

Article

Ceratozamia dominguezii (Zamiaceae): A New Cycad Species from Southeastern Mexico

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Abstract: *Ceratozamia dominguezii* (Zamiaceae), a new species endemic to the lowland karstic tropical rainforests of southeastern Veracruz, Mexico, is described. The new species is part of the *C. robusta* species complex, a group of closely related species that share unique characteristics in the genus, such as robust trunks, large strobili, and long leaves. Compared with the other species in the complex (i.e., *C. robusta*, *C. leptoceras*, *C. aurantiaca* and *C. subroseophylla*), *C. dominguezii* has the longest rachides, and is characterized by having papyraceous leaflets, a unique caramel color in emerging leaves, and a dark-violet color in the central portion of distal faces of male and female sporophylls. *Ceratozamia dominguezii* occurs within the Uxpanapa floristic refuge, which is hypothesized to have sheltered a numerous group of tropical elements during the Neogene glaciations. The recognition of *C. dominguezii* contributes to clarifying the present diversity of cycads in the genus *Ceratozamia*, and adds discussion on the role of floristic refugia in the divergence of Neotropical plants in Mexico.

Keywords: cycads; endangered species; floristic refugia; Mesoamerica; morphological analyses; species complex



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1. Introduction

Over a century and a half after the Neotropical genus *Ceratozamia* Brongn. was first established [1], only 12 species were recognized [2]. However, the pace of species discovery within the genus has accelerated considerably in recent years, with the number of accepted species nearly tripling to 34 since the year 2000 [3]. This notable burst of species discovery has been achieved through the efforts of researchers surveying previously unexplored areas for cycads as well as the critical examination of herbarium specimens (e.g., [4–8]). The increase in species discovery in recent years is consistent with the prediction by Walters et al. [9], who suggested that the number of species in *Ceratozamia* will approximate 40 once the field explorations and the taxonomic determinations of known populations are completed. Identifying the entirety of the constituent species within *Ceratozamia* will contribute to a better understanding of its evolutionary history, and this in turn will allow for the identification of evolutionarily significant units [10] within the genus to aid in future conservation efforts.

Species of the genus *Ceratozamia* can be found in a wide range of elevations, from 0 to 2000 m a.s.l., mainly in tropical forests, oak forests and cloud forests in mountainous regions of Mexico, Guatemala, Belize and Honduras [11]. Most species (26 of 34) occur in the States of Oaxaca, Chiapas and Veracruz, in southeastern Mexico: An area that represents the richest floristic region in the country [12]. This high biodiversity can be explained by the high neo- and paleoendemism [13] originated by processes of diversification

mainly influenced by climatic fluctuations which occurred between 5 and 20 million years ago [14,15]. Indeed, Wendt [16] identified the mountains of Uxpanapa, Veracruz and the “arc area” (a mountain chain that extends from Uxpanapa to northern Chiapas) as one of several regions that could have served as refugia for warm-tropical communities during the glaciation cycles that took place from 20 million years to 10,000 years ago. Recent studies on cycads have supported this hypothesis [15,17,18]; yet little is known about the influence of these refugia on the evolution of *Ceratozamia*.

In the year 2000, we started reviewing the taxonomy and distribution of the *Ceratozamia robusta* Miq. species complex, a group of closely related species characterized by having robust trunks, large strobili, and long leaves [19]. The complex occurs in the mountainous areas of Chiapas, Guerrero, Oaxaca and Veracruz, Mexico and ranges into adjacent Guatemala and Belize (Figure 1). It is currently comprised of *C. robusta*, *C. subroseophylla* Mart.-Domínguez and Nic.-Mor., *C. aurantiaca* Pérez-Farr., Gut. Ortega, J.L. Haynes and Vovides, and *C. leptoceras* Mart.-Domínguez, Nic.-Mor., D.W.Stev and Lorea-Hern., the latter occurring in the State of Guerrero [20], each species distinguished from the others by qualitative and quantitative traits such as the color of emerging leaves, size and color of strobili, or size and shape of leaves and leaflets [8]. In the process of reviewing specimens of the *C. robusta* complex, we located a few specimens deposited at HEM, XAL and MEXU herbaria (acronyms according to [21]) which were collected in the floristic refuge of Uxpanapa (Veracruz) and required closer scrutiny to ensure its taxonomic status. These plants, previously identified as *C. robusta*, were originally discovered and first collected in 1975 by Dr. Mario Vázquez Torres of the Institute of Biological Sciences of Universidad Veracruzana.

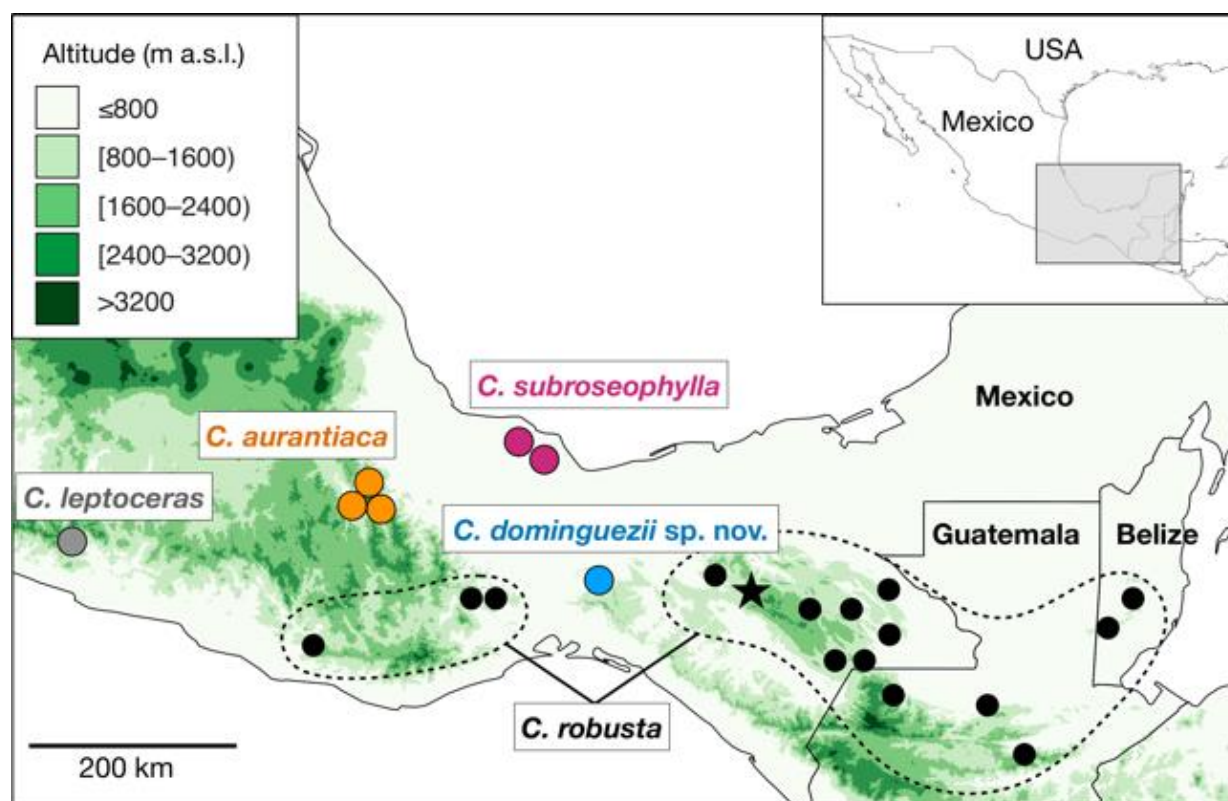


Figure 1. Distribution map of the known populations of the *Ceratozamia robusta* species complex. The putative new species from Uxpanapa (*C. dominguezii* sp. nov.) appears in the mid-portion of the distribution range (blue circle). Black circles surrounded by a dotted line indicate the occurrence of populations of *C. robusta*. The star symbol indicates the neotype locality of *C. robusta* (Parque Nacional Cañón del Sumidero, Chiapas, Mexico). The species *C. aurantiaca*, *C. subroseophylla* and *C. leptoceras* are also part of the species complex [8]. Green color scale indicates the elevation in meters above sea level (m a.s.l.) as recorded in the raster layers of 30 s resolution of the NASA Shuttle Radar Topographic Mission (SRTM) 90 m Digital Elevation Database v4.1 deposited in DIVA-GIS (<https://www.diva-gis.org/>; accessed on 14 October 2021).

In mid-2019, we located populations of this *Ceratozamia* in the wild in order to better understand its variation and ecology and collect more specimens. At this time, we observed that the plants from Uxpanapa appeared to differ from the contemporary circumscription of *C. robusta*. For example, the leaves of these plants were larger than those of any other known species in the genus (Figure 2). Additionally, the distal sporophyll faces of mature seed and pollen strobili were a dark-violet color that fades to yellowish-brown at the margin, a distinct difference to the brownish margins found in *C. robusta*. These observations led us to consider the possibility that the plants from Uxpanapa could represent a new species. Previous studies of *C. robusta sensu lato* have led to the discovery of new species [7,8], so we tested whether this was also the case for populations from Uxpanapa, by evaluating their morphological variation and testing its delimitation as a species when compared to other species within the *C. robusta* species complex.



Figure 2. The putative new cycad species from Uxpanapa, Veracruz, Mexico. (A) The plants from this locality resembles *Ceratozamia robusta*, but have significantly longer leaves, and papyraceous, smooth and wider leaflets that are more separated along the rachis. (B) The first author (M.A.P.-F.) showing the large size of leaves.

2. Materials and Methods

The morphological variation among species in the *C. robusta* species complex and the new putative taxon (Table 1, Figure 1) was first evaluated through the observation of qualitative diagnostic characters related to the trunk, leaves and leaflet shape and texture (Table 2), as they were effective in distinguishing the different taxa in the complex [8]. Additionally, we measured seven leaf and leaflet traits commonly used as diagnostic characters in *Ceratozamia* [7,8] and compared them among species (Table 3). For this, we

measured the seven traits on 15 adult plants from one population from Uxpanapa, and added it to the dataset used in Pérez-Farrera et al. [8], which included data for the species *C. robusta*, *C. subroseophylla* and the recently described species *C. aurantiaca*.

Table 1. Species compared in this study. *n* = number of samples analyzed in morphometric analyses. The number of analyzed samples of *Ceratozamia aurantiaca*, *C. robusta* and *C. subroseophylla* correspond to those used in the study by Pérez-Farrera et al. [8].

Species	Elevation (m a.s.l.)	Locality	<i>n</i>
<i>Ceratozamia</i> from Uxpanapa (<i>C. dominguezii</i> sp. nov.)	130	Uxpanapa, Veracruz, Mexico	15
<i>C. aurantiaca</i>	480	Teutila, Sierra Norte, Oaxaca, Mexico	16
<i>C. robusta</i>	1200	San Fernando, Parque Nacional Cañón del Sumidero, Chiapas, Mexico (neotype population)	20
<i>C. subroseophylla</i>	500	Santiago Tuxtla, Veracruz, Mexico (type population)	11

Table 2. Comparison of morphological traits variation among species of *Ceratozamia robusta* complex.

Trait	<i>Ceratozamia</i> from Uxpanapa (<i>C. dominguezii</i> sp. nov.)	<i>C. aurantiaca</i>	<i>C. subroseophylla</i>	<i>C. robusta</i>	<i>C. leptoceras</i>
Trunk	Erect to decumbent	Erect to decumbent	Erect to decumbent	Erect	Erect to decumbent
Color of emerging leaves	Caramel color	Orange-brown to orange	Yellowish-brown	Reddish-brown	Green to copper-green
Crown of leaves	Open	Open	Open	Closed	Open
Texture of leaflets	Papyraceous	Coriaceous	Papyraceous	Papyraceous	Membranaceous
Veins in abaxial part of leaflets	Not visible	Not visible	Visible	Not visible	Visible
Apex of female cone	Acuminate	Mucronate	Mucronate	Acuminate	Acute

Table 3. Mean and standard deviation of measures of the seven quantitative traits examined in the four examined taxa. Bold texts in each column indicate the higher values among the four species. Note that the putative new species (*Ceratozamia Uxpanapa*) has the longer rachis, widest separation between median leaflets and widest basal leaflets.

Trait	<i>Ceratozamia</i> from Uxpanapa (<i>C. dominguezii</i> sp. nov.)	<i>C. aurantiaca</i>	<i>C. robusta</i>	<i>C. subroseophylla</i>
A (Length of petiole)	60.82 (16.61)	54.66 (13.11)	67.6 (11.22)	84.46 (11.93)
B (Length of rachis)	172.83 (35.30)	135.13 (28.26)	126.91 (20.9)	132.25 (28.26)
C (Number of leaflet pairs)	31.14 (7.27)	24.93 (4.611)	28.85 (4.90)	34.90 (5.30)
D (Length of median leaflets)	34.6 (4.73)	33.61 (5.90)	32.07 (3.05)	34.70 (4.45)
E (Distance between median leaflets)	40.05 (10.53)	35.91 (8.17)	29.732 (4.745)	23.006 (5.33)
F (Width of median leaflets)	37.28 (5.96)	40.11 (3.85)	32.38 (3.07)	34.12 (3.399)
G (Width of basal leaflets)	11.77 (1.47)	11.50 (2.45)	9.2945 (1.46)	11.29 (2.05)

We performed the following statistic tests as implemented in PAST v.3.4 [22] to determine whether the morphometric variation can distinguish between species. For the univariate analyses, the Welch's ANOVA was used to test whether the means of the trait variation across species was significantly different. Additionally, for each trait, the Tukey's Q of pairwise differentiation between species was calculated to distinguish which traits significantly differ in one species with respect to the others. For multivariate analyses, a

linear discriminant analysis (LDA) was conducted to test whether the overall variation among species can distinguish the four species determined a priori; namely the putative new species from Uxpanapa, and the three species in the *C. robusta* species complex. The pairwise Mahalanobis distances were calculated to test whether the four species are significantly separated, which would imply morphological differentiation completely sorted among species. The information of three more traits (H: Height of trunk; I: Diameter of trunk; J: Number of leaves) were added to the dataset because we noticed in preliminary runs that they improved to separate the groups in the LDA and other multivariate analyses. However, we had information of these traits for *C. robusta* and *C. aurantiaca*, and we were unable to obtain data for these traits in the other species.

3. Results

The putative new species from Uxpanapa can be distinguished from each of the three compared species utilizing different qualitative traits (Table 2). Most remarkable is the unique caramel color (similar to light-brown) of the emerging leaves, which are orange in *C. aurantiaca*, yellowish-brown in *C. subroseophylla*, reddish-brown in *C. robusta* and green to copper-green in *C. leptoceras*. Likewise, the measurements of morphometric traits were informative to understand general differences between the putative new species in respect to three closely related species in the *C. robusta* species complex (Table 3, Figure 3). The plants from Uxpanapa have the longest rachides (mean = 172.83 ± 35.30 cm), longer distances between median leaflets (mean = 40.05 ± 10.53 mm), and widest basal leaflets (mean = 11.77 ± 1.47 mm) among the examined species. *C. subroseophylla* presents the longest petioles (mean = 84.46 ± 11.93 cm), the most leaflet pairs (34.9 ± 5.3) and the longest median leaflets (mean = 34.70 ± 4.45 cm). *C. aurantiaca* has the widest median leaflets (mean = 40.11 ± 3.85 mm). Surprisingly, *C. robusta*, although it has been historically considered as the largest sized species (due to its long leaves and robust trunks) in the genus [23], did not rank first in any of the examined traits.

The ANOVA test demonstrated that six of the seven quantitative traits have significantly different mean values among the four compared species (Table 4). The length of median leaflets showed no significant differentiation ($p = 0.1908$), suggesting that this trait has little diagnostic utility within the *C. robusta* species complex. The Tukey's Q values of pairwise differentiation gave more detailed information on how the examined species can be distinguished (Table 5). Concordant with our prior observations, the plants from Uxpanapa were found to have significantly longer rachides than the other species (Figures 2 and 3B, Table 5). In addition, the plants from Uxpanapa have significantly longer rachides than *C. aurantiaca* ($p < 0.005$), significantly longer distance between median leaflets than *C. robusta* ($p < 0.005$) and *C. subroseophylla* ($p < 0.001$), and significantly narrower median leaflets ($p < 0.05$) and wider basal leaflets than *C. robusta* ($p < 0.005$).

The LDA summarized the total variation among species in three axes, each representing 68.97% (axis 1), 22.35% (axis 2) and 8.683% (axis 3) of the total variation. Axis 1 clearly separates *C. subroseophylla* from *C. robusta*, *C. aurantiaca* and the plants from Uxpanapa (Figure 4A). The longest biplots B and E suggest that the length of rachis and the distance between median leaflets were the main traits that dispersed the four groups. Axes 2 and 3 do not improve the segregation, showing that a few individuals from Uxpanapa overlap with the convex hulls of *C. aurantiaca* (Figure 4B). The confusion matrix obtained from LDA (Table 6) confirmed that only two individuals from Uxpanapa may be confused with either *C. aurantiaca* (1 individual) or *C. robusta* (1 individual). Additionally, one individual of *C. aurantiaca* may be confused as the putative species from Uxpanapa. However, the squared Mahalanobis distances were significantly high in all pairwise comparisons, suggesting that the overall morphometric variation is completely sorted among the examined taxa, confirming that the population from Uxpanapa represents a different species (Table 7).

In summary, the presented evidence suggests that the plants from Uxpanapa, Veracruz, have the longest leaves within the *C. robusta* species complex, when compared to the type population of each species. Additionally, overall, plants look similar to *C. aurantiaca* but

have leaflets with a papyraceous (vs. coriaceous) texture, and emergent leaves that are of a unique caramel color not found in other members of the group. Additionally, the central portion of distal faces of the sporophylls of both the pollen and seed cones of the Uxpanapa plants are dark-violet that fades to yellowish-brown towards the margins, a unique trait within the genus. Because this suite of characters distinguishes these plants from the rest in the genus, we propose that the *Ceratozamia* populations from Uxpanapa should be recognized as a new species, and we name it as *Ceratozamia dominguezii* sp. nov.

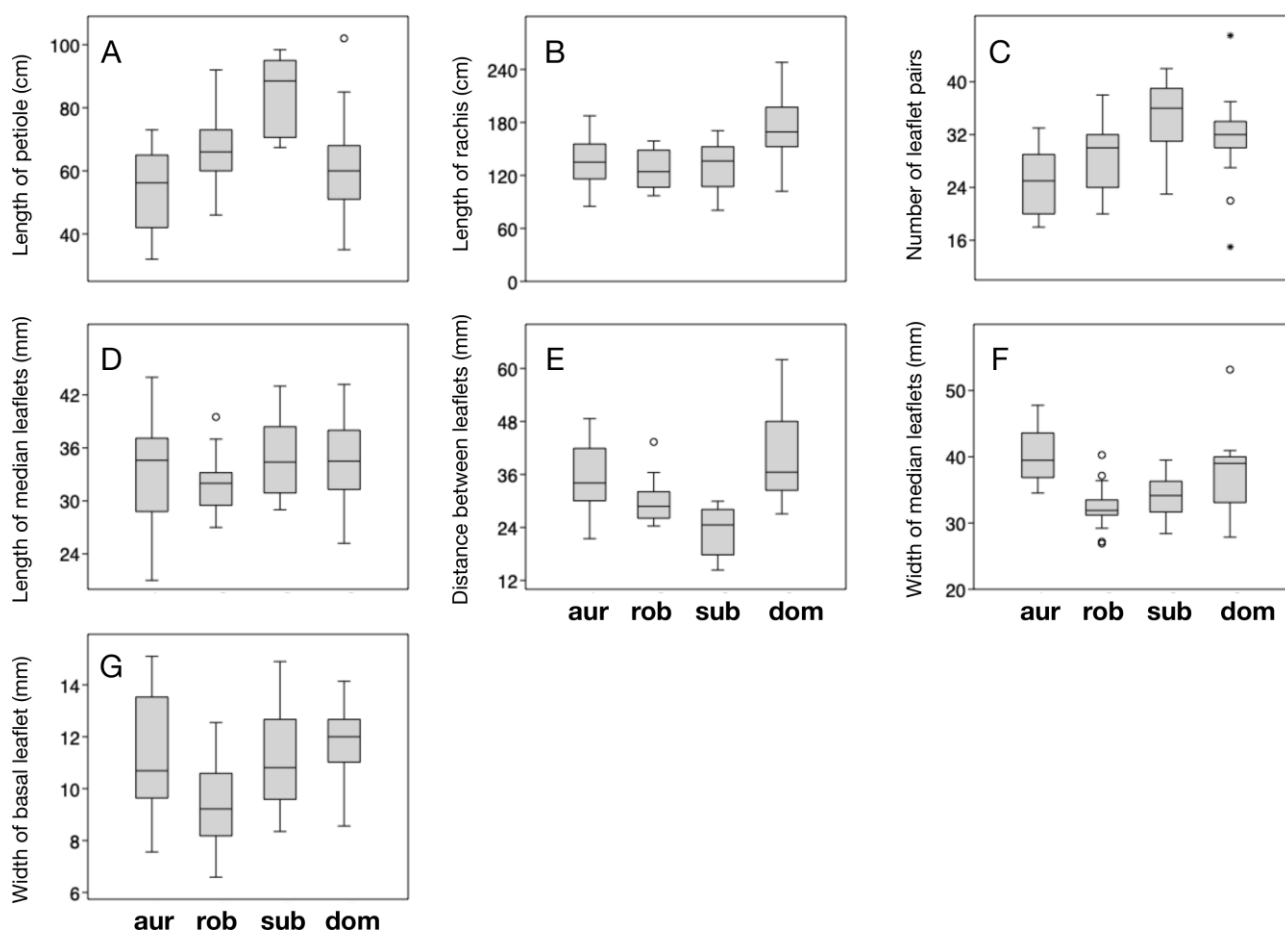


Figure 3. Morphometric variation among the four compared species: *Ceratozamia aurantiaca* (aur), *C. robusta* (rob), *C. subroseophylla* (sub), and the putative new species from Uxpanapa (dom; *C. dominguezii* sp. nov.). The plots (A–G) correspond to the traits listed in Table 3. Whiskers indicate standard errors and circles and asterisks indicate outliers.

Table 4. Morphometric differentiation of seven traits among the four *Ceratozamia* species examined. Overall differentiation estimated as Welch’s *F* in ANOVA and *p*-values are indicated. D.f. = degree freedom.

Key	Trait	<i>F</i>	D.f.	<i>p</i>
A	Length of petiole	12.7	27.96	<0.001
B	Length of rachis	6.455	27.78	0.001
C	Number of leaflet pairs	8.683	28.07	<0.001
D	Length of median leaflets	1.698	27.23	0.1908
E	Distance between median leaflets	13.05	27.97	<0.001
F	Width of median leaflets	14.45	28.48	<0.001
G	Width of basal leaflets	9.147	28.07	<0.001

Table 5. Pairwise Tukey's Q values of differentiation between species of seven morphometric traits. Abbreviations: Traits A–G correspond to those listed in Tables 3 and 4. *, $p < 0.05$; **, $p < 0.005$; ***, $p < 0.001$.

		<i>Ceratozamia</i> from Uxpanapa (<i>C. dominguezii</i> sp. nov.) vs. <i>C. aurantiaca</i>	<i>Ceratozamia</i> from Uxpanapa (<i>C. dominguezii</i> sp. nov.) vs. <i>C. robusta</i>	<i>Ceratozamia</i> from Uxpanapa (<i>C. dominguezii</i> sp. nov.) vs. <i>C. subroseophylla</i>	<i>C. aurantiaca</i> vs. <i>C. robusta</i>	<i>C. aurantiaca</i> vs. <i>C. subroseophylla</i>	<i>C. subroseophylla</i> vs. <i>C. robusta</i>
A	Length of petiole	1.782 ^{ns}	1.962 ^{ns}	6.841 ^{***}	3.743 [*]	8.622 ^{***}	4.879 ^{**}
B	Length of rachis	5.167 ^{**}	6.294 ^{***}	5.562 ^{**}	1.128 ^{ns}	0.3951 ^{ns}	0.7325 ^{ns}
C	Number of leaflet pairs	4.28 [*]	1.581 ^{ns}	2.597 ^{ns}	2.698 ^{ns}	6.877 ^{**}	4.179 [*]
D	Length of median leaflets	0.8264 ^{ns}	2.131 ^{ns}	0.09188 ^{ns}	1.304 ^{ns}	0.9183 ^{ns}	2.223 ^{ns}
E	Distance between median leaflets	2.121 ^{ns}	5.291 ^{**}	8.74 ^{***}	3.17 ^{ns}	6.619 ^{**}	3.449 ^{ns}
F	Width of median leaflets	2.599 ^{ns}	4.496 [*]	2.9 ^{ns}	7.095 ^{***}	5.499 ^{**}	1.596 ^{ns}
G	Width of basal leaflets	0.5448 ^{ns}	5.092 ^{**}	0.9928 ^{ns}	4.547 [*]	0.4481 ^{ns}	4.099 [*]

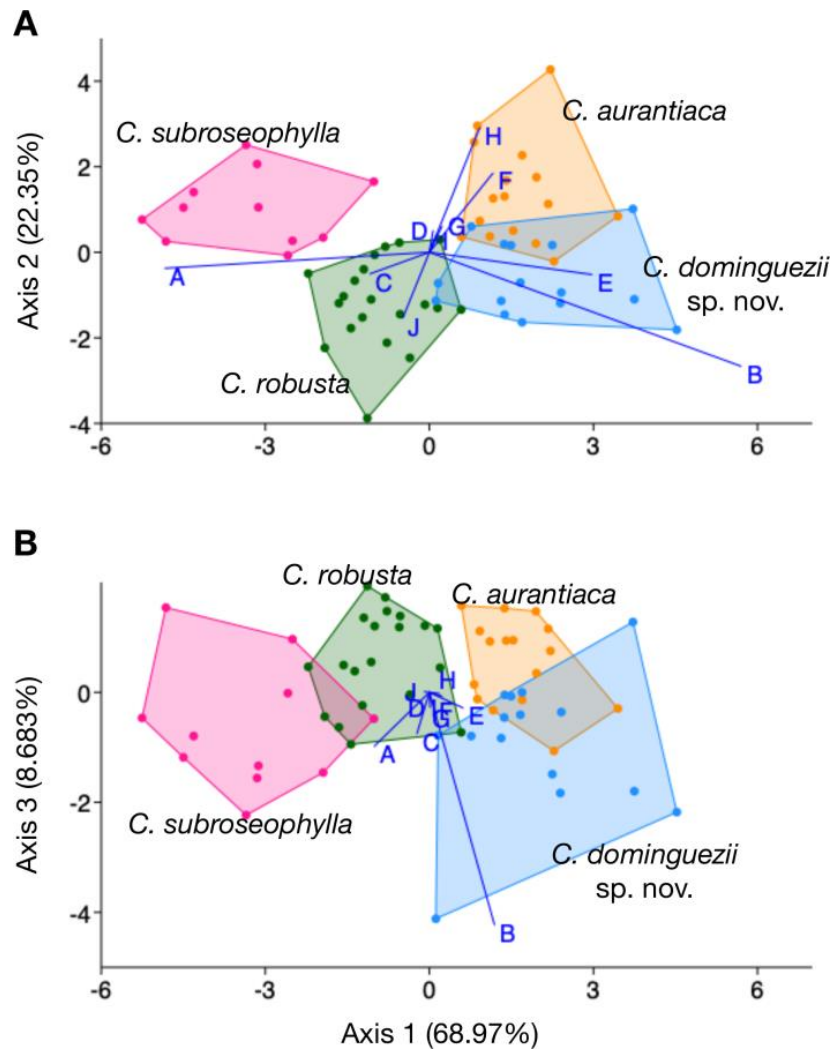


Figure 4. Linear discriminant analysis plot showing the dispersion of the variation of individuals of four examined species. Plot (A) shows the variation dispersed along the two main axes (axes 1 and 2); plot (B) shows axes 1 and 3. Axes 1, 2, and 3 summarize 68.97%, 22.35% and 8.683% of the total variation. Biplots A–J represent the loading of each trait along the axes: A, length of petiole; B, length of rachis; C, number of leaflet pairs; D, length of median leaflets; E, distance between median leaflets; F, width of median leaflets; G, width of basal leaflets; H, high of trunk; I, diameter of trunk; J, number of leaves.

Table 6. Confusion matrix constructed with the linear discriminant analysis (LDA). Rows indicate given groups (number of individuals that we consider as *C. aurantiaca*, *C. robusta*, *C. subroseophylla* or *C. dominguezii* sp. nov., according to their population type) and columns indicate predicted groups by the LDA.

	<i>C. aurantiaca</i>	<i>C. robusta</i>	<i>C. subroseophylla</i>	<i>Ceratozamia</i> from Uxpanapa (<i>C. dominguezii</i> sp. nov.)	Total
<i>C. aurantiaca</i>	15	0	0	1	16
<i>C. robusta</i>	1	18	0	1	20
<i>C. subroseophylla</i>	0	0	11	0	11
<i>Ceratozamia</i> from Uxpanapa (<i>C. dominguezii</i> sp. nov.)	1	0	0	14	15
Total	17	18	11	16	62

Table 7. Squared Mahalanobis distances (below the diagonal) and *p* values (above the diagonal) among the four examined species. All values are significant ($p < 0.001$), suggesting complete morphological sorting among species.

	<i>C. aurantiaca</i>	<i>C. robusta</i>	<i>C. subroseophylla</i>	<i>Ceratozamia</i> from Uxpanapa (<i>C. dominguezii</i> sp. nov.)
<i>C. aurantiaca</i>		<0.001	<0.001	<0.001
<i>C. robusta</i>	14.11		<0.001	<0.001
<i>C. subroseophylla</i>	28.372	28.744		<0.001
<i>Ceratozamia</i> from Uxpanapa (<i>C. dominguezii</i> sp. nov.)	14.011	37.327	30.915	

New species description:

Ceratozamia dominguezii Pérez-Farr. and Gut.-Ortega sp. nov. (Figures 5–9).

Holotype:—MEXICO. Veracruz, Uxpanapa, 130 m a.s.l. Pérez-Farrera M.A, 29 May 2021, 4013 ♂, (HEM). Isotypes: (XAL; MEXU).

Ceratozamia dominguezii can be distinguished by having long rachides with very separated median leaflets, emergent leaves of caramel color, papyraceous leaflets, and distal faces of mega- and microsporophylls with a dark-violet color that fades to yellowish-brown at the margin.

Additional specimens examined:—MEXICO. Veracruz: Uxpanapa, 16 January 1975, Mario Vázquez 1760 (MEXU, XAL, MO); Jesús Carranza, 12 April 1982, Mario Vázquez et al., 2430 (MEXU); Jesús Carranza, 19 February 2009, David Jimeno DJS1045 (MEXU, UV); Uxpanapa, 8 May 2019, Miguel A. Pérez Farrera, Michael Calonje and Cesar Daniel Coutiño Ovando 3763 (HEM); 4 November 2019, Miguel A. Pérez Farrera and Hector Gómez Domínguez 3800 (HEM); 23 October 2020, Miguel A. Pérez Farrera and Héctor Gómez Domínguez 3868 (HEM); 4 September 2021 Miguel A. Pérez Farrera and Pedro Díaz Jiménez 4064 ♀ (HEM).

Plant rupicolous, arborescent, unbranching. *Stem* cylindrical, erect, sometimes decumbent with age, covered with persistent leaf bases, 32–132 cm tall, 20.69–30 cm in diameter. *Cataphylls* persistent, brown and densely tomentose at emergence, triangular apex acuminate. *Leaves* pinnate, 22–43 per crown, forming a semi-open crown, erect, ascending, olive green, keeled lightly in the basal part of leaves, 165.5–316.0 cm long, 50.4–68.4 cm wide, caramel color at emergence, turning green at maturity. *Petiole* terete, 35–103 cm long, densely armed with thick prickles. *Rachis* green, terete, 102–248 cm long, erect, with sparse prickles diminishing into the distal end of the rachis. *Leaflets* 15–37 pairs, papyraceous, subopposite to alternate in the basal part of the leaf, opposite to subopposite in the median part, linear, subfalcate to falcate, margin entire, apex acute to acuminate, asymmetric; base broad attenuate, articulation green adaxially, light green abaxially 0.85–1.4 cm wide, veins 30–33, parallel, inconspicuous, slightly translucent; median leaflets 25–43 cm long, 2.7–4.5 cm wide, spaced 2.7–6.2 cm between leaflets. *Microstrobilus* solitary, conical, erect, orange tomentose when emerging, 34–50 cm long, 5–6 cm diameter, peduncle densely tomentose, 8–9 cm long, 3 cm diameter. *Microsporophyll* cuneiform, 17.37–22.96 mm long, 8.79–13.38 mm wide, distal face bicornate, with dark-violet color at the central portion, which fades to brown-yellowish towards the margins, horns 1.5–2.7 mm long, separated by 120–135° angle, sporangia zone on abaxial surface 10.22–14.81 mm long, microsporangia 220–240 grouped in 3–4 per sorus. *Megastrobilus* solitary, cylindrical, erect, 44–48 cm long, 10–12 cm diameter; apex mucronate, light orange pubescent at emergence, peduncle tomentose, 7–9 cm long, 2.2–3.2 cm in diameter. *Megasporophylls* peltate, bicornate, 4–5.5 cm wide, 2.2–2.5 cm tall, distal face pubescent, when mature, distal face presents a dark-violet color at the central portion, which fades to brown-yellowish towards the margins (including horns). *Seed* ovoid, sarcotesta cream when immature, sclerotesta beige when mature, 1.5–2.0 cm diameter, 2.5–2.9 cm long, with micropylar ridges.

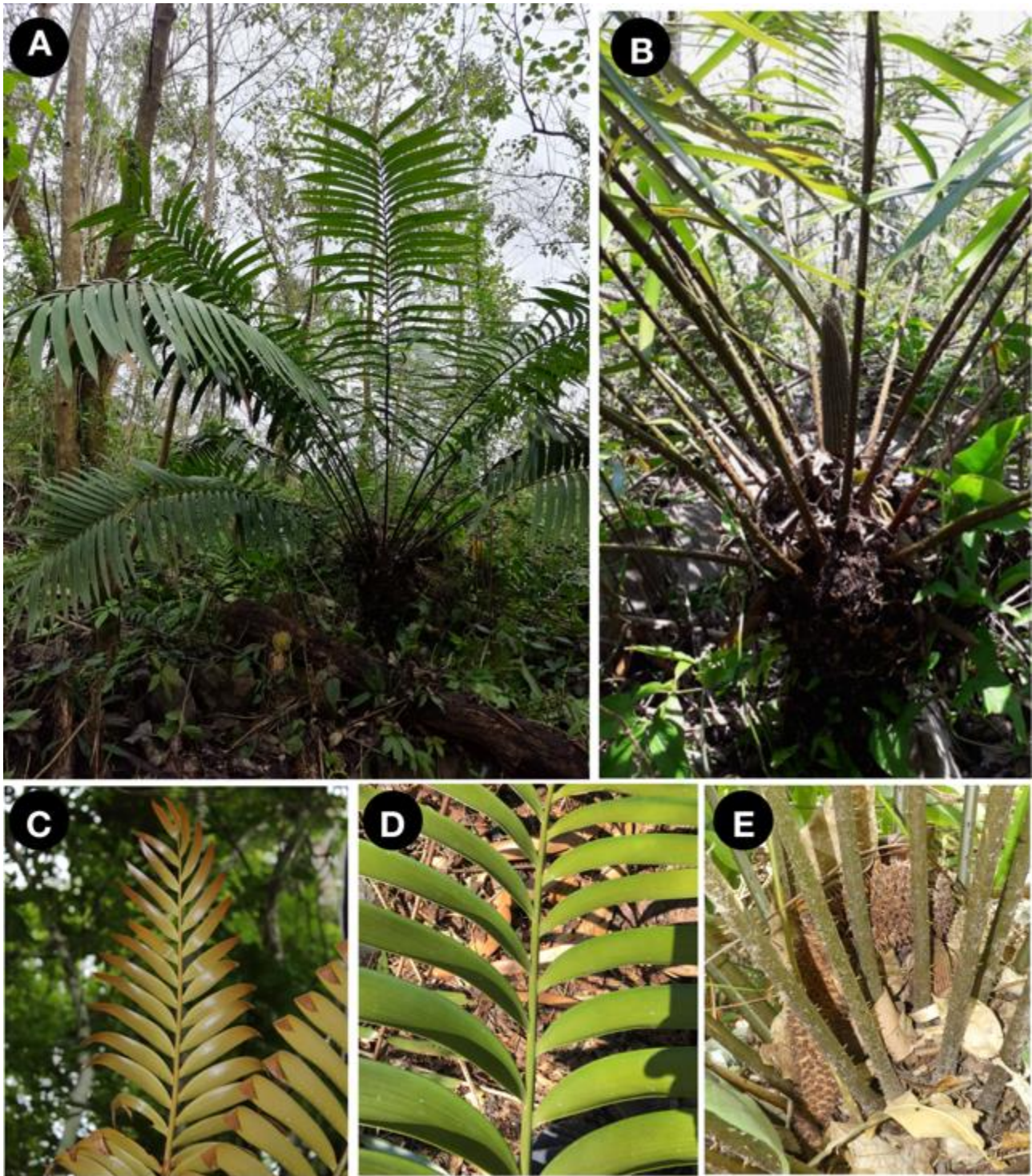


Figure 5. *Ceratozamia dominguezii* sp. nov. (A) Adult plant showing the open crown of erect leaves. (B) Apex of the semi-hypogeous robust trunk, details of long petioles armed with thick prickles, and microstrobilus. (C) Emerging leaf displaying distinctive caramel coloration. (D) Close-up of leaflets arrangement on the rachis. (E) Close-up of petiole bases.



Figure 6. Color variation in emerging leaves of *Ceratozamia dominguezii* sp. nov. (A) Emerging leaves of caramel color, (B,C) while maturing, leaves gradually acquire a green color.



Figure 7. Reproductive structures of *Ceratozamia dominguezii*. (A) Male cone. (B) Female cone.

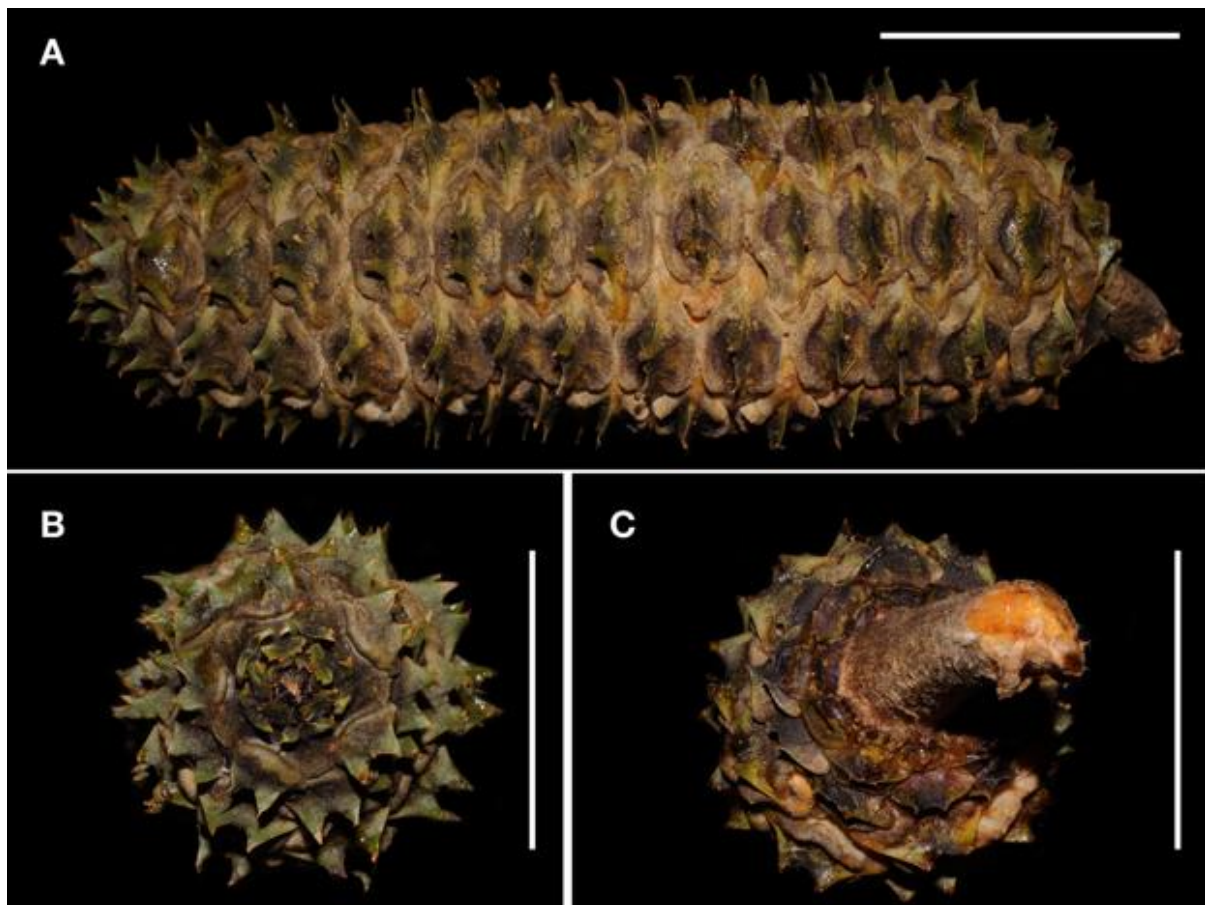


Figure 8. Megastrobilus of *Ceratozamia dominguezii*. Note the distal faces of sporophylls of dark-violet color that fades to brown-yellowish towards the margins. (A) Lateral view of megastrobilus and peduncle. (B) View from above. (C) View from below. Scales = 10 cm.

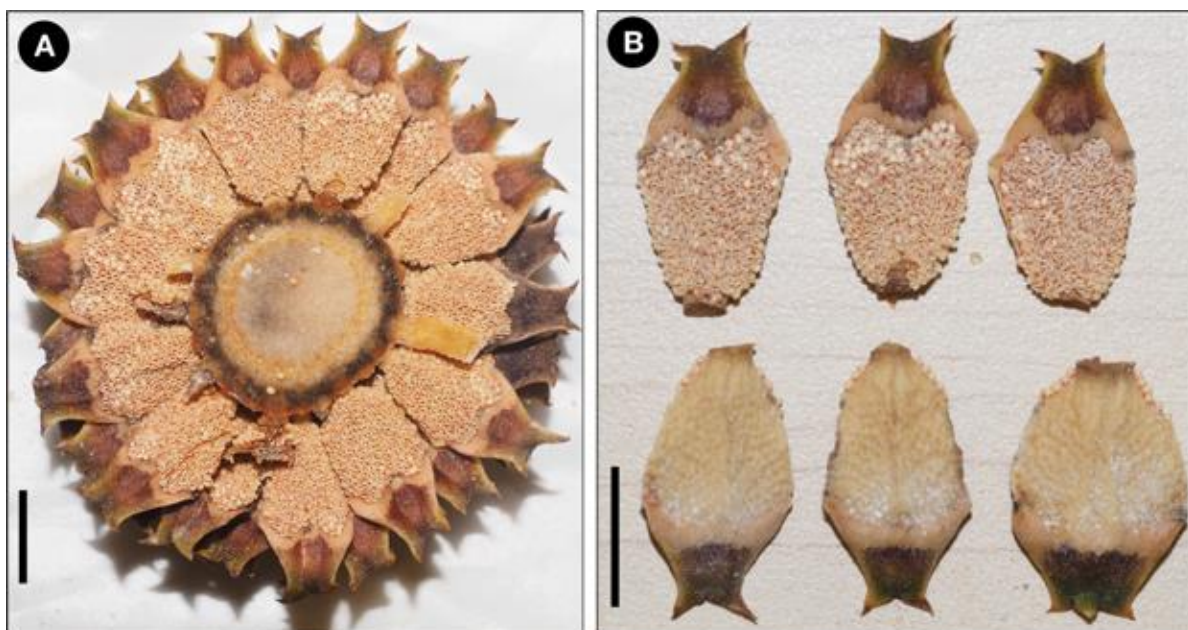


Figure 9. (A) Transversal view of megastrobili showing details of megasporophylls, abaxial side. (B) Megasporophylls: abaxial side (above) and adaxial side (below). Scales in both panels = 1 cm.

Habitat description: *Ceratozamia dominguezii* grows between 100 and 130 m a.s.l., in karst tropical forest, according to the vegetation classification of Rzedowski [24]. Associated flora includes *Brosimum alicastrum* Sw., *Pseudobombax ellipticum* (Kunth) Dugand, *Swietenia macrophylla* King, *Bursera simaruba* (L.) Sarg., *Stenanona* sp., *Coccoloba* sp., *Amphitecna* sp., *Plumeria rubra* L., *Astrocaryum mexicanum* Liebm. ex Mart., *Chamaedorea ernesti-augustii* H. Wendl., *Ch. pinnatifrons* H. Wendl., *Ch. oblongata* Mart., *Ch. elatior* Mart., *Ch. tepeljilote* Liebm., *Begonia nelumbonifolia* Schltld. and Cham., *Anthurium pedatoradiatum* Schott, *A. schlechtendalii* Kunth, *Monstera deliciosa* Liebm., and *Philodendron radiatum* Schott.

Etymology: the specific epithet was chosen to honor Héctor Gómez-Domínguez (M.Sc.), retired technician from the Eizi Matuda Herbarium (Chiapas) whose field explorations and specimen collections resulted in the discovery of several new cycad species from southern Mexico.

4. Discussion

Although the *Ceratozamia* populations from Uxpanapa, Veracruz, have historically been considered as *C. robusta*, our results demonstrate that the set of morphological traits presented by these populations are not consistent with the concept of *C. robusta*, as defined by plants occurring at or near its type locality. The neotype of *C. robusta* [25] is from Parque Nacional Cañón del Sumidero, northwest of Tuxtla Gutiérrez, Chiapas (Table 1), a locality that is relatively close to Uxpanapa (Figure 1). However, the plants from Uxpanapa (here recognized as *C. dominguezii*) have significantly longer rachides (Figure 3B), wider distances between leaflets along the rachis (Figure 3E), wider median leaflets (Figure 3F) and wider basal leaflets (Figure 3G, Table 5). This taxon is also distinguishable from *C. robusta* and the rest of the species in the complex based on qualitative traits (Table 2), most notable being the unique caramel color of emerging leaves (Figure 6), and the dark-violet coloration at the central portion of distal faces of strobili (Figures 7 and 8).

The occurrence of *C. dominguezii* and the distribution of the other species in the *C. robusta* species complex can be informative about the evolutionary history of this group (Figure 1). The Isthmus of Tehuantepec has been identified as a main geographic barrier causing the divergence of lineages at either side [17]. *Ceratozamia dominguezii* and *C. robusta* occur at the eastern side of the isthmus, whereas *C. subroseophylla*, *C. aurantiaca*, and *C. leptoceras* occur at the western side. However, there is evidence of historical connectivities between the two sides. Wendt [16] identified that the regions of Uxpanapa (home of *C. dominguezii*), the northern mountains of Chiapas (home of *C. robusta* in Chiapas), as well as the Izabal floristic refugium region (home of *C. robusta* in Guatemala and Belize, Los Tuxtlas (home of *C. subroseophylla*), and the northern mountains of Oaxaca (home of *C. aurantiaca*) harbor highly similar karstic, tropical rainforests, although each with their own endemic species. These areas are thought to represent floristic refugia that allowed the persistence of paleoendemic groups such as *Oreomunnea* Oerst. and *Ceratozamia* [26] during the climatic fluctuations which occurred since the Miocene to the Late Pleistocene [16]. Events of vicariance in plant lineages inhabiting throughout these areas may have occurred during these times, since events of vicariance are expected to have influenced cycad divergence leading to speciation [15,17,18,27]. Future phylogenetic analyses may clarify the times of divergence, as well as its position and delimitation in the phylogeny of the genus.

To date, we have identified four populations of *C. dominguezii* in Uxpanapa, Veracruz, Mexico. However, Veracruz is one of the states with the highest deforestation rate in the country [28], and the forest of Uxpanapa is one of the most severely affected [29]. Uxpanapa also hosts two other cycad species: *Ceratozamia euryphyllidia* Vázq. Torres, Sabato and D.W.Stev., a distantly related species belonging to the *C. miqueliana* species complex [30,31], and *Zamia purpurea* Vovides, J.D.Rees and Vázq. Torres. Both species are listed as Critically Endangered in the Red List of the International Union for the Conservation of Nature [32]. We propose that *C. dominguezii* should be considered under the same status, CR, given the same threat and according to the criteria B2ab(i,ii,iii,iv,v) [32].

Conservation measures for in-situ protection and representation of this species in ex-situ collections are urgently necessary.

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