*, the position of the megastrobilus in *C. santillanii* and *C. chinantlensis* is erect (Table 1).

3.2. Morphometric Analyses

The morphometric variation among the three evaluated species is shown in Figure 2, and Tukey's Q values for assessing the pairwise differentiation among the species are listed in Table 3. Based on the statistically differentiated estimates, *C. chinantlensis* can be distinguished from the other two species by the number of leaves (trait C), the length of the rachis (trait E), and the length (trait I) and width (trait J) of the median leaflets. In addition, it can be further distinguished from *C. zoquorum* based on the diameter of the trunk (trait B) and the width of the leaves (trait H).

An LDA summarized 100% of the morphometric variation into two axes, with each axis representing 85.19% and 14.81% of that variation. When plotted (Figure 3), the polygons formed by the three species do not overlap, supporting their complete separation based on the overall variation. The biplots of the LDA plot suggest that the number of leaves (trait C) and the width of articulations of the median leaflets contribute most significantly to separate *C. chinantlensis* from both *C. zoquorum* and *C. santillanii* along axis 1 (Table 3). Likewise, the confusion matrix obtained from the LDA completely sorted the three species

with only one minor exception: one individual of *C. chinantlensis* was misclassified as *C. santillanii* and one *C. santillanii* individual was misclassified as *C. chinantlensis* (Table 4). The estimates of the squared Mahalanobis distance between species suggest that, based on the overall variation, *C. chinantlensis* is closer to *C. santillanii* (17.25) than to *C. zoquorum* (33.24), while the distance between *C. santillanii* and *C. zoquorum* was 14.65. All this clear evidence allows us to describe the new species *Ceratozamia chinantlensis*.

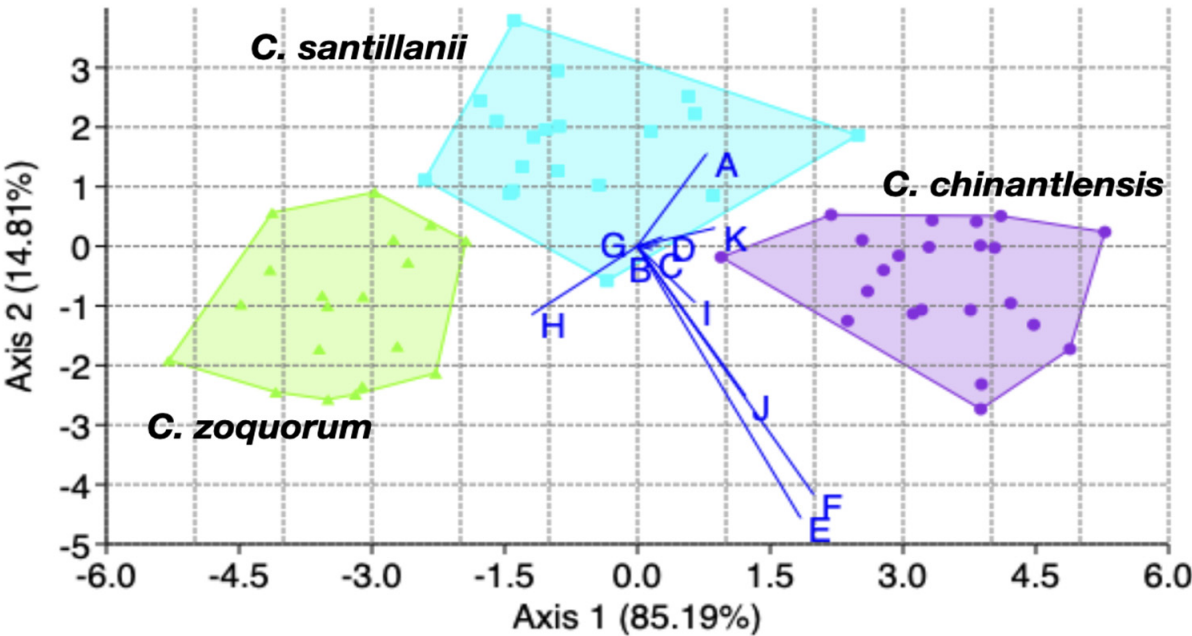


Figure 3. Linear discriminant analysis plot that summarizes the morphometric variation into two axes, each representing 85.19% and 14.81% of the total variation. Biplots A–K correspond to the vegetative traits listed in Table 2. *Ceratozamia chinantlensis* (circles), *C. zoquorum* (triangles), *C. santillanii* (squares).

Table 4. Confusion matrix obtained from the linear discriminant analysis. Rows indicate the given groups, and columns indicate the predicted groups. Bold values (number of individuals) in the diagonal indicate the correct classification of the three species.

	<i>C. chinantlensis</i>	<i>C. santillanii</i>	<i>C. zoquorum</i>	Total
<i>C. chinantlensis</i>	21	1	0	22
<i>C. santillanii</i>	1	18	0	19
<i>C. zoquorum</i>	0	0	19	19
Total	22	19	19	60

3.3. New Species Description

Ceratozamia chinantlensis Pérez-Farr., Ramírez-Oviedo S. M. & Gut.-Ortega *sp. nov.* (Figures 4–11).

Holotype: MEXICO. Oaxaca, La Chinantla, Distrito de Tuxtepec, 28 June 2024, Pérez-Farrera M.A & A. G. Rocha-Loredo, M.G Martínez-Mtz, G. Moreno-Méndez. 4466 ♂ (HEM). **Isotypes:** (XAL, MEXU). *Ceratozamia chinantlensis* is distinguished by its circinate vernation and dark beige color; tomentose, pruinose, or glaucous arched emerging leaves with light copper to bronze coloration, changing to avocado green color at maturity; light copper to bronze leaflet articulations on the adaxial side; erect and short trunks when young, becoming decumbent when old; erect megastrobili that are avocado green; and erect microstrobili.

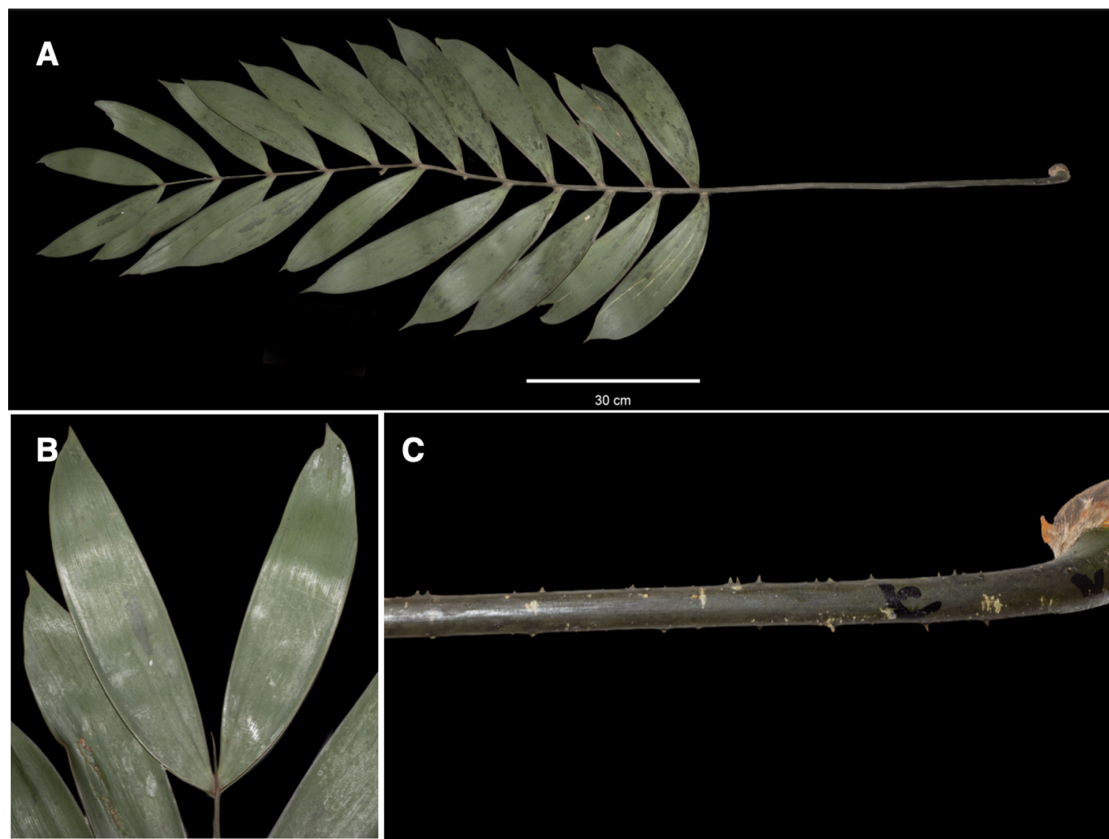


Figure 4. *Ceratozamia chinantlensis* sp. nov. (A) Leaf of an adult individual. (B) Close-up of the apical portion of the leaf. (C) The petiole of *C. chinantlensis* possesses short and thick prickles.



Figure 5. Leaves of adult *Ceratozamia chinantlensis*. (A) Emerging leaf. (B) Mature leaf.

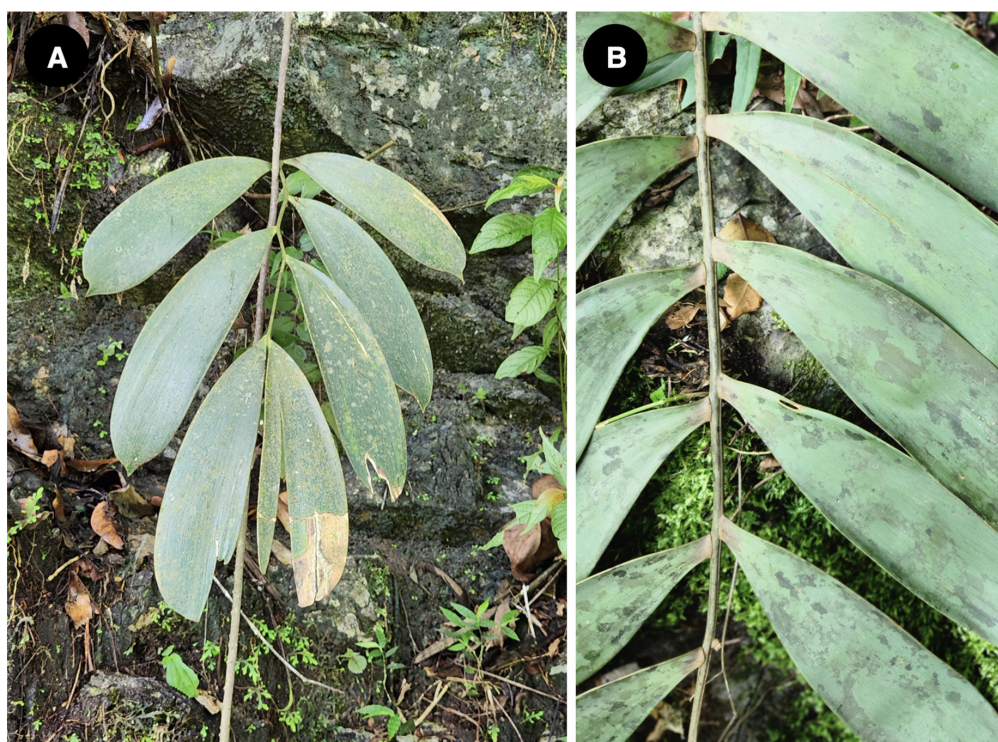


Figure 6. Close-up on leaves of *Ceratozamia chinantlensis*. Juvenile with rachis flexuous form when young (A) and detail of articulations of mature leaf (B).

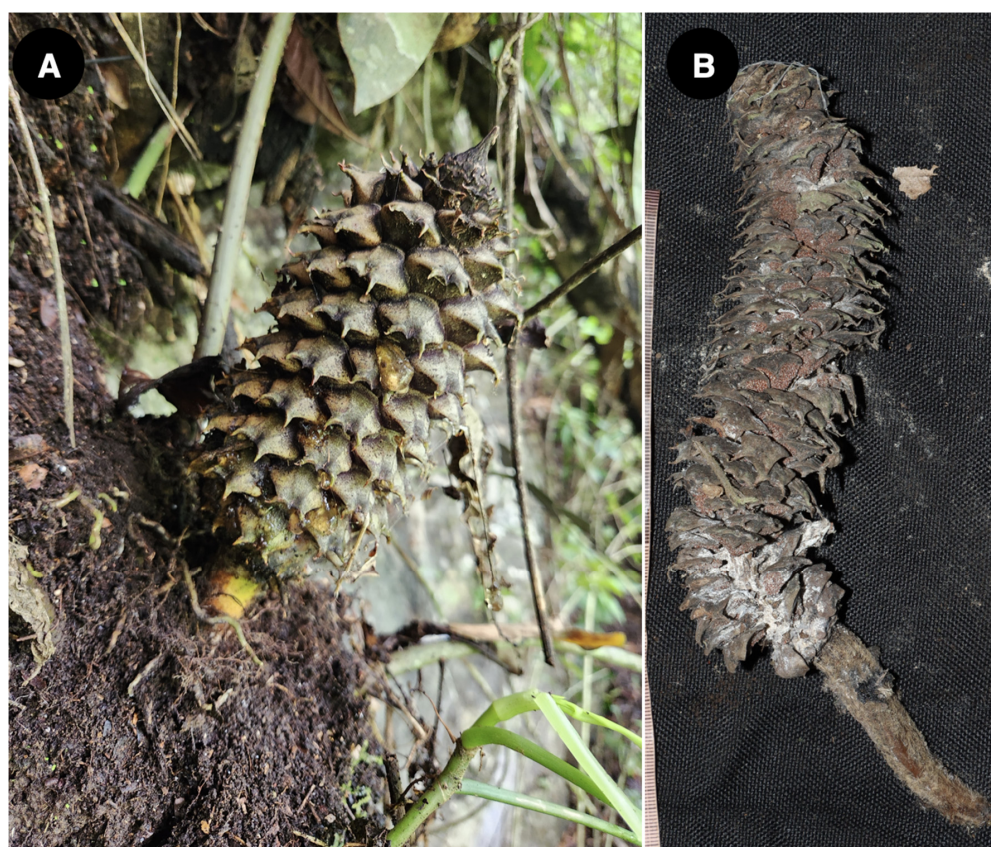


Figure 7. Mature seed cone (A) and dry and detached pollen cone (B) of *Ceratozamia chinantlensis*.



Figure 8. *Ceratozamia chinantlensis* in habitat. The rupicolous habit is present in all individuals of this species. (A) Adult plant with open crown, (B) Plant stem.

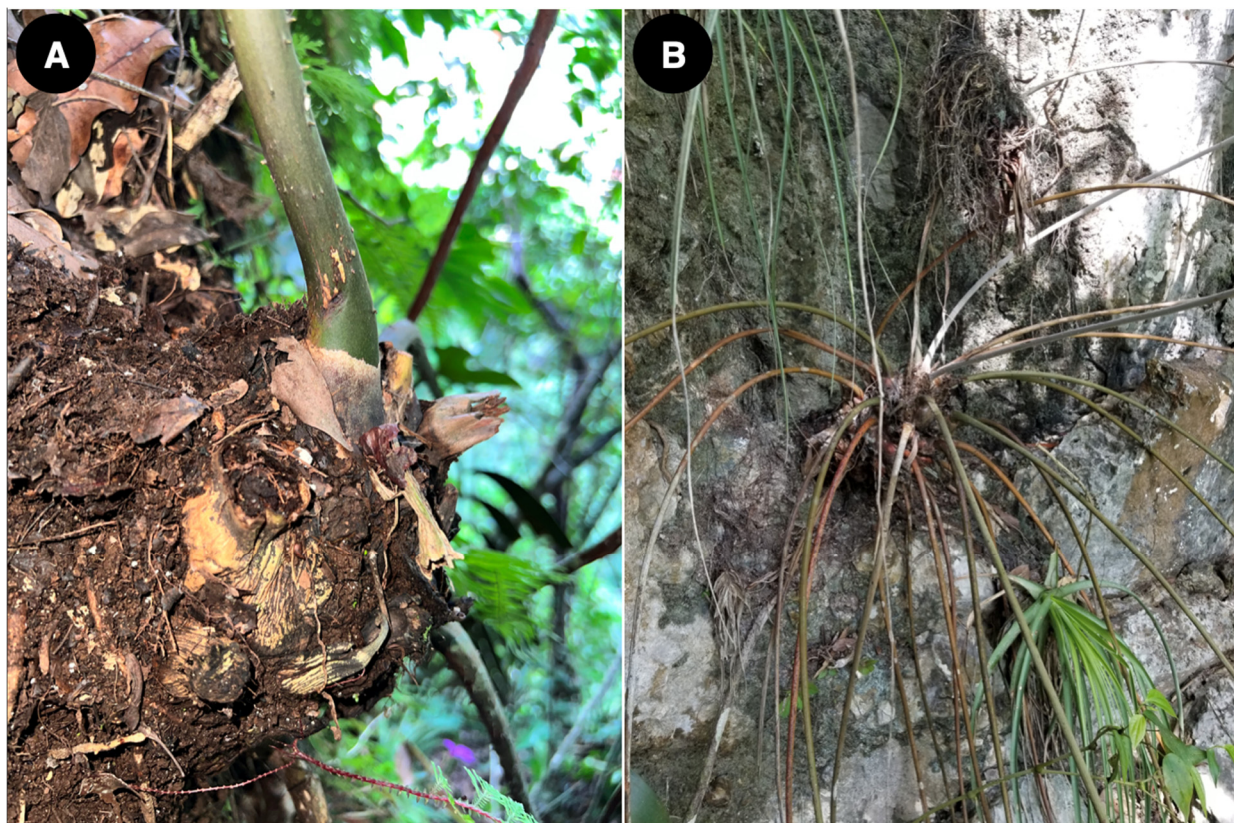


Figure 9. (A) Trunk and base of the leaf with details of the petiole. Note the prickles in the petiole. (B) Multiple petioles emerging from a single trunk.



Figure 10. (A) Seedling and (B) juvenile of *Ceratozamia chinantlensis*.

Additional specimens examined (paratypes): MEXICO. Oaxaca, La Chinantla, Distrito de Tuxtepec, 28 July 2024, Martínez-Mtz M.G & Moreno-Mendez G., Rocha-Loredo A.G. 162 (HEM); 28 July 2024, Pérez-Farrera M.A. & M.G Martínez-Mtz, G. Moreno-Mendez, A.G. Rocha-Loredo. 4467 ♂ (HEM); Moreno-Mendez G. & Martínez-Mtz M. G., Pérez-Farrera M.A., Rocha-Loredo A.G. 116 (HEM); 15 August 2024, Ramírez-Oviedo S.M 180 ♂ (HEM). **Plant habit:** Rupicolous. **Stem:** Unbranching to rarely bifurcated, short, cylindrical, and thick; erect when young, becoming decumbent when old; covered with persistent leaf bases; 15–80 cm tall and 10–19 cm in diameter. **Cataphylls:** Persistent, brown, and densely tomentose at emergence; triangular with an acuminate apex. **Leaves:** Pinnate, 3–8 per crown, forming an open crown; erect when emerging, ascending when young, and descending with age, sometimes distally supine; 165–331 cm long and 32.6–64 cm wide; bronze when emerging, glaucous, turning avocado green; vernation circinate; dark beige color; tomentose. **Petiole:** Terete to trilateral in foveate caniculation; papaya orange color at the proximal end, changing to avocado green at the distal end; 52–143 cm long; armed with short, thick, scattered prickles. **Rachis:** Avocado green; terete to trilateral in foveate caniculation, 76.7–184 cm long; straight to flexuous form when young, with few individuals maintaining a slight flexuous form upon maturity or becoming erect and straight, with short and thick prickles; proximally sparse in number and diminishing distally. **Leaflets:** 6–14 pairs; long, linear to oblanceolate; extremely coriaceous; basally subopposite to alternate; medially subopposite to opposite; apically opposite; basally slightly subfalcate, medially and apically linear to subfalcate; margin entire and revolute; apex acute to acuminate; asymmetric. Median leaflets are 28.8–51 cm long and 5.8–8.3 cm wide; spaced 5.6–18.2 cm between leaflets; base broad attenuate; articulation light green to yellowish when young, changing to light copper when mature adaxially and brown abaxially; 1.2–2.5 cm wide; veins 38–46, parallel, conspicuous; seedling eophylls 2. **Microstrobilus:** Solitary, conical, and erect; 21.4–30.5 cm long and 3.72–4.51 cm in diameter (when dry); peduncle densely tomentose, light brown; 6.3–6.8 cm long and 0.92–1.24 cm in diameter. **Microsporophylls:** Cuneiform; 12.9–18 mm

long and 13.5–15.4 mm wide; distal face bicornate, surface facing downwards; sporangia zone on abaxial surface 5.6–10.1 mm long (when dry); microsporangia grouped in 3–4 per sorus. *Megastrobilus*: Solitary, cylindrical, and erect; 17.2–18 cm long and 8.59–9.07 cm in diameter; beige-brown; apex acuminate with blackish sericeous indumentum at maturity; peduncle short, beige with gray appressed sericeous indumentum; 6–7 cm long and 2.54–2.57 cm in diameter. *Megasporophylls*: Peltate; avocado green in the distal to middle surface; bicornate with horns oriented downwards; 1.5–2.4 cm wide and 1.3–1.7 cm tall; distal face pubescent blackish toward the basal margin and middle surface between horn bases when mature; horns yellowish-brown. *Seeds*: Ovoid; sarcotesta cream when immature, sclerotesta beige when mature, with micropylar ridges.

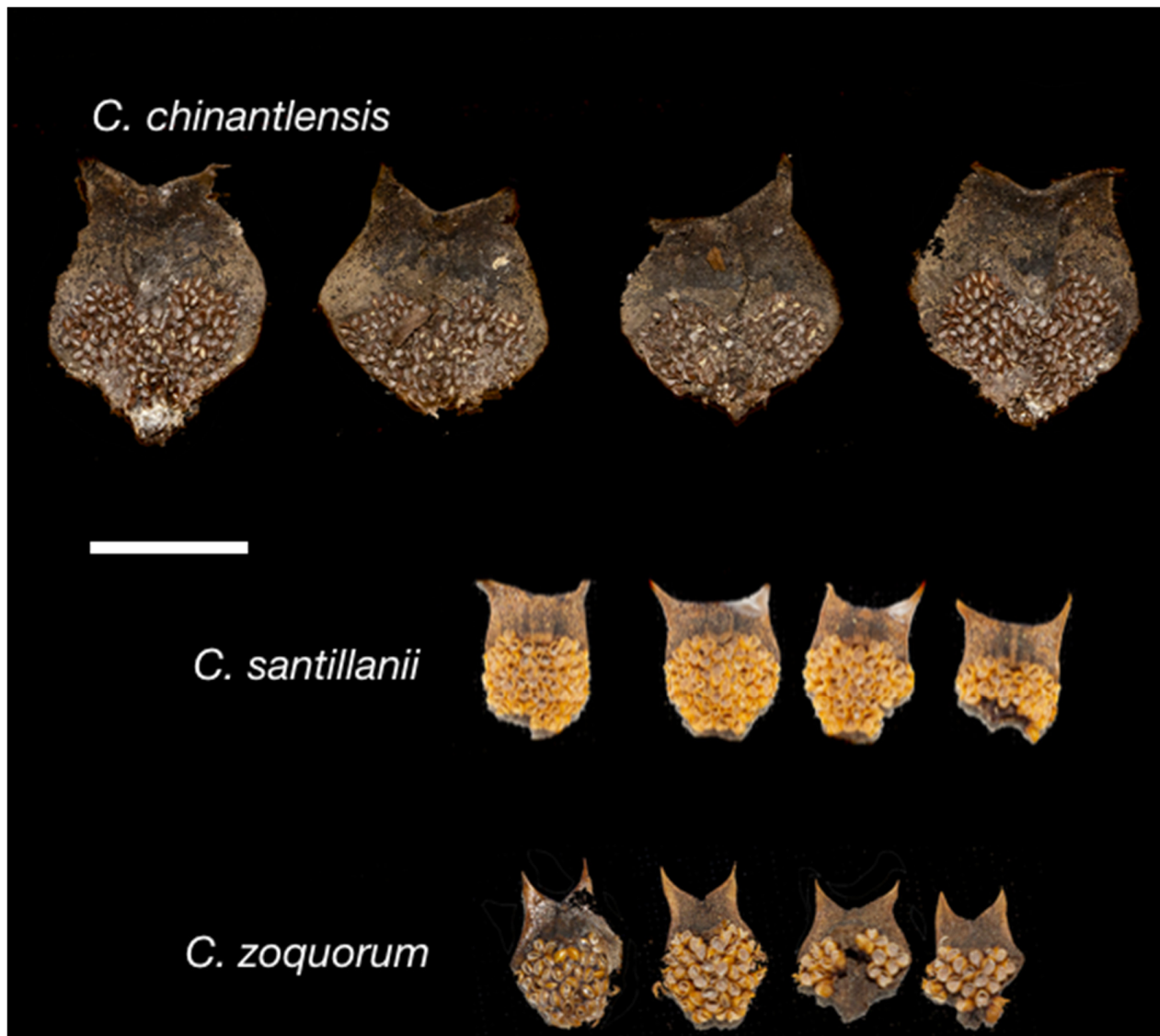


Figure 11. Microsporophylls of *Ceratozamia chinantlensis* compared with those of *C. santillanii* and *C. zoquorum*. Scale = 1 cm.

Distribution and Habitat: *Ceratozamia chinantlensis* appears to be restricted to La Chinantla, Oaxaca, Mexico. It grows in karstic landscapes, composed of carbonatic rocks in tropical rainforests between 100 and 700 m. Lithology comprises Tithonian marine deposits composed of siliciclastic and calcareous rocks from the Chivillas Formation [19]. This species is accompanied by other plants at different strata. Tree stratum: *Simira salvadorensis* (Standl.) Steyererm, *Cecropia pachystachya* Trécul. *Brosimum alicastrum* Sw., *Cedrela odorata* L.,

Dendropanax arboreus (L.) Decne. y Planch., *Clusia guatemalensis* Hemsl., *Inga* sp., *Bursera* sp., *Trichilia* sp., *Eugenia* sp., *Ficus* sp. Understory stratum: *Cnidoscopus chayamansa* McVaugh, *Palicourea tomentosa*, *Chamaedorea tepejilote* Liebm., *Chamaedorea elatior* Mart., *Chamaedorea pinatifrons* (Jacq.) Oerst., *Chamaedorea elegans* Mart., *C. ernesti-augusti* Wendland, *Astrocaryum mexicanum* Liebm. ex Martius, *Miconia* sp., *Piper* sp., *Solanum* sp. Shrub stratum: *Anthurium huixtlense* Matuda, *Anthurium schlechtendalii* Kunth, *Tectaria transiens* (C.V.Morton) A.R.Sm., *Pitcairnia imbricata* (Brog.) Agave sp., *Calathea* sp., *Prosthechea cochleata* (L.) WE Higgins, *Philodendron sagittifolium* Liebm., *Begonia* sp., *Pitcairnia* sp., *Philodendron* sp. Epiphytes and hemiepiphytes: *Monstera acuminata* Koch, *Syngonium chiapense* Matuda, *S. podophyllum* Schoott, *Peperomia* sp., *Polypodium* sp., *Epidendrum* sp., *Elaphoglossum* sp., *Tillandsia* sp., *Werauhia* sp.

Etymology: *Ceratozamia chinantlensis* is named based on its location provenance in La Chinantla, Oaxaca, Mexico.

Conservation status: Only four populations of *C. chinantlensis* have been located, each of them with less than 50 adult individuals. Currently, in most populations, we found seedling recruitment. The distribution of this species is restricted to an area no larger than 15 km². All populations are found growing in evergreen tropical forests. Due to the limited number of populations, geographic distribution, and the number of individuals per population, the species should be considered Critical (CR). The *C. chinantlensis* populations are situated within an area that has been historically affected by the extraction of *Dioscorea mexicana* and *Vanilla planifolia*.

4. Discussion

Based on qualitative data (Table 1), *C. chinantlensis* looks morphologically distinct from its neighboring congeners *C. aurantiaca* (Robusta subclade), *C. whitelockiana* (Matudae clade), and *C. miqueliana* (Miqueliana subclade) (classification according to [4]). While *C. chinantlensis* is a cliff-dwelling species, *C. aurantiaca* has a “robustoid” morphology, with thick trunks and large leaves densely armed with thick prickles, and looking more similar to a *C. robusta* Miq. [20]. *Ceratozamia miqueliana* is also notably distinct from *C. chinantlensis*, as they differ in the shape of leaves (oblong in *C. miqueliana* and long, linear to oblanceolate in *C. chinantlensis*), the texture of leaflets, and the generally more robust and thicker trunks of *C. miqueliana*. *Ceratozamia whitelockiana* is also different from its neighboring species, including *C. chinantlensis*. They differ in the shape of trunks, the color of emerging leaves, the texture of leaflets, and the apex of the megastrobilus. Similar to *C. aurantiaca* and *C. miqueliana*, *C. whitelockiana* can be easily distinguished from *C. chinantlensis* by viewing the general form of their leaves, leaflets, and trunks. In addition, *C. chinantlensis* is rupicolous and develops on cliffs, unlike its neighboring species *C. whitelockiana*, *C. aurantiaca*, and *C. miqueliana*. As the comparison with neighboring species cannot help us to determine a diagnosis of *C. chinantlensis*, we concluded that *C. chinantlensis* may be more easily confused with *C. santillanii* and *C. zoquorum* if they are placed side by side. Both *C. santillanii* and *C. zoquorum* are geographically separated from *C. chinantlensis* (Figure 1), but given the morphological characteristics of *C. chinantlensis*, a morphological comparison with these two species might be more appropriate for making a taxonomic diagnosis, as previously discussed. Further phylogenetic analysis may clarify the position of *C. chinantlensis* within the phylogenetic tree of the genus.

The discovery of *C. chinantlensis* was achieved through the current efforts of our research team and colleagues to explore remote areas via traditional floristic surveys. In these projects, the objectives usually include making inventory lists of species in areas with high biodiversity, but occasionally, new species can be identified [21–25]. The discovery of *C. chinantlensis* and the recent description of *Z. magnifica* [13] are two outcomes of these efforts as we started our own surveys in La Chinantla. As reported in the case of *Z. magnifica* [13], local people from La Chinantla actively protect the plants, and our surveys and material collection would be impossible without their consent, support, and permission.

We expect that this observation can discourage any attempts at illegal or non-consented plant collection in this region.

The geographic occurrence of *Ceratozamia chinantlensis* supports the argument that this region has been underexplored from a floristic point of view. Until 2023, there were no abundant herbaria records of *Ceratozamia* in La Chinantla, and while the findings of *C. chinantlensis* and *Z. magnifica* were surprising, the occurrence of cycads in La Chinantla was predictable from a biogeographic perspective. La Chinantla represents one of the hyper-humid forests that were once connected to other homologous forests along Mesoamerica [11,26,27]. These forests harbored both Holarctic and tropical species that took refuge during climatic cycles since the Miocene [11]. While climate change, particularly aridification, fragmented these forests, lineages were left in isolation, facilitating cycad divergence and diversification [28]. The discovery of *C. chinantlensis*, together with that of the recently discovered *Z. magnifica*, suggests the great potential of La Chinantla to harbor even greater flora diversity than we expected. In addition, in the case of the cycads, both *C. chinantlensis* and *Z. magnifica* are easily differentiated from all their neighbors, suggesting that they might be relict species [29]. Consequently, this implies an important role of La Chinantla as a refuge for relict species. Therefore, the effective management and conservation of La Chinantla should be further prioritized.

The recognition of *C. chinantlensis* increases the number of *Ceratozamia* species to 42 [7]. With this, the species of cycads in Mexico totals 77, quickly getting closer to 85, the number of species in Australia, the country with the highest cycad species diversity worldwide. While we believe that the cycad diversity in many countries remains to be discovered and described, the rapid increase in the number of cycad species in Mexico demonstrates that dedicating efforts and resources to traditional floristic exploration in remote areas (further discussed in [30]) can still reveal a vast, hidden biological diversity.

Author Contributions: Conceptualization, M.A.P.-F. and S.M.R.-O.; Methodology, M.A.P.-F., S.M.R.-O., M.G.M.-M., G.M.M., A.G.R.L. and J.S.G.-O.; software, M.A.P.-F. and J.S.G.-O.; validation, M.A.P.-F. and J.S.G.-O.; formal analysis, M.A.P.-F. and J.S.G.-O.; investigation, M.A.P.-F., S.M.R.-O., M.G.M.-M., G.M.M., A.G.R.L. and J.S.G.-O.; resources, M.A.P.-F. and S.M.R.-O.; data curation, M.A.P.-F. and J.S.G.-O.; writing—original draft preparation, M.A.P.-F., S.M.R.-O., M.G.M.-M., G.M.M., A.G.R.L. and J.S.G.-O.; writing—review and editing, M.A.P.-F., S.M.R.-O., M.G.M.-M., G.M.M., A.G.R.L. and J.S.G.-O.; visualization, J.S.G.-O.; supervision, M.A.P.-F.; project administration, M.A.P.-F.; funding acquisition, M.A.P.-F. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Montgomery Botanical Center's Plant Exploration Fund.

Data Availability Statement: Qualitative data are contained within the article. Quantitative data available on request from the authors.

Acknowledgments: Thanks to Mayra Herrera, Floriano Isidro Juan, Q.C. Jose Manuel Sánchez Ruíz, Ramiro Sánchez, Angel Sánchez, Coqueto Sánchez, Bernardo Ramírez Roque, Estanislao Ortiz, Felix Ortiz Osorio, and Xihuitl Tecuixpo Baroco for their help during fieldwork. Also, thanks to Biol. Josefa Anahi Espinosa Jiménez for her help in the identification of the herbarium material and for describing the habitat of *C. chinantlensis*. This work was supported by an anonymous donor to the Montgomery Botanical Center to MAPF. Additional support was also provided by Traditionally Texan to SMRO. AGRL especially thanks the Fondo de Conservación El Triunfo who financed some exploration trips to La Chinantla during 2024 through an anonymous donor. JSGO acknowledges support from the RIKEN Special Postdoctoral Researchers Program. All material examined was collected under permit No. SPARN/DGVS/02086/24 of SEMARNAT, Mexico.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Pérez-Farrera, M.A.; Gutiérrez-Ortega, J.S.; Haynes, J.L.; Chemnick, J.; Salas-Morales, S.H.; Calonje, M.; Vovides, A.P. *Ceratozamia aurantiaca* (Zamiaceae): A new cycad species from the northern rainforests of Oaxaca, Mexico. *Taxonomy* **2021**, *1*, 243–255. [CrossRef]

2. Vovides, A.P.; Pérez-Farrera, M.A.; Salinas-Rodríguez, M.M.; Galicia, S.; Díaz-Jiménez, P.; Calonje, M.; Gutiérrez-Ortega, J.S. Morphological and anatomical analyses clarify the species definition of *Ceratozamia latifolia* Miq. (Zamiaceae) and lead to the description of a new species: *Ceratozamia reesii*. *Phytotaxa* **2022**, *575*, 224–252. [CrossRef]
3. Martínez-Domínguez, L.; Nicolalde-Morejón, F.; González-Aguilar, M.A.; Vergara-Silva, F.; Stevenson, D.W. *Ceratozamia gigantea* (Zamiaceae), a new species of cycad, endemic to the mountain karst forests of Tabasco, Mexico: What the reproductive structures revealed. *Kew Bull.* **2024**, *79*, 543–558. [CrossRef]
4. Gutiérrez-Ortega, J.S.; Pérez-Farrera, M.A.; Matsuo, A.; Sato, M.P.; Suyama, Y.; Calonje, M.; Vovides, A.P.; Kajita, T.; Watano, Y. The phylogenetic reconstruction of the Neotropical cycad genus *Ceratozamia* (Zamiaceae) reveals disparate patterns of niche evolution. *Mol. Phylogenetics Evol.* **2024**, *190*, 107960. [CrossRef]
5. Habib, S.; Gong, Y.; Dong, S.; Lindstrom, A.; Stevenson, D.W.; Wu, H.; Zhang, S. Phylotranscriptomics shed light on intrageneric relationships and historical biogeography of *Ceratozamia* (Cycadales). *Plants* **2023**, *12*, 478. [CrossRef]
6. Vovides, A.P.; Pérez-Farrera, M.A.; Gutiérrez-Ortega, J.S.; Avendaño, S.; Medina-Villarreal, A.; González-Astorga, J.; Galicia, S. A revision of the *Ceratozamia miqueliana* (Zamiaceae) species complex based on analyses of leaflet anatomical characters. *Flora* **2020**, *270*, 151649. [CrossRef]
7. Calonje, M.; Stevenson, D.W.; Osborne, R. The World List of Cycads. 2024. Available online: <http://www.cycadlist.org> (accessed on 6 August 2024).
8. Brongniart, A.T. Note sur un nouveau genre de Cycadeés du Mexique. *Ann. Des Sci. Nat.* **1846**, *3*, 5–10.
9. Velasco Tapia, B.P. MEX/00G31/IG/99: Manejo Integrado de Ecosistemas en tres Ecorregiones Prioritarias. Comisión Nacional de Áreas Naturales Protegidas. Mexico. 2009. Available online: https://simec.conanp.gob.mx/TTH/Tuxtlas/Tuxtlas_TTH_1980_2007.pdf (accessed on 8 October 2024).
10. Meave, J.A.; Rincón-Gutiérrez, A.; Ibarra-Manríquez, G.; Gallardo-Hernández, C.; Romero-Romero, M.A. Checklist of the vascular flora of a portion of the hyper-humid region of La Chinantla, Northern Oaxaca Range, Mexico. *Bot. Sci.* **2017**, *95*, 722–759. [CrossRef]
11. Meave, J.A.; Rincón, A.; Romero-Romero, M.A. Oak forests of the hyper-humid region of La Chinantla, Northern Oaxaca Range, Mexico. In *Ecology and Conservation of Neotropical Montane Oak Forests*; Springer: Berlin/Heidelberg, Germany, 2006; pp. 113–125.
12. INEGI. Vectorial Map of Land Use and Vegetation, Serie V, Scale 1:250,000. 2013. Available online: https://www.inegi.org.mx/contenidos/temas/mapas/usuarios/metadatos/guia_interusuarios.pdf (accessed on 8 October 2024).
13. Pérez-Farrera, M.A.; Gutiérrez-Ortega, J.S.; Martínez-Martínez, M.G.; Calonje, M. *Zamia magnifica* (Zamiaceae, Cycadales): A New rupicolous cycad species from Sierra Norte, Oaxaca, Mexico. *Taxonomy* **2023**, *3*, 232–249. [CrossRef]
14. Wendland, H. *Ceratozamia miqueliana*; Index Palmarum: Hahn, Hannover, 1854; p. 68.
15. Chemnick, J.; Gregory, T.J. A new species of *Ceratozamia* (Zamiaceae) from Oaxaca, Mexico with comments on distribution, habitat, and relationships. *Phytologia* **1996**, *79*, 51–57.
16. Pérez-Farrera, M.A.; Vovides, A.P.; Martínez-Camilo, R.; Meléndez, N.M.; Iglesias, C. A reassessment of the *Ceratozamia miqueliana* species complex (Zamiaceae) of southeastern Mexico, with comments on species relationships. *Syst. Biodivers.* **2009**, *7*, 433–443. [CrossRef]
17. Pérez-Farrera, M.A.; Vovides, A.P.; Iglesias, C.G. A new species of *Ceratozamia* (Zamiaceae) from Chiapas, Mexico. *Bot. J. Linn. Soc.* **2001**, *137*, 77–80. [CrossRef]
18. Hammer, Ø.; Harper, D.A. Past: Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* **2001**, *4*, 1.
19. Mendoza-Rosales, C.C.; Silva-Romo, G.; Centeno-García, E.; Campos-Madrigal, E.; Rodríguez-Otero, M. La Formación Chivillas en Tehuacán, Puebla, México: Definición, análisis de facies y procedencia. *Boletín Soc. Geológica Mex.* **2013**, *65*, 457–480. [CrossRef]
20. Miquel, F.A.W. Over eenige nieuwe of zeldame Cycadeën in den Hortus Botanicus Amsterdam. Eerste gedeelte. *Tijdschrift voor de wísen natuúrkundige wetenschappen, uitgegeven door de eerste klasse van het Kon. Ned. Instituut van Wetenschappen, Letteren en Schoone Kunsten* **1847**, *1*, 33–43.
21. Maas, P.J.; Maas-van de Kamer, H.; André, T.; Skinner, D.; Valderrama, E.; Specht, C.D. Eighteen new species of Neotropical Costaceae (Zingiberales). *PhytoKeys* **2023**, *222*, 75. [CrossRef]
22. Alvarado-Cárdenas, L.O.; García-Mendoza, A.J.; Sandoval-Gutiérrez, D. *Ruehssia magalloniae* (Apocynaceae; Asclepiadoideae), una especie nueva del bosque mesófilo de montaña de la Sierra Norte de Oaxaca, México. *Bot. Sci.* **2023**, *101*, 608–618. [CrossRef]
23. Flores-Fausto, C.; Ramírez-Roa, A. Novelty in the Gesneriaceae from the Mixe and Yautepec districts, Oaxaca, Mexico: New records, a preliminary list, and a new species. *Rev. Mex. Biodivers.* **2022**, *93*, e933989.
24. Moreno-Méndez, G.; Ortiz-Rodríguez, A.E. A new species of Annonaceae, endemic to the limestone karst forests of Chiapas, Mexico. *Acta Botánica Mex.* **2020**, *127*, e1625. [CrossRef]
25. Zamudio, S.; Mata-Rosas, M.; Salinas-Rodríguez, M.M.; Hernández-Rendón, J. *Pinguicula warijia* sp. nov. (Lentibulariaceae), a newly rediscovered species from the Sierra Obscura, northern Mexico. *Phytotaxa* **2023**, *578*, 219–227. [CrossRef]
26. Wendt, T. Composition, floristic affinities, and origins of the canopy tree flora of the Mexican Atlantic slope rain forests. In *Biological Diversity of Mexico: Origins and Distributions*; Ramamoorthy, T.P., Bye, R., Lot, A., Fa, J., Eds.; Oxford University Press: New York, NY, USA, 1993; pp. 595–680.
27. Graham, A. Studies in neotropical paleobotany. II. The Miocene communities of Veracruz, Mexico. *Ann. Mo. Bot. Gard.* **1976**, *63*, 787–842. [CrossRef]

28. Gutiérrez-Ortega, J.S.; Pérez-Farrera, M.A.; Sato, M.P.; Matsuo, A.; Suyama, Y.; Vovides, A.P.; Molina-Freaner, F.; Kajita, T.; Watano, Y. Evolutionary and ecological trends in the Neotropical cycad genus *Dioon* (Zamiaceae): An example of success of evolutionary stasis. *Ecol. Res.* **2024**, *39*, 131–158. [[CrossRef](#)]
29. Grandcolas, P.; Nattier, R.; Trewick, S. Relict species: A relict concept? *Trends Ecol. Evol.* **2014**, *29*, 655–663. [[CrossRef](#)] [[PubMed](#)]
30. Villaseñor, J.L.; Meave, J.A. Floristics in Mexico today: Insights into a better understanding of biodiversity in a megadiverse country. *Bot. Sci.* **2022**, *100*, 14–33. [[CrossRef](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.