

Article

Zamia magnifica (Zamiaceae, Cycadales): A New Rupicolous Cycad Species from Sierra Norte, Oaxaca, Mexico

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Abstract: *Zamia magnifica* (Zamiaceae), a new species endemic to Sierra Norte, Oaxaca, Mexico, is described. *Zamia magnifica* is characterized by having a rupicolous habit, pendent leaves bearing leaflets that are densely tomentose and pink to caramel in color when emerging, and broad oblong leaflets that are coriaceous in texture with few non-prominent denticulations and ovulate strobili with short (<4 cm) peduncles. It is compared to *Z. furfuracea* and *Z. meermanii*, the Mesoamerican *Zamia* species to which it shares the closest morphological resemblance.

Keywords: cycad; karst; rupicolous plants; southern Mexico; tropical rainforest



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1. Introduction

Cycads represent an ancient lineage of seed plants that now forms the second most diverse group of gymnosperms, just after the conifers [1]. The modern cycads are classified into ten genera, four of which (*Zamia*, *Dioon*, *Ceratozamia* and *Microcycas*) occur exclusively in the New World [2]. Within the New World, cycads are distributed into three distinct biogeographic regions [2]: (i) the Caribbean region which hosts two genera (*Microcycas* and *Zamia*) and nine species, (ii) the South America and Central American Isthmus region which hosts only a single genus (*Zamia*) with 49 species, and (iii) the Mesoamerican region (here referred to as ‘Mesoamerica’ and including the Mesoamerican Dominion and Mexican Transition Zone [3], which hosts three genera and 83 species [4].

Because the Mesoamerican region has the highest species and genus richness in the New World, it is considered a global hotspot for cycad diversity. Specifically, the region includes the entirety of the genera *Ceratozamia* (39 spp.) and *Dioon* (18 spp.) and almost a third of the genus *Zamia* (26 out of 84 total species). The latter is the most species rich, morphologically variable, ecologically diverse, and broadly distributed, with the highest species richness occurring in the South America and Central American Isthmus region [5]. Although the taxonomy of the genus *Zamia* remains in flux, the majority of discoveries in recent years have occurred in South America, including the description of nine new species, e.g., [6–12], and numerous taxonomic and nomenclatural clarifications, e.g., [13–15]. In contrast, the taxonomy of Mesoamerican *Zamia* species has remained relatively stable in recent years. A taxonomic revision of the genus in Mesoamerica was published in 2009 [16], and since then, only four new species [17–20] and a few taxonomic clarifications [21–23] have been published. In this contribution, we add to the body of knowledge of Mesoamerican *Zamia* by describing a novel rupicolous species that was recently discovered in the karstic mountainous area of Sierra Norte, Oaxaca, Mexico and comparing it to the two species to which it bears the closest morphological resemblance: the Belizean species *Z. meermanii* Calonje and the Mexican species *Z. furfuracea* L.f.

2. Materials and Methods

Fieldwork focused on investigating the putative new species was conducted in the August of 2022 in Sierra Norte, Oaxaca, Mexico (Figure 1). This included the collection of morphometric data, plant material (12 leaves from different adult plants, two seed cones, and four pollen cones), herbarium specimens, and photographs. This amount of collected material was decided by the local people, who actively protect the plants and who guided us to the location where the plants occur. A review of our extensive collective database of herbarium specimen data and images confirmed that the species of interest was unique and had not been collected previously. The collected material was subjected to diagnosis, and we found that the most morphologically similar species were the Belizean species *Z. meermanii* and the Mexican species *Z. furfuracea* (Figure 1). Thus, we examined qualitative traits that could be used to identify the differences between these species and conducted morphometric analyses to compare them (Table 1). For *Z. meermanii*, we used morphometric data collected in August of 2008 in Soldier Creek, Belize District, Belize, during the course of the fieldwork that resulted in the original species description [17]. For *Z. furfuracea*, in situ morphometric data were collected in Alvarado, Veracruz, Mexico in March of 2023. A total of 12 individuals of the putative new species, 15 of *Z. meermanii*, and 9 of *Z. furfuracea* were compared morphometrically utilizing twelve traits typically used in species delimitation in cycads, e.g., [24–27] (Table 1). All statistical tests were performed in the PAST v3.14 software [28]. To estimate the global differentiation among species, we used the ANOVA and Kruskal–Wallis tests. This approach deals with the differences in the sample size variation among species. We also used a Linear Discriminant Analysis (LDA) to estimate how much the three species can be distinguished when considering the multivariate data.

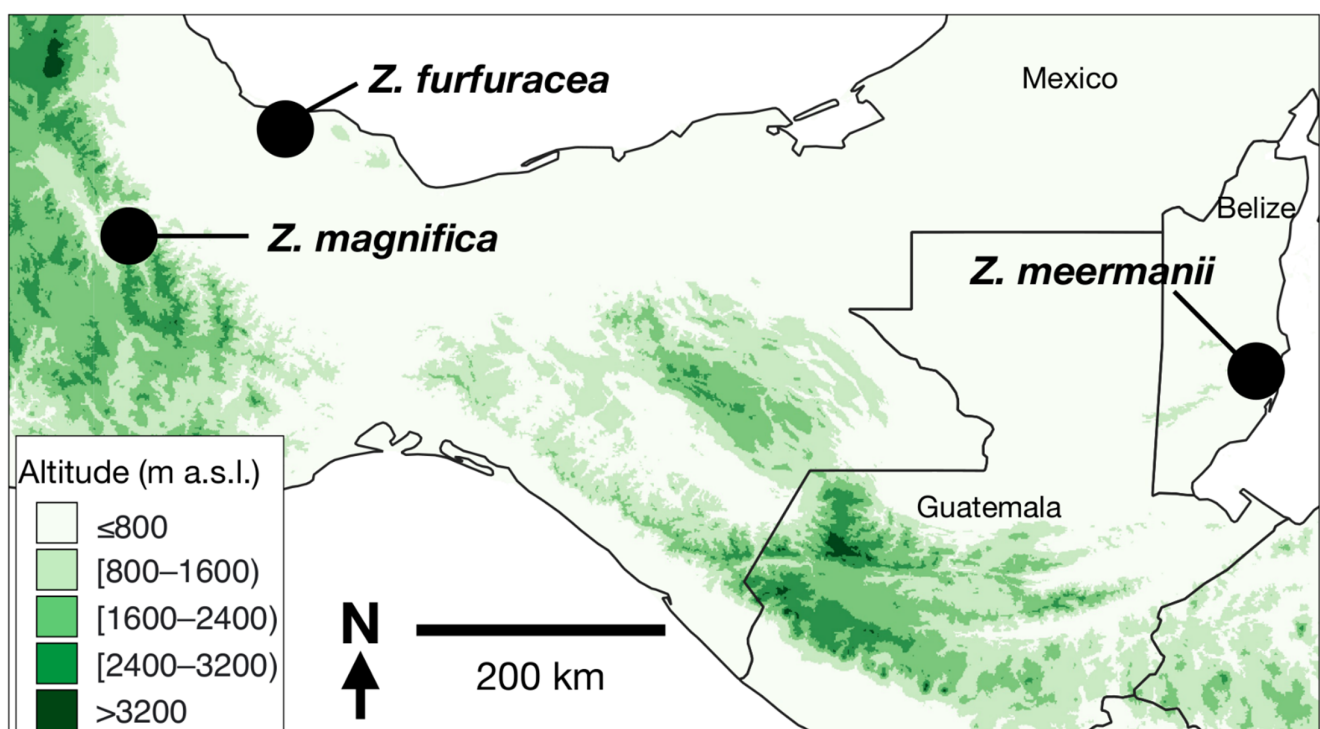


Figure 1. Locations of the three species that we compared in this study: *Zamia magnifica* from La Chinantla, Sierra Norte, Oaxaca, Mexico; *Z. furfuracea* from Alvarado, Veracruz, Mexico; *Z. meermanii* from Soldier Creek, Belize Department, Belize.

Table 1. List of 12 morphometric traits evaluated in *Z. magnifica* and two closely related species: *Z. meermanii* and *Z. furfuracea*. Overall differentiation estimated as Welch's *F* in ANOVA and *p*-values are indicated. D.f. = degrees of freedom.

Key	Trait	Welch's <i>F</i>	D.f.	<i>p</i>
A	Number of leaves	104.1	13.05	<0.001
B	Number of leaflets	4.036	21.96	<0.05
C	Length of petioles (cm)	154.6	20.75	<0.001
D	Length of rachis (cm)	42.13	19.61	<0.001
E	Length of basal leaflets (cm)	36.37	17.78	<0.001
F	Length of median leaflets (cm)	88.63	20.31	<0.001
G	Length of apical leaflets (cm)	81.41	19.07	<0.001
H	Width of basal leaflets (cm)	60.22	18.91	<0.001
I	Width of median leaflets (cm)	82.84	20.5	<0.001
J	Width of apical leaflets (cm)	72.89	19.47	<0.001
K	Distance between median leaflets (cm)	86.12	19.17	<0.001
L	Width of articulation of median leaflets (cm)	13.42	20.16	<0.001

3. Results

3.1. Morphometric Analysis

Welch's ANOVA demonstrated that the 12 quantitative traits have overall significantly different mean values among the three compared species (Table 1). However, in pairwise comparisons, the number of leaflets did not show significant Tukey's *Q* values (Table 2, Figure 2), suggesting that it is not useful as a diagnostic trait. In contrast, all the remaining 11 traits were significantly differentiated in any of the three pairwise comparisons. In particular, the number of leaves, length of petioles, length of basal leaflets, length of median leaflets, length of apical leaflets, width of median leaflets, width of apical leaflets, and distance between median leaflets were the traits that are significantly differentiated among the three species (their mean values do not overlap). The length of rachis, the width of basal leaflets, and the width of articulations of median leaflets were significantly differentiated between *Z. magnifica* and *Z. meermanii*, and between *Z. magnifica* and *Z. furfuracea*, but not between *Z. meermanii* and *Z. furfuracea*.

Table 2. Pairwise Tukey's *Q* values of differentiation between the new species (mag = *Z. magnifica*) and the other two species examined species (fur = *Z. furfuracea* and mee = *Z. meermanii*) of 12 morphometric traits. Abbreviations: * *p* < 0.05; *** *p* < 0.001; ns, no significant.

Key	mag vs. mee	mag vs. fur	mee vs. fur
A	5.966 ***	8.489 ***	15.46 ***
B	0.9178 ns	2.713 ns	1.994 ns
C	13.74 ***	20.07 ***	8.365 ***
D	10.09 ***	12.11 ***	3.396 ns
E	5.448 ***	9.419 ***	4.912 ***
F	9.546 ***	15.71 ***	7.661 ***
G	7.622 ***	13.47 ***	7.3 ***
H	11.46 ***	13.96 ***	4.076 ns
I	14.72 ***	18.3 ***	5.619 ***
J	13.41 ***	15.09 ***	3.87 *
K	9.617 ***	14.7 ***	6.537 ***
L	4.641 ***	6.724 ***	2.769 ns

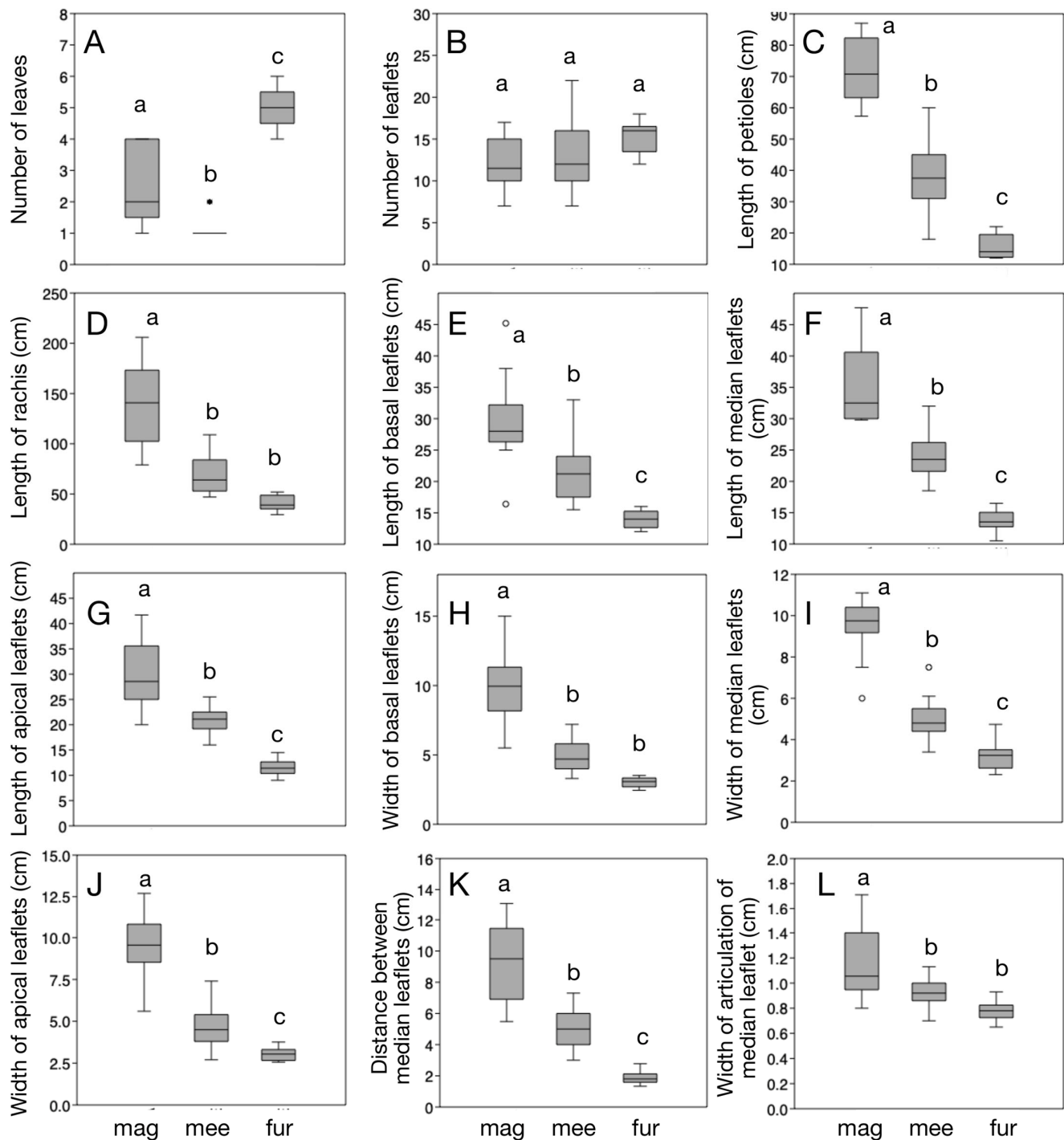


Figure 2. Morphological variation and differentiation of 12 traits in *Zamia magnifica* (mag), *Z. meermanii* (mee), and *Z. furfuracea* (fur). Panels (A–L) correspond to the traits listed in Tables 1 and 2. Different lowercase letters above the bars indicate significant differentiations, as obtained in the Tukey's Q pairwise estimations. Dots and open dots above or below the boxplots indicate outliers.

The LDA summarized the total variation among species in two axes, each representing 67.97% (axis 1), 32.03% (axis 2) of the total variation (Figure 3). The biplots C and D suggest that the length of petioles and rachides were the main traits that dispersed the three groups. The confusion matrix obtained from LDA (Table 3) confirmed that 100% of the individuals evaluated were classified correctly, suggesting a complete sorting among species. The squared Mahalanobis distances (Table 4) were significantly high in all pairwise comparisons

($p < 0.5$), also suggesting that the overall morphometric variation is completely sorted among the examined taxa, confirming that the *Z. magnifica* represents a different species.

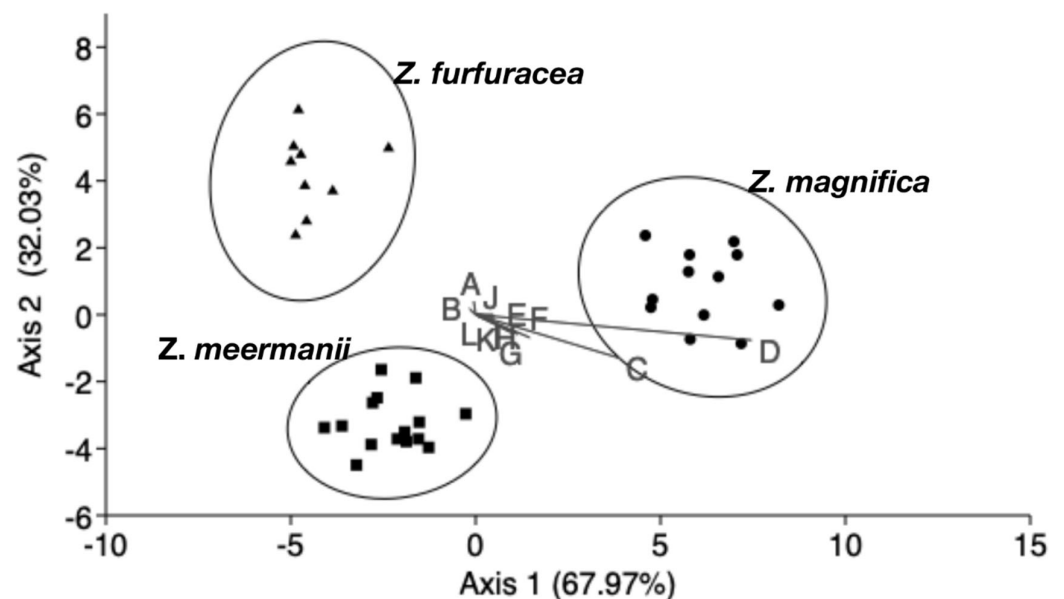


Figure 3. Linear Discriminant Analysis plot. The two main axes summarize 100% of the total variation. The 95% ellipses of species do not overlap, indicating a clear overall differentiation among the three species: *Zamia magnifica* (circles), *Z. furfuracea* (triangles), *Z. meermanii* (squares). The biplots A–L correspond to the traits listed in Table 1. The length and direction of the biplots indicate the relative importance of each trait in representing the variation among species.

Table 3. Confusion matrix constructed with the Linear Discriminant Analysis (LDA). Rows indicate given groups (number of individuals considered *Z. magnifica*, *Z. meermanii*, or *Z. furfuracea*) and columns indicate groups predicted by the LDA.

	<i>Z. magnifica</i>	<i>Z. meermanii</i>	<i>Z. furfuracea</i>	Total
<i>Z. magnifica</i>	12	0	0	12
<i>Z. meermanii</i>	0	15	0	15
<i>Z. furfuracea</i>	0	0	9	9
Total	12	15	9	36

Table 4. Squared Mahalanobis distances (below diagonal) and p -values (above diagonal) among the three analyzed species. All values are significant, suggesting complete sorting among species.

	<i>Z. magnifica</i>	<i>Z. meermanii</i>	<i>Z. furfuracea</i>
<i>Z. magnifica</i>		<0.001	<0.001
<i>Z. meermanii</i>	90.604		<0.05
<i>Z. furfuracea</i>	169.31	15.892	

3.2. Taxonomic Treatment

Zamia magnifica Pérez-Farrera, Gutiérrez-Ortega, and Calonje sp. nov. (Figures 4–10).



Figure 4. (A) *Zamia magnifica* sp. nov. in habitat. (B) Leaves of *Z. magnifica* (next to first author) are among the largest in the genus.

Holotype.—MEXICO. Oaxaca, Sierra Norte, Santiago Tuxtepec, 80 m, Pérez-Farrera 4285, and Mauricio G. Martínez-Mtz, Diego Villar Morales, male, 3 August 2022. (HEM!).
Isotypes: (XAL!, MEXU!).

Zamia magnifica is distinguished from its congeners by its rupicolous habit, pendent leaves bearing leaflets that are densely tomentose and pink to caramel in color when emerging, and has broad oblong leaflets that are coriaceous in texture with few non-prominent denticulations, and ovulate strobili with short (<4 cm) peduncles.

Additional specimens examined.—MEXICO. Oaxaca, Sierra Norte, Santiago Tuxtepec, 80 m a.s.l., Pérez-Farrera 4286, and Mauricio G. Martínez-Mtz, Diego Villar Morales, male, 3 August 2022. (HEM!); Mauricio G. Martínez-Mtz 9, 10, 11, 12 and Pérez-Farrera, Diego Villar Morales, 3 August 2022. (HEM!).



Figure 5. (A) Leaf of adult *Zamia magnifica*. (B) Details of base of petiole.

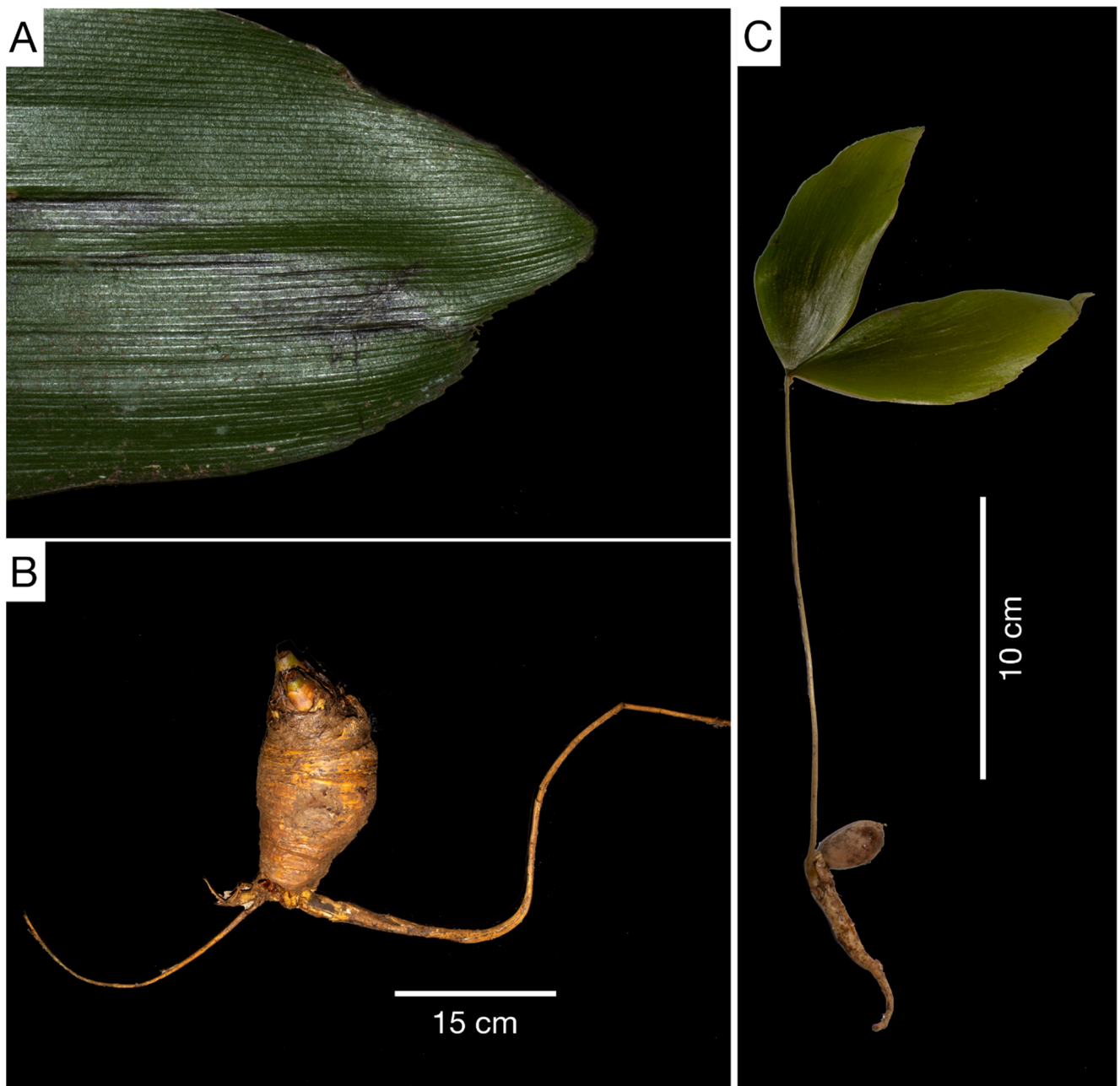


Figure 6. (A) Close up view of leaflet of *Zamia magnifica*. Note the visible veins. (B) Trunk of juvenile. (C) Seedling with eophyll.

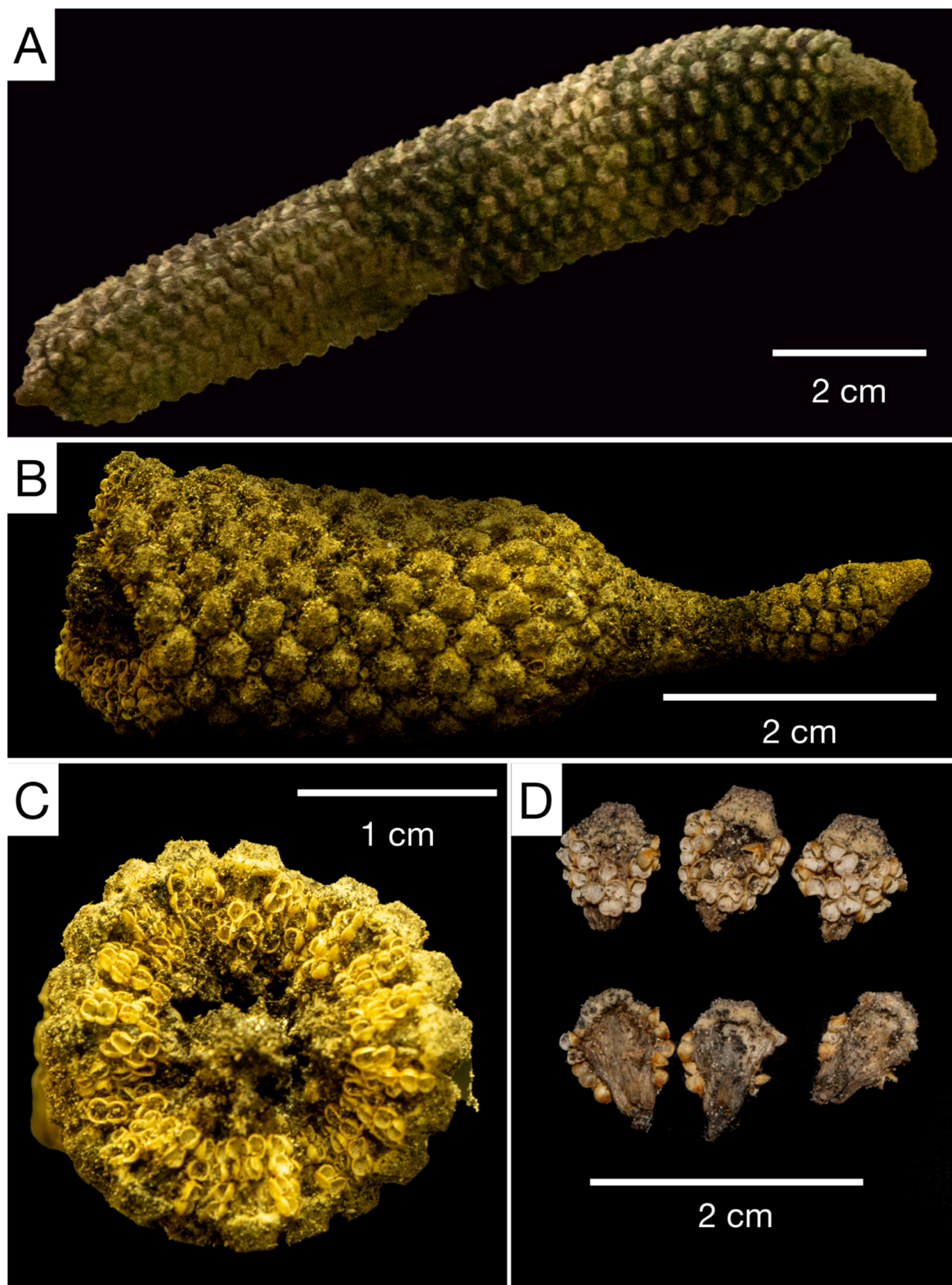


Figure 7. Pollen cone of *Zamia magnifica*. (A) Fertile region of strobilus (without peduncle). (B) Distal portion of strobilus. (C) Cross section showing microsporophylls. (D) Microsporophylls, abaxial (top) and adaxial (bottom) surfaces.

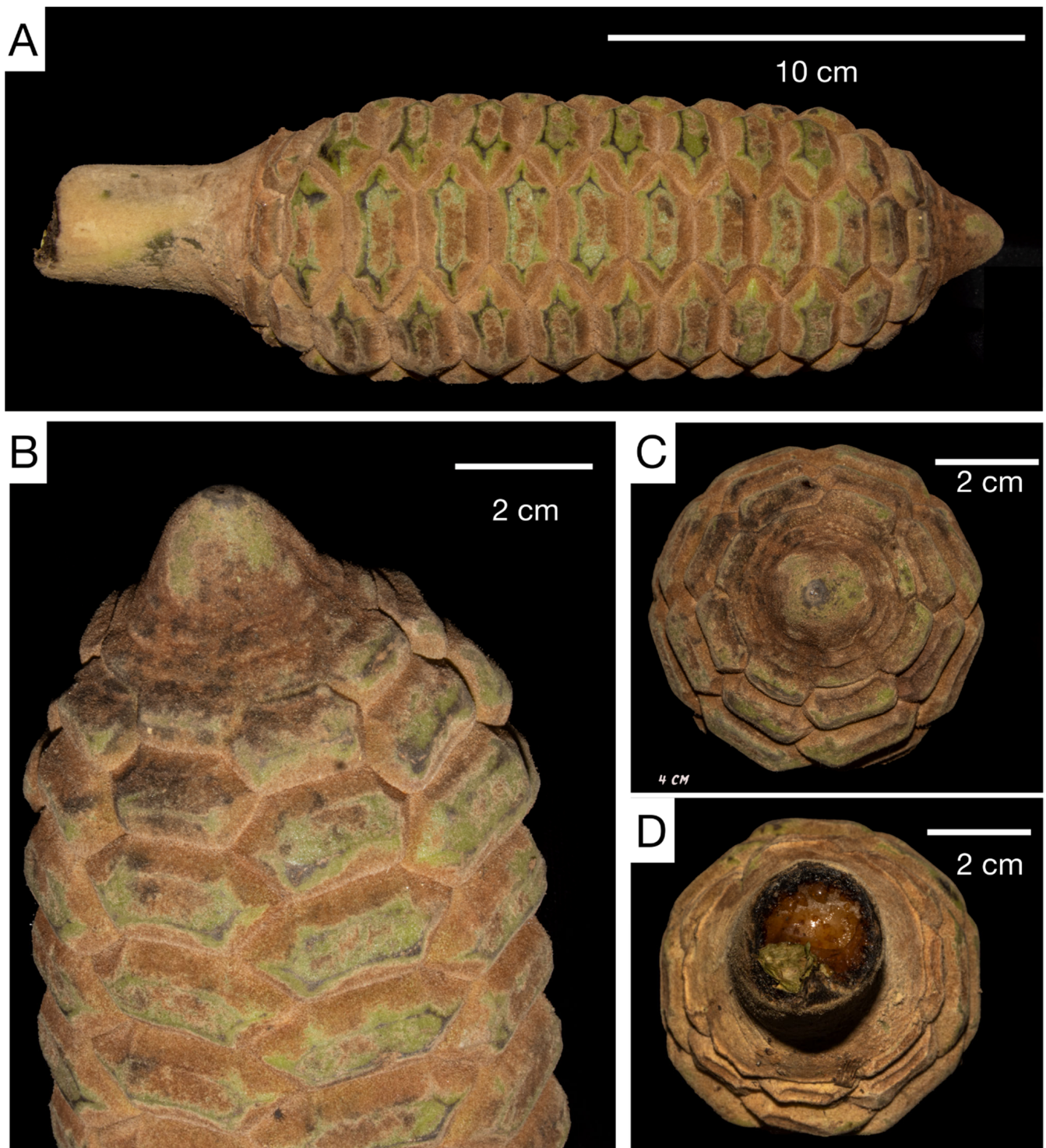


Figure 8. Seed cone of *Zamia magnifica*. (A) Entire strobilus with peduncle. (B) Apex. (C) Apical view. (D) Basal view.

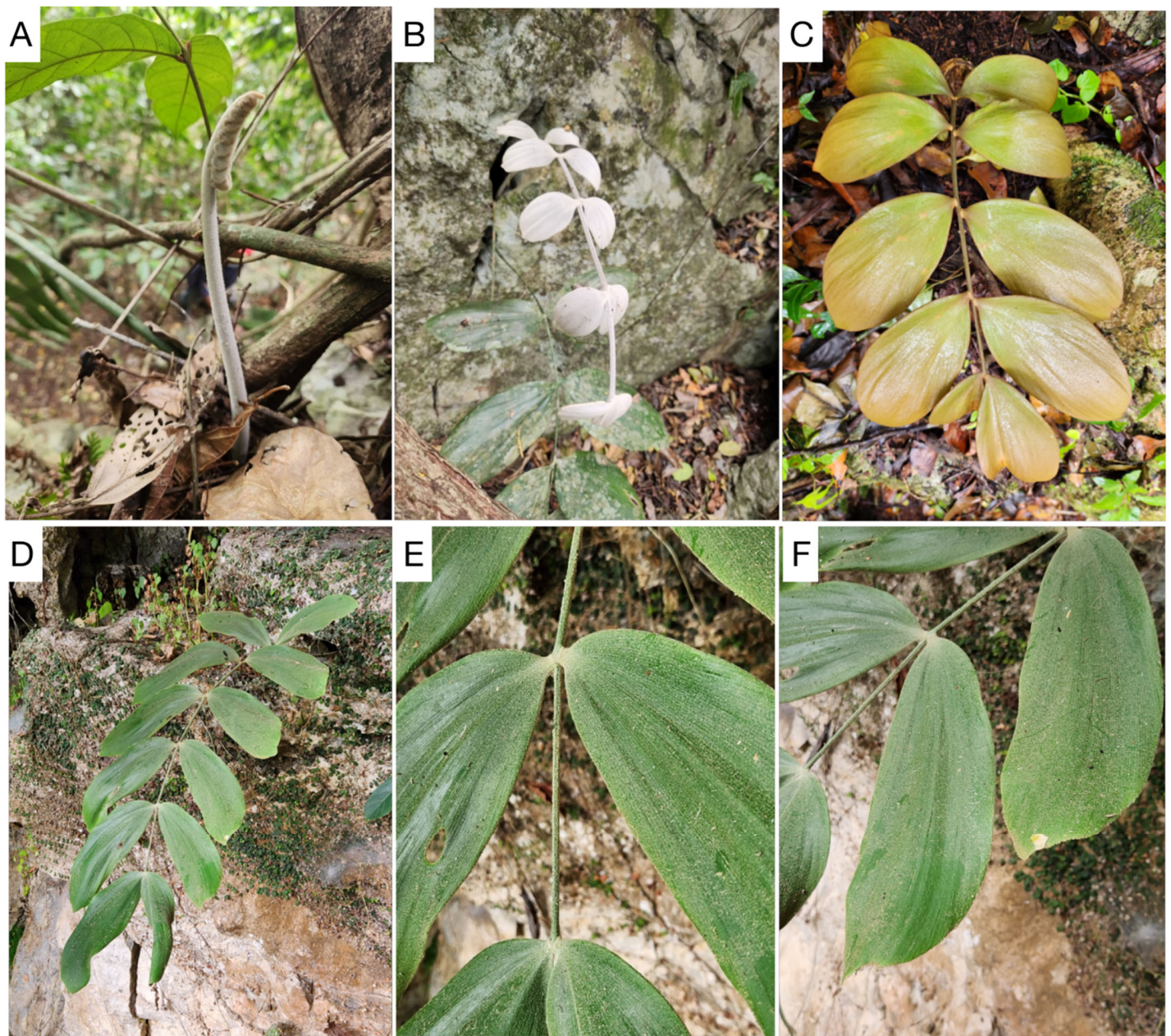


Figure 9. *Zamia magnifica* in habitat. (A) Emergent leaf showing inflexed ptyxis. (B) Emergent leaf expanding, showing dense cover of white tomentum. (C) Immature leaf color change. (D) Mature leaf. (E) Articulation of leaflets and tomentose rachis. (F) Median leaflet.

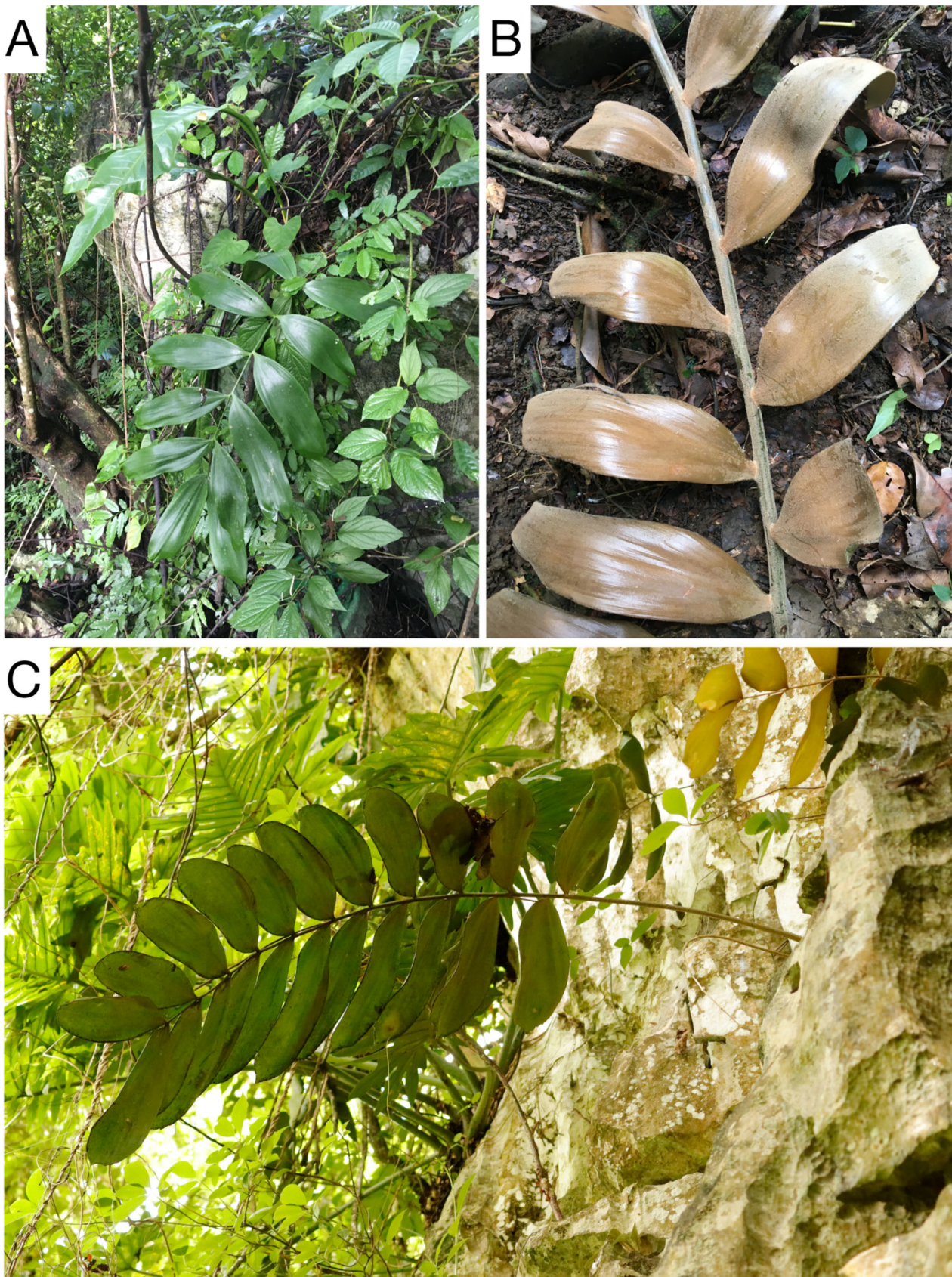


Figure 10. *Zamia magnifica* in habitat. (A) Mature leaf hanging from cliff. (B) Close up view of immature leaf. (C) Rupicolous habit of *Z. magnifica*.

Description. Stem pachycaulous, hypogeous, erect, or decumbent, solitary to profusely branching, 10–38 cm in height, 10–17 cm in diameter. *Cataphylls* persistent, brown, and densely tomentose at emergence. *Leaves* 3–4 per stem, pendent, 160.8–324.0 cm long, 38.7–60.0 cm wide, densely tomentose and pink in the emergence changing to caramel color, transitioning finally to dark green and sparsely tomentose at maturity. *Petiole* terete, 57.3–87.0 cm long, sparsely armed with very few minute prickles diminishing from the petiole to rachis. *Rachis* terete, 93–206 cm, unarmed or sparsely armed with few minute prickles in the proximal third. *Leaflets* 10–17 pairs, oblong to oblanceolate, subcoriaceous, alternate in the basal part of the rachis, subopposite in the median, opposite in the apical part of the rachis, apex acute to rounded, crenulately toothed on the distal fourth, asymmetric or symmetric, base attenuate; median leaflets $29.8\text{--}47.7 \times 6.0\text{--}11.1$ cm, inter-leaflet distance 5.0–13.1 cm; articulations green, 0.8–1.7 cm wide. *Eophylls* with two leaflets. *Pollen strobili* 1–3, cylindrical, erect, $10.75\text{--}15.00 \times 1.90\text{--}2.33$ cm, light green turning tan to light brown or light orange color at maturity; peduncle tomentose, $3.2\text{--}5.5 \times 1.2\text{--}1.5$ cm. *Microsporophylls* spirally arranged in 18–21 orthostichies of 32–37 sporophylls each, cuneiform, distal face 5.7–7.9 mm long, 4.0–5.6 mm wide, abaxial surface bearing 18–24 microsporangia aggregated into a single group. *Ovulate strobili* solitary, cylindrical, erect, 9.1–15.8 cm, 7.2–7.8 cm in diameter, yellowish at maturity; apex acute, 1.6–2.0 cm long, peduncle tomentose, light yellow at maturity, $9.1\text{--}10 \times 1.4\text{--}2.7$ cm. *Megasporophylls* arranged in 7–8 orthostichies of 9–10 sporophylls each, cuneiform, peltate, distal end hexagonal truncate, 24.8–37 mm short axis, 23.2–32.5 mm wide axis, distal face brown pubescent, yellowish when immature, green at maturity. *Seeds* ovate, sarcotesta reddish orange, 18.6–23.5 mm long, 12.5–15.2 mm in diameter.

Habitat description. The vegetation type where this cycad is found is *tropical rainforest*, according to the classification of Breedlove [29]. *Zamia magnifica* is sympatric with *Dioon spinulosum*. Both species occur in karst tropical rainforest and gallery forest in lowland forest in the Sierra de Juarez, Oaxaca dominated by: *Swietenia macrophylla* King, *Inga* sp., *Cedrela odorata* L., *Trophis* sp., *Bursera simaruba* (L.) Sarg., *Oreopanax* sp., *Dendropanax* sp., *Attalea butyracea* (Mutis ex L. f.) Wess. Boer, *Chamaedorea elatior* Mart., *C. tepejilote* Liebm., *C. oblongata* Mart., *C. pinnatifrons* (Jacq.) Oerst., *C. metallica* O.F. Cook ex H.E. Moore, *C. sartorii* Liebm., *Cecropia peltata* L., *Bactris mexicana* Mart., *Cnidocolus* sp., *Piper* sp., *Heliconia* sp., epiphytes and hemiepiphytes as *Monstera* sp., *Philodendron* sp., *Syngonium neglectum* Schott, *Tillandsia* sp., *Maxillaria* sp., *Anthurium schlechtendalii* Kunth, *Spathiphyllum* sp. The region is characterized by sedimentary and metamorphic rocks as well as lephosols, cambisols, fluvisol, and humic acrisol soils. There are also sedimentary rocks from the Cretaceous period of the Mesozoic era, generally on abruptly steep slopes of about 40–45° and it is found within the range of 80–100 m a.s.l. [30,31].

Etymology. The epithet ‘magnifica’, derived from the Latin *magnificus* (‘magnificent’), refers to the strikingly beautiful aspect of the species due to its large and spectacular pendent leaves.

Uses. The local people mentioned that they use the seeds of *Z. magnifica* as an insecticide. They grind the seeds and add sugar or honey and deposit the mix in an open recipient. Flies eventually eat from the mix and die due to the toxic compounds.

Distribution and conservation status. The species should be classified as Critically Endangered (CR) according to the IUCN (2001), due to its restricted distribution (La Chinantla, Sierra Norte, Oaxaca) and its limited number of populations (only one population) with around 2000 individuals (considering seedlings, juveniles, and adults). The area where the population occurs is approximately 4477 ha (44.8 km²) in size, and plants are actively protected by the local people, making studies and collection of them impossible without their consent and permission. However, much of the surrounding habitat is being transformed into pastures for raising cattle and for coffee and corn cultivation. As is the case with many cycad species in Mexico, its conservation both ex situ and in situ is urgent.

4. Discussion

Zamia magnifica occurs in one locality in the La Chinantla region, in Sierra Norte, Oaxaca. La Chinantla region is an area that has been suggested to be a Neogene refuge [32], where a high floristic richness and great endemism of ancient and rare taxa occur [33,34]. About 1021 species have been reported in this locality [33,35,36]. The plant communities that are below 1000 m altitude in the Sierra Norte have been greatly altered due to human activities [33], being converted to grazing areas or pastures for cattle, and cultivation areas for corn and coffee. However, some hills consist of rich karstic tropical forests that contain great levels of endemism. Other notable species such as *Beaucarnea recurvate*, *Chamaedorea metallica*, *Ceratozamia whitelockiana*, *C. aurantiaca*, *Dioon spinulosum*, *D. rzedowskii*, *Gaussia gomez-pompae*, and *Licaria chinanteca* also live in these forests.

Zamia magnifica is one of four obligate cliff-dwelling *Zamia* species in Mesoamerica, the others being *Z. cremnophila* Vovides, Schutzman, and Dehgan from Mexico, *Z. sandovalii* C.Nelson from Honduras, and *Z. meermanii* from Belize. The species is easily distinguished from *Z. cremnophila* and *Z. sandovalii* by its leaflets alone, which are oblong to oblanceolate and crenulately toothed at the apex, compared to those of the other two species which are lanceolate and prominently toothed at the distal half. Among the rupicolous Mesoamerican species, *Z. magnifica* most closely resembles the Belizean species *Z. meermanii*, as both species share pendent leaves that are densely tomentose and colorful at emergence, bearing obovate to oblanceolate leaflets that are inconspicuously toothed at the apex. However, the leaflets of *Z. meermanii* are concave and strongly coriaceous in texture, whereas those of *Z. magnifica* are distinctly convex and moderately coriaceous. The new leaves of *Z. magnifica* are whitish pink, and the color changes to caramel with white to tan tomentum. The leaves of *Z. meermanii* are cream-colored, and covered with saffron-orange tomentum (Table 5). Morphometrically, *Z. magnifica* can be distinguished from *Z. meermanii* in 11 out of 12 traits we evaluated (all traits except the number of leaves) (Table 2). *Zamia magnifica* attains much larger dimensions overall than *Z. meermanii*, typically bearing much longer leaves (142–290 cm vs. 71–147 cm) and median leaflets that are much longer (29–48 cm vs. 18–32.0 cm) and broader (6–11 vs. 3.4–7.5 cm). Furthermore, *Z. magnifica* has microsporophylls with 18–24 microsporangia aggregated into a single group, whereas *Z. meermanii* has 22–28 microsporangia occurring in two distinctly separate groups. In addition, the stems of *Z. meermanii* are typically solitary, whereas in *Z. magnifica* they can be profusely branching on older individuals (see Figure 4A).

Table 5. Morphological variation among *Zamia magnifica* and species affine: (*Z. furfuracea* and *Z. meermanii*).

Trait	<i>Z. magnifica</i>	<i>Z. meermanii</i>	<i>Z. furfuracea</i>
Habitat	Karstic terrain	Karstic terrain	Sand dunes
Trunk	Branching with age	Typically solitary	Branching with age
Color emergence of leaves	Pink	Reddish-brown	Ochre to light brown
Texture of leaflets	Subcoriaceous with caducous tomentum	Coriaceous with caducous tomentum	Coriaceous with persistent tomentum
Leaflets	Widely obovate	Obovate to oblanceolate or narrowly oblong	Obovate to oblanceolate
Peduncle of ovulate strobilus	Thick and short	Thick and short	Thin and long
Color of mature ovulate strobilus	Light orange	Light brown	Yellowish green
Color of mature pollen strobilus	Light orange	Cream to brown	Light brown
Ovulate strobilus apex shape	Acute or obtuse	Apiculate	Apiculate

Zamia magnifica also shares some morphological resemblance to the Veracruz endemic species *Z. furfuracea*, as both species have leaves that are densely tomentose at emergence, bearing leaflets that are similar in shape (oblong to oblanceolate), and are inconspicuously toothed at the apex. However, *Z. furfuracea* is a terrestrial species (vs. rupicolous) with spreading (vs. pendent) leaves, the emerging leaves in *Z. furfuracea* are ochre to light brown (vs. pink), and seed strobili with longer and thinner peduncles (Table 5) (14–16 vs. 9.1–10 cm).

Eleven out of 12 vegetative traits were significantly differentiated between the two species (all traits except the number of leaves) (Table 2). *Zamia furfuracea* is a much smaller plant overall, having much smaller leaves (48–66 cm vs. 142–290 cm) and leaflets that are much shorter (10.5–16.5 vs. 29–48 cm) than *Z. magnifica*.

Definitely, *Z. magnifica* is the Mexican *Zamia* species with the largest leaves (up to 290 cm). The second Mexican *Zamia* would be *Z. splendens* Schutzman, with leaves of around 2 m long. Some plants of *Z. variegata* Warsz. in Belize may also produce large leaves (at more than 2.5 m long), especially in plants living in areas with frequent flooding (personal obs.) or in cultivation [1]. Furthermore, it is notable that *Z. magnifica* produces some of the largest seeds among the Mexican *Zamia*; we found seeds 1.9–2.4 cm long and 1.1–1.5 cm wide, whereas the Mexican *Zamia* with the largest seeds is *Z. soconuscensis* (2.2–2.6 cm long, 1.4–1.9 cm wide).

Recent phylogenetic work in the genus *Zamia* [5] has helped clarify the relationships between the Mesoamerican species of *Zamia*, with four major groups evident: (i) The Fischeri clade, being sister to the rest of the mainland American species (excluding *Z. integrifolia* L.f.), consists of the three species from northeastern Mexico: *Z. fischeri* Miq., *Z. vazquezii* D.W.Stev., Sabato and De Luca, and *Z. inermis* Vovides, J.D.Rees and Vázq.Torres. (ii) The Furfuracea subclade, being a broadly distributed group (Mexico, Guatemala, Belize, and Honduras), consists of seven species: *Z. herrerae* S.Calderón and Standl., *Z. paucijuga* Wieland, *Z. prasina* W.Bull, *Z. variegata*, *Z. sparteae* A.DC., *Z. furfuracea*, and *Z. loddigesii* Miq. (iii) The Purpurea clade consists of six species that are associated mostly with the Northern Area of the Chiapas Highlands biogeographic province [3]: *Z. lacandona* Schutzman and Vovides, *Z. grijalvensis* Pérez-Farr., Vovides and Mart.-Camilo, *Z. purpurea* Vovides, J.D.Rees and Vázq.Torres, *Z. cremnophila*, *Z. splendens*, and most likely *Z. katzeriana* (Regel) E.Rettig (see below). (iv) The Tuerckheimii subclade is restricted to evergreen tropical rainforests in Guatemala, Belize, and Honduras, and consists of seven species: *Z. decumbens* Calonje, Meerman, M.P.Griff. and Hoese, *Z. onan-reyesii* C.Nelson and Sandoval, *Z. tuerckheimii* Donn.Sm., *Z. meermanii*, *Z. sandovalii*, *Z. standleyi* Schutzman, and most likely *Z. oreillyi* C.Nelson (see below). Calonje et al. [5] did not include *Z. katzeriana* or *Z. oreillyi* C.Nelson in their molecular phylogenetic analysis, but the former is believed to belong to the Purpurea clade [23], and the latter, based on its morphological characteristics and geographical distribution, is likely in the Tuerckheimii subclade. Although *Z. magnifica* has yet to be included in phylogenetic analyses, we hypothesize the species most likely belongs to the Furfuracea subclade due to its geographic distribution and morphology. *Zamia magnifica* shares a similar leaflet morphology to *Z. furfuracea* (member of the Furfuracea clade), as well as the densely tomentose new leaves that characterize that group. Geographically, *Z. magnifica* occurs within the geographic distribution range of the Furfuracea clade, and because there is a strong congruence between geographic distribution and phylogenetic relationships in *Zamia* [5], the distribution is a piece of evidence that favors the idea of *Z. magnifica* being in the Furfuracea clade. Based on the distribution ranges of the *Zamia* clades, an alternative might be that *Z. magnifica* belongs to the Purpurea clade. However, the Purpurea clade is limited to the east of the Isthmus of Tehuantepec (whereas *Z. magnifica* occurs to the west). This geographic disjunction is notable, as the Isthmus of Tehuantepec has been recognized as a formidable geographic barrier affecting the distribution and diversification of *Dioon* [37] and *Ceratozamia* [38], which disfavors this alternative hypothesis of *Z. magnifica* in the Purpurea clade. Future phylogeographic studies will contribute to untangle the relationships among *Zamia* species in these geographic regions.

The distribution of *Z. magnifica* is restricted to certain cliffs where rocks are exposed, and plants are usually very difficult to access. We hypothesize that the cliff-dwelling habit in *Z. magnifica* might have evolved from a terrestrial habit ancestor, and originated locally in La Chinantla as a response to avoid competition with other terrestrial species. The same might be true for the other cliff-dwelling *Zamia* species, implying that the habit has multiple origins in the genus, and that each origin might be triggered by distinct or similar local biotic or abiotic factors. However, little is known about this aspect. For example, what are

the physiological and anatomical features that may enable these possible cases of adaptation to the cliff-dwelling habit? A recent study on *Zamia* found little correlation between leaflet anatomical trait variation and phylogeny or macro-environmental variation [39], leaving open the possibility that the effect of micro-environmental variation on selection or biotic factors such as competition are possible causes. In the case of *Z. magnifica*, it is possible that rodents or other small mammals or birds feeding on the sarcotesta deposit the seeds in the fissures of rocks where plants grow, but which are the exact species that disperse the seeds is still unknown. Nevertheless, we expect that the discovery of *Z. magnifica* may encourage more researchers to clarify the evolutionary and ecological consequences of the cliff-dwelling habit of cycads.

5. Conclusions

This research presented *Z. magnifica*, a species for which there are no previous records in herbaria, as far as we know. The discovery of *Z. magnifica* suggests that the botanical explorations in southern Mexico are still promising, and expeditions to remote places may lead to an even a better comprehension of the cycad diversity. Understanding the full diversity may help us to disentangle the evolutionary history of these plants and contribute to their effective conservation.

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