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Zamia multidentata (Cycadales, Zamiaceae), a new arborescent species of *Zamia* from Acre, Brazil

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Abstract

Zamia multidentata is described and illustrated here as a new species from the Amazon basin, state of Acre, Brazil. The new species shares morphological similarities with the Amazonian species *Z. hymenophyllidia*, and *Z. urep,* to which it is compared. The combination of slender (to 6.2 cm) caulescent stems, strongly serrulate elliptic leaflets with long acuminate tips and a pronounced adaxially raised longitudinal crease, as well as seed strobili with long peduncles (15 cm +) and flat megasporophylls distinguish the new species *Zamia multidentata* from all other known species in the genus.

Keywords: Amazon Rainforest, Serra do Divisor, Sierra del Divisor

Introduction

The genus *Zamia*, with eighty-four currently accepted species (Calonje *et al.* 2023), is the most widespread and speciose cycad genus in the New World. The genus was described over 250 years ago by Carl Linnaeus (1763), yet the majority of species have been described since the early 1980's. The remarkable amount of taxonomic interest in the genus evidenced in recent years continues unabated, with new species still being described almost every year. Currently the least understood assemblage of species of *Zamia* are those occurring in the Amazon basin. The region hosts ten currently accepted species (i.e. *Z. amazonum* Stevenson (2001: 33), *Z. boliviana* de Candolle (1868: 540), *Z. brasiliensis* Calonje & Segalla in Segalla & Calonje (2019: 4), *Z. hymenophyllidia* Stevenson (2001: 43), *Z. lecointei* Ducke (1915: 9), *Z. lindosensis* Stevenson *et al.* (2018: 364), *Z. macrochiera* Stevenson (2004: 185), *Z. poeppigiana* Mart. & Eichler in Eichler (1863: 414), *Z. ulei* Dammer (1907: 117), and *Z. urep* B.Walln. (1996: 1056), the majority of which have been phylogenetically evaluated and form a monophyletic assemblage (Calonje *et al.* 2019). However, perhaps partially due to the complex logistics of working in the Amazon, the taxa occurring here remain understudied and in need of taxonomic revision.

A survey conducted in 2015 in Mâncio Lima (Acre, Brazil) by Ricardo Soares Pimenta, Juliano Borin, and José Fernando Tribst identified a thin-stemmed arborescent species reported by local resident Francisco Assis F. Silva as a potentially undescribed species that would require further study to verify. The opportunity to formally document the species arose in September 2020, when the species was detected in the Serra do Divisor National Park (Acre, Brazil; SDNP) during the course of ongoing research on Amazonian *Zamia* systematics. A preliminary herbarium specimen survey suggested that the taxon had never been collected before, and a close examination of its reproductive and vegetative morphology in the field provided confirmation that the species is novel and readily distinguishable from all currently described species. Here we describe and illustrate this new species and compare it to *Z. hymenophyllidia* and *Z. urep*, the two species with which it shares the closest morphological resemblance.

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Materials and methods

Field expeditions focusing on studying the putative new species of *Zamia* were conducted in September 2020 and June 2021 within SDNP in the Municipality Mâncio Lima, Acre, Brazil. The national park, located to the northeast of the state of Acre, is at the border of Brazil and Peru, in the Upper Rio Juruá region in the Cruzeiro do Sul microregion (Associação SOS Amazônia 1998). In addition, field research in the Municipalities of Leticia and Puerto Nariño, Amazonas, Colombia focusing on *Z. hymenophyllidia* was conducted in November 2017 and January 2022. Fieldwork at both locations included morphometric data collection, photographic documentation, and herbarium specimen collection. Living plants of *Z. hymenophyllidia* (Accessions 16022A & 16027A) and *Z. urep* (Accession 15233A) were also studied in cultivation at Nong Nooch Tropical Botanic Garden (NNTBG, Chonburi, Thailand). Herbarium specimens and specimen photographs of *Zamia hymenophyllidia* and *Z. urep* deposited at the following herbaria were consulted: AMAZ, COAH, COL, F, FMB, FTG, GH, HUA, K, LZ, MO, NY, UDBC, USM, W (acronyms according to Thiers 2022, continuously updated), and are listed in Appendix I. Specimens and field observations were georeferenced, and mapped in ArcGIS (Version 10.8.2; ESRI, 2021) and relevant morphological measurements were recorded from specimen images with the software ImageJ (Schneider *et al.* 2012). In order to reduce the subjectivity inherent in describing colors, for the species description we identified colors based on the RHS Colour Chart (Royal Horticultural Society [Great Britain], 2015) numbers (e.g. RHS 173C), and color names from "Color Names for the RHS Colour Chart" (UPOV 2019) as implemented in the R Statistical Software (v4.2.2; R Core Team 2022) package ColorNameR (Sánchez Beeckman 2021). Color values were obtained from photographs by using the eyedropper tool in Adobe Photoshop (v24.0; Adobe inc., 2022) to sample the average CIELAB color values for an area of 31x31 pixels. These values were input into ColorNameR to obtain the closest RHS colors and color names to be used in this paper. Estimates for annual temperature ranges within the area of occupancy of the species were obtained by extracting values at occurrence points using CHELSA bioclimatic variables (v1.2; Karger *et al.* 2017, 2018). Specific locality information associated with the visited locations and herbarium specimens is purposefully withheld in this paper and provided only at the municipality level to minimize the risk of illegal harvesting of the species discussed herein.

Taxonomic treatment

Zamia multidentata **Calonje, Segalla & R.S.Pimenta** *sp. nov.* (Figs. 1–3)

Diagnosis:—The combination of slender (to 6.2 cm) caulescent stems, strongly serrulate elliptic leaflets with long acuminate tips and a pronounced adaxially raised longitudinal crease, as well as seed strobili with long peduncles (15 cm +) and flat megasporophylls distinguish the new species *Zamia multidentata* from all other known species in the genus.

Type:—BRAZIL. Acre: Mâncio Lima: 220m, 26 Sep 2020, *R. Segalla & L.V. Lima SDMR 01* (holotype RB!, isotypes UFMT!, INPA!, UFACPZ!).

Description:—*Stem* epigeous, cylindrical, typically solitary, 16–45 × 4.0–6.2 cm. *Cataphylls* caducous, triangular to narrowly triangular, 3.7–7.02 cm long and 1.8–2.5 cm wide at base, abaxial surface densely covered with light yellow orange (RHS 158D) felted indumentum. *Ptyxis* slightly reflexed. *Leaves* 8–14 per crown, held relatively upright, slightly spreading, 114–152 cm long and 35.1–44.9 cm wide. *Petiole* 35–83 cm long and 10.7–21.7 mm thick, with abruptly swollen base to 35.79 mm wide, moderately to strongly armed with prickles 1.7–5.0 mm long., petiole and rachis densely covered with grey (RHS N189D) pubescent indumentum on new leaves, gradually shedding it to reveal medium yellow green (RHS 159D) to dark brown (RHS N200A) epidermis on older leaves. *Rachis* 43.0–78.5 cm long, lightly armed with prickles mostly in the proximal fourth, with occasional solitary prickles occurring beyond. *Leaflets* 10–26, papyraceous to chartaceous, oppositely to sub-oppositely arranged, articulate insertion on rachis 2.9–4.4 mm wide, spaced to 2.0 to 5.5 cm apart at leaf center, ovate to elliptic with long acuminate apex, distinctly raised longitudinal crease, margins strongly serrulate beyond proximal fourth with 30–49 teeth, median section traversed by 36–47 parallel veins, light green (RHS 138D) on new leaf flushes, at maturity turning medium brown green (RHS 136C) to light green (RHS 145B) adaxially, light green abaxially (RHS 135D), basal leaflets 10.0–21.0 cm × 3.0–7.0 cm, median leaflets 18.2–21.7 cm × 4.3–9.3 cm, apical leaflets 13.5–20.0 cm × 5.0–8.3 cm. *Eophylls* 13–17 cm long, petiole 12–16 cm long, rachis 0.6–1.0 cm long bearing 4 leaflets. *Eophyll leaflets* oval to ovate with long acuminate apices, margins strongly serrulate in the distal half, the basal leaflets 7.2–8.0 × 3.5–3.6 cm, the apical leaflets 7.0–7.8 × 2.6–2.7 cm. *Pollen strobili* 1–5 per stem apex, fertile portion conical-cylindrical, at pollen shedding stage 8.2–8.3

× 1.4–1.5 cm, covered with medium brown (RHS 173C) to grey brown (RHS N199C) felted indumentum, strobilus apex acute 3.0–6.0 mm long and 4.7–5.3 mm wide at base, peduncle 8.8–9.1 × 0.7–0.8 cm, densely covered with light yellow (RHS 163D) tomentose indumentum, strobilar axis glabrous. *Microsporophylls* spirally arranged in 7–8 orthostichies of 14–16 fertile sporophylls each, median sporophylls 4.9–5.2 × 5.0–5.2 mm. *Microsporophyll shield* a distinctly extruded hexagonal prism covered with dark yellow orange (RHS 173C) to grey brown (RHS N199C) felted indumentum, 2.1–2.5 mm tall and encompassing 2/5 to 1/2 of sporophyll length, 3.6–4.6 × 2.2–2.5 mm at the base, the distal face distinctly indented and slightly reduced to approximately ¾ the size of the base. *Fertile portion of microsporophyll* with adaxial surface glabrous, abaxial side lightly covered with grey-brown (RHS 199B) pubescent indumentum and patches of strong orange red (RHS 169A) pubescent indumentum restricted to the areas immediately surrounding individual microsporangia. *Microsporangia* present only on the abaxial side of the microsporophyll, slightly ovate, 1.1–1.2 × 0.9–1.0 mm, typically aggregated into a single group of 13–17 sporangia, but occasionally separated into two distinct marginal groups of 6–8 sporangia each. *Ovulate strobili* one per stem apex, fertile portion cylindrical, at maturity 16.2–18.0 × 4.7–5.6 cm, with acute apex 12–13 mm long and 84–99 mm wide at base, covered with dark brown purple (RHS N186C) felted indumentum on newly emerging strobili turning orange brown (RHS 172C) to medium brown (RHS 172A) at maturity; peduncle 15–19 × 1.2–1.4 cm, covered with purple grey (RHS 201C) indumentum when newly emerging, at maturity indumentum persisting in medium yellow brown (RHS 164B) patches or shedding to reveal grey brown glabrous epidermis (RHS 199A). *Megasporophylls* spirally arranged in 6–9 orthostichies of 6–10 sporophylls each, 20 × 10 mm, megasporophyll shield not extruded but relatively flat, 1.8–3.0 mm thick, 20–21 mm wide, and 14–17 mm tall, the distal facet shallowly indented, narrow and elongated and encompassing approximately 1/13th to 1/16th of the area of the base. *Seeds* ovoid-pyramidal, sarcotesta medium red (RHS 44A) to orange red (RHS 32A) at maturity, 17.4–18.6 × 9.0–11.0 mm, sclerotesta ovoid, glabrous, light yellow-brown (RHS 161C), 13.0–16.4 × 8.6–9.8 mm.

Etymology: From the Latin *multi* ('many') and *dentatus* ('toothed'), referring to the numerous teeth found along the margins of the leaflets of this species.

Habitat, geology and soils:—*Zamia multidentata* occurs in the upper Juruá River basin (Daly *et al.* 2016) within the "Southwest Amazon Moist forests Ecoregion", a region of high endemism and species richness in vascular plants (Olson *et al.* 2001). To date it has been only been observed within a vegetation type officially classified in Brazil as "Open Alluvial Ombrophilous Forest with Palms" (IBGE 2012), where it occurs on the alluvial soils of the Moa river floodplain adjacent to the Serra do Divisor, an isolated mountain range in the southwestern Amazon characterized by fiercely dissected peaks and ridges rising out of the surrounding lowland rainforest (Salisbury *et al.* 2013). The soils originated from Holocene sediments and have a high content of fine sands resulting from the erosion of Cretaceous sandstone from the Serra do Divisor (Mendonça *et al.* 2020). The soils are lower in organic carbon but richer in nutrients than those from the Serra do Divisor, are high in Al^{3}+ and have a mixed mineralogy with 2:1 clays, hydroxyl-Al interlayered smectite, and kaolinite (Mendonça *et al.*, 2020).

Climate:—The region of the Serra do Divisor mountainous complex is inserted in a transitional climatic band between the Humid and the Super-humid (relative humidity index close to 100) with rainfall (2,500 to 2,750 mm per year) frequent throughout the year, since even during the driest months (June to September) the totals are usually greater than 60 mm (Associação SOS Amazônia 1998). In the other months of the year, totals greater than 180 mm predominate, and over 300 mm in the months of November to April (Associação SOS Amazônia 1998). The mean annual air temperature is 25.0° C, with a mean minimum daily temperature of 20.8° C in the coldest month, and a mean maximum daily temperature of 28.6° C in the warmest month.

Ecology:—The species was rare in the surveyed area, with scattered individuals occurring in the forest understory, usually on flat to gentle slopes. Accordingly, very few seedlings or juvenile plants were observed. As this species to our knowledge has not been studied or collected before, little is known its population dynamics, reproductive phenology, or the plant-animal interactions affecting it. Although most South American species of *Zamia* are pollinated by beetles in the genus *Pharaxonotha* Reitter (Coleoptera: Erotylidae) (Segalla *et al.* 2021, Tang *et al.* 2018), the pollination agents for this species remain unknown. Similarly, the seed dispersal agents are not known, and no evidence of herbivory by caterpillars of the genus *Eumaeus* (Segalla & Morellato 2019) was observed in habitat. Strobili emerge from April to June, with the reproductive period when the seed strobili become receptive and the pollen strobili become dehiscent occurring from May through June. Pollinated ovulate strobili mature for approximately one year after pollination, with seed dehiscence occurring from May to July the year following cone emergence. New leaves are produced from October through December.

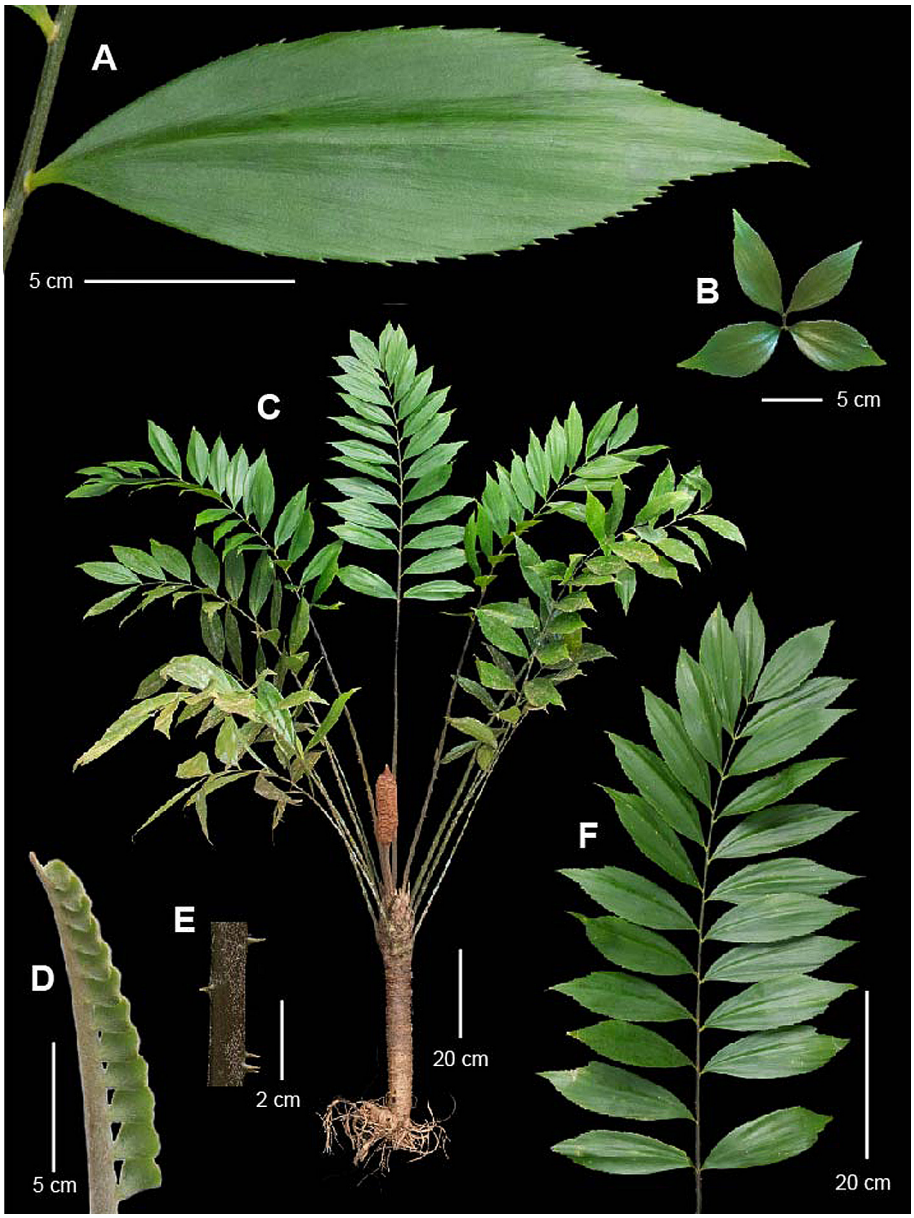

FIGURE 1. Vegetative characteristics of *Zamia multidentata*. A. Median leaflet attached to rachis, B. Top view of eophyll, C. Habit of adult individual with ovulate strobilus. D. Newly emerging leaf showing slightly reflexed ptyxis and indumentum covering rachis, E. Middle section of petiole showing some patches of indumentum and prickles, F. Leaf. All photographs used for the preparation of the illustration were taken at the type locality.

Distribution and conservation status:—The Sierra do Divisor's ridge divides Brazil's Jurua river basin from Peru's Ucayali basin and serves as the international boundary between the two countries (Salisbury *et al.*, 2013). On the Brazilian side of the boundary lies the Serra do Divisor National Park, and on the Peruvian side its transboundary sister reserve, the Sierra del Divisor National Park. The adjacent transnational parks are part one of the largest contiguous blocks of protected areas in the Amazon, but despite their protected status, the region is threatened by anthropogenic activities including agriculture, hunting and subsistence fishing, tourism, and plant extraction for timber, charcoal, firewood, and horticulture (Associação SOS Amazônia 1998; Daly *et al.* 2016; Esteves & Luz 2019). The location surveyed in this study, selected as the type locality, is protected within the Serra do Divisor National Park (SDNP), whereas the other known locality occurs outside of the park boundaries in an area that has been actively deforested in the last 40 years and where habitat transformation and deforestation continue unabated. The two known locations of *Zamia multidentata* are approximately 30 km away from each other within the Moa river floodplain at an elevational range of 200–220 m. The species was infrequent within the SDNP location visited, and local field guides reported being aware of past extraction of wild plants in the region for horticultural purposes. Although no Peruvian collections

are currently known, the species occurs approximately 20 km from the Peruvian border, so its distribution range may possibly extend into this country as well. Based on the two known locations for this species, the continuing decline in habitat quantity/quality in at least one of these locations, the reported threat to the species from commercial extraction for horticulture, and the small Extent of Occurrence (25 sq. km) and Area of Occupancy (8 sq. km), we recommend a listing of this species by the IUCN as Endangered based on criteria B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v); C2(i) (sensu IUCN Standards and Petitions Committee 2022).

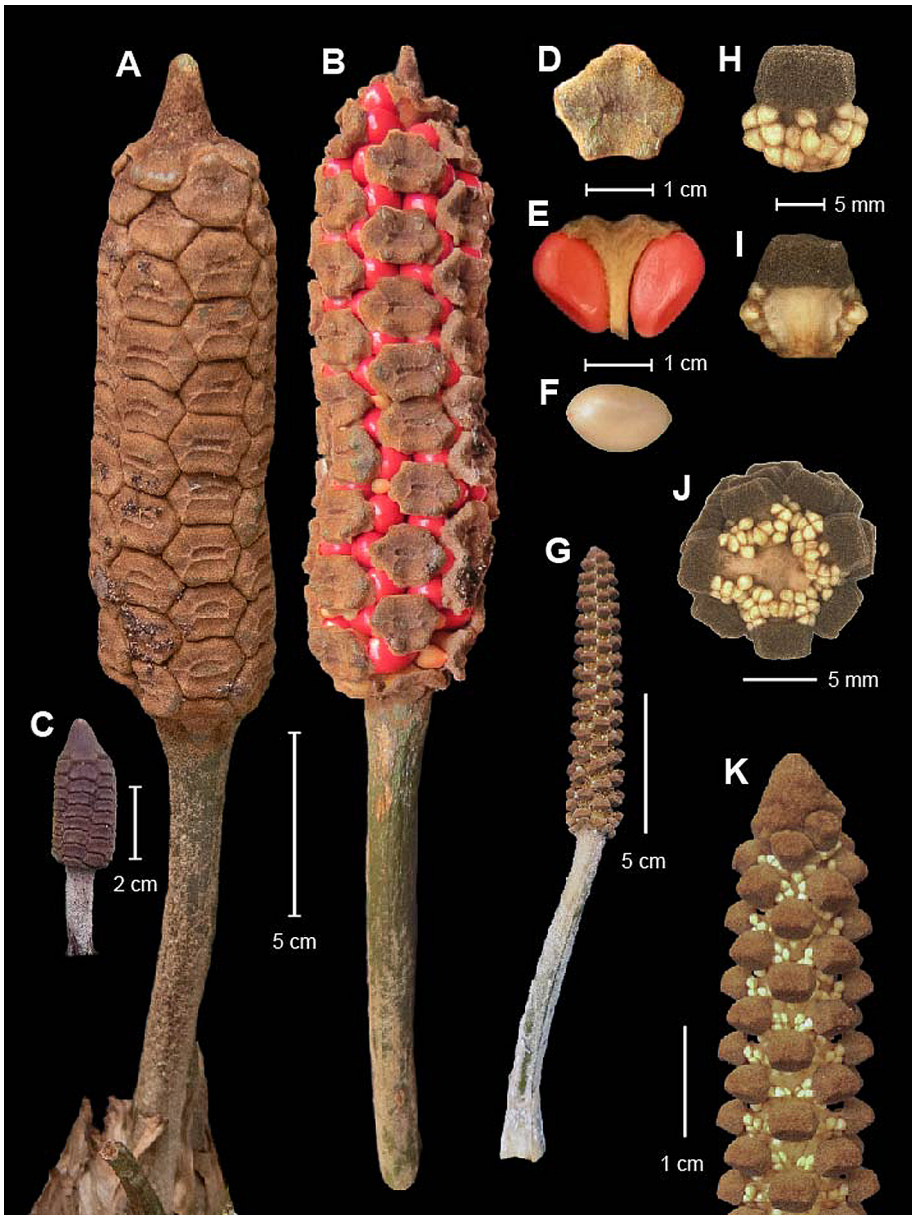

FIGURE 2. Reproductive characteristics of *Zamia multidentata*. A. Near mature ovulate strobilus, B. Mature ovulate strobilus with ripe seeds, C. Immature ovulate strobilus. D. Megasporophyll shield, E. Megasporophyll with two mature seeds with sarcotesta intact, F. Seed sclerotesta, G. Pollen strobilus at pollen dehiscence stage, H. Microsporophyll abaxial view, I. Microsporophyll adaxial view, J. Pollen strobilus cross section showing microsporophyll arrangement, abaxial side, K. Close up of distal half of pollen strobilus. All photographs used for the preparation of the illustration were taken at the type locality.

Morphological affinities:—*Zamia multidentata* shares some morphological similarities with the Amazonian species *Z. urep* and *Z. hymenophyllidia,* including elliptic leaflets with long acuminate tips as well as ovulate strobili with long peduncles. *Z. multidentata* most closely resembles *Z. hymenophyllidia*, with which it shares the presence of a pronounced adaxially raised longitudinal crease on the leaflets, and slender (less than 7 cm wide) caulescent stems. Whether these morphological affinities correspond to a close phylogenetic relationship is currently unknown. While all species of *Zamia* from the Amazon basin phylogenetically evaluated to date appear to belong to the same clade, the fine-scale relationships between the constituent species in this clade remain unresolved and their resolution will require

the use of new high-throughput sequencing technologies (Calonje *et al.*, 2019). Nevertheless, as within the Amazon basin these three species are the most likely to be confused morphologically, we hereafter discuss the morphological differences and similarities between them in order to aid in their identification.

FIGURE 3. *Zamia multidentata* in habitat. A. Adult plant in habitat with post-receptive ovulate strobilus, B. Abaxial side of leaf, with Márcio Sombra, C. Adult plant with Rosane Segalla for scale, D. Adult plant growing near river. The nutrient poor sandy soils of the region evident on the opposing riverbank. All photographs taken at type locality.

The three species can be readily distinguished by their leaflet morphology alone (Fig. 4), as they vary in their dentation, number and prominence of leaflet veins, and the presence or absence of an adaxially raised longitudinal crease (Table 1). *Zamia multidentata* leaflets have a larger number of veins and teeth than the other two species. The presence of an adaxially raised longitudinal crease is present in both *Z. multidentata* and *Z. hymenophyllidia*, but absent in *Z. urep* which has relatively flat leaflets. The veins are extremely prominent on the adaxial leaflet surface of *Z. urep*, less so in *Z. hymenophyllidia* (though highly prominent in dried specimens), and not prominent in *Z. multidentata*. The color of newly emerging and expanding leaflets is green in both *Z. multidentata* and *Z. hymenophyllidia*, and medium yellow brown (RHS 163A) in *Z. urep*.

Zamia multidentata and *Z. hymenophyllidia* have caulescent trunks whereas *Z. urep* is acaulescent. In addition to differences in vegetative characters, *Z. multidentata* has microsporophylls typically bearing more microsporangia (12–17) than either *Z. hymenophyllidia* (10–12) or *Z. urep* (9–10) (Table 1). Finally, although the three species are

endemic to the Amazon basin, their geographic ranges do not overlap and are separated by hundreds of kilometers from each other (Fig. 5).

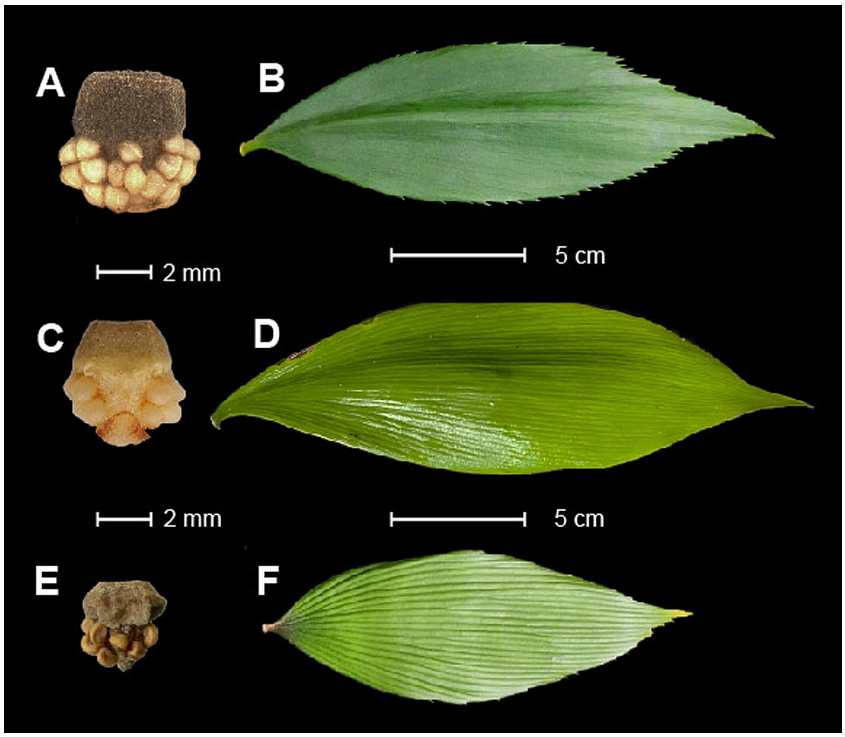

FIGURE 4. Comparison of microsporophylls and leaflets of *Zamia multidentata*, *Z. hymenophyllidia*, and *Z. urep*. A. Microsporophyll of *Z. multidentata*, abaxial side, B. Median leaflet of *Z. multidentata*, adaxial side, C. Microsporophyll of *Z. hymenophyllidia*, Nong Nooch Tropical Botanical Garden (NNTBG) accession 16022A, originally collected from Loreto, Perú. D. Median leaflet of *Z. hymenophyllidia*, adaxial side, photographed in Leticia, Amazonas, Colombia, E. Microsporophyll of *Z. urep*, abaxial side, F. Median leaflet of *Z. urep*, adaxial side. Photographs of *Z. multidentata* from material collected at type locality, photographs of *Z. urep* from NNTBG accession 15233A.

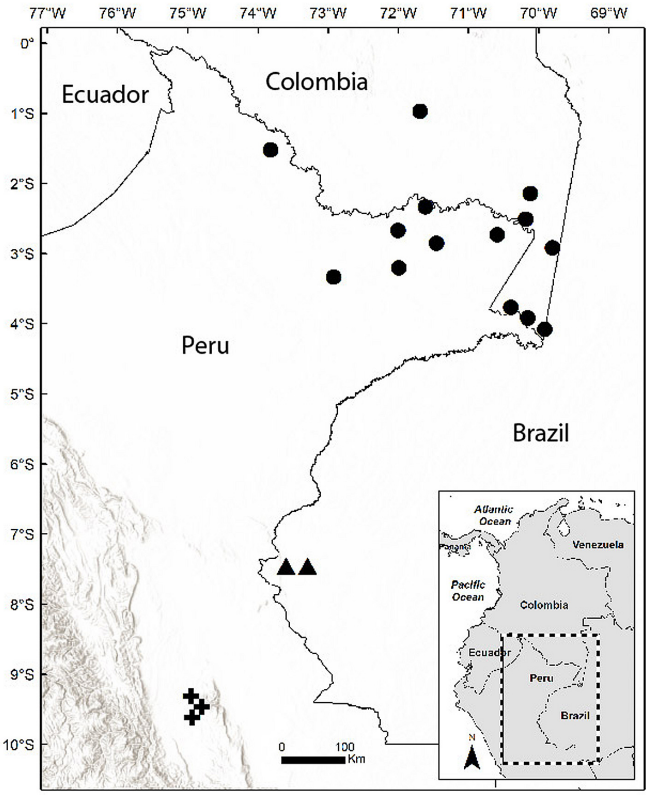

FIGURE 5. Disjunct geographic distribution of *Zamia multidentata* (triangles), *Z. hymenophyllidia* (circles), and *Z. urep* (crosses).

Most Amazonian *Zamia* species have subterranean stems, and prior to this description, the massive species *Z. poeppigiana*, with its stems reaching 3 m tall and 30 cm in diameter (Calonje *et al.*, 2011), was considered the only truly arborescent species. Our field surveys documented that an arborescent habit is also widespread in *Zamia multidentata*, albeit it produces much shorter and more slender stems reaching up to 45 cm tall and 6.2 cm in diameter. Furthermore, we report that *Zamia hymenophyllidia*, previously considered a subterranean-stemmed species (Stevenson, 2001), is an arborescent species producing similarly slender stems to *Z. multidentata*. Although most plants observed in our survey for this species in Leticia (Amazonas, Colombia) were acaulescent, we did observe a small number of plants in habitat with short slender stems up to 12 cm tall and 4 cm wide, and specimens report stems for this species up to 40 cm tall (*Barona 5044* [COAH!]) and 7 cm in diameter (*Bernal et al. 2545* [COL!]). The slender (7 cm or less) caulescent stems produced by *Z. multidentata* and *Z. hymenophyllidia* are unusual in the genus, as most arborescent species have considerably thicker stems typically exceeding 8 cm at maturity. The extremely slender stems of these two species are perhaps only comparable to those of younger plants of *Z. obliqua* Braun (1875: 376) which at maturity can have stems from 6.5 to 15 cm in diameter.

Discussion

The combination of slender (to 6.2 cm) caulescent stems, strongly serrulate (30–49 teeth) elliptic leaflets with long acuminate tips and a prominently raised adaxial longitudinal crease, and seed strobili with long peduncles (15 cm +) and flat megasporophylls, distinguish *Zamia multidentata* from all other species in the genus. With this contribution we add to the body of knowledge of the poorly studied and understood zamias of the Amazon basin and build upon previous contributions by members of the authorship team to the taxonomy and biology of this group, including: the recircumscription of *Z. poeppigiana* (Calonje *et al.* 2011), the description of *Z. brasiliensis* (Segalla & Calonje 2019), and an increased understanding of the reproductive biology (Segalla *et al.*, 2021) and ecological interactions (Segalla & Morellato 2019) of *Z. boliviana*.

TABLE 1. Quantitative and qualitative distinctions between *Z. multidentata*, *Z. hymenophyllidia*, and *Z. urep*.

	Z. multidentata	*Z. hymenophyllidia*	*Z. urep*
Stem habit	Caulescent	Caulescent	Acaulescent
Median leaflet length (cm)	18.2–21.7	16–24	11–20
Median leaflet width (cm)	4.3–9.3	4.5–7.2	3–6
Median leaflet teeth number	30–49	0–11	18–29
Leaflet adaxially raised longitudinal crease	Present	Present	Absent
Median leaflet veins at center	36–47	21–28	19–24
Adaxial leaflet vein prominence	Low	Moderate	High
New leaf color	Green	Green	Brown
Microsporangia per microsporophyll	12–17	10–12	9–10

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first preliminary survey of this species, and to local resident Francisco Assis F. Silva, for first locating and bringing this species to RP's attention. We thank the Sociedad Colombiana de Cycadas, the Grupo de investigación Ecología Evolutiva y Conservación (EECO), and the Universidad Nacional de Colombia for supporting field research in Leticia (Amazonas, Colombia) focusing on *Zamia hymenophyllidia*. We thank Anders Lindstrom and Nong Nooch Tropical Botanic Garden (Chonburi, Thailand) for providing access to MC to the garden's ex situ cycad living collection for study. We thank Miguel Ángel Pérez-Farrera and an anonymous reviewer for taking the necessary time and effort to critically review the manuscript, and Mario Coiro and Simon Lavaud for providing valuable feedback on a draft version of the manuscript.

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Appendix 1. Specimens examined of *Z. hymenophyllidia* and *Z. urep*:—

Z. hymenophyllidia. Type: COLOMBIA. Amazonas: Tarapacá, 200 m, 9 Mar 1999, *D. Cárdenas et al. 10089* (holo-: COAH! No. 50000!, iso-: NY);

COLOMBIA. Amazonas: La Chorrera, 29 Sep 2017, *A. Barona & S. Dutcha* 4683 (COAH No. 100431!); La Pedrera, 94 m, 15 Apr 2018, A. Barona 5044 (COAH No. 100379!); 198 m, 31 Jul 1997, *D. Cárdenas López et al.* 8473 (COAH no. 30073!), 8477 (COAH 30065!); Leticia, 16 Aug 2000, *J. Arias et al. 858* (HUA No. 136517!); 17 Aug 2000, *J. Arias et al.* 883 (HUA No. 136414!); 104 m, 25 May 2018, *A. Barona 5164* (COAH Nos. 104155!, 104157!); 150 m, 4 Mar 2001, *R. Bernal et al. 2545* (COL Nos. 462223!, 462047!); 150 m, 3 Mar 2001, *R. Bernal et al. 2528* (COL No. 462332!); 100 m, 11 Jun 2013*, D. Cárdenas et al.* 43554 (COAH No. 29347!); 100 m, 12 Jun 2013, *D. Cárdenas et al.* 43555 (COAH No. 29324!); 100 m, 16 Jun 2013, *D. Cárdenas et al.* 43559 (COAH No. 43015!); 100 m, 20 Jan 1988, *A. Gentry & J.A. Villa-Lopera 60827* (MO No. 4626404!); 100–120 m, 25 Nov 2017, *C. López-Gallego et al.* 78, 80, 87 (HUA!); 100 m, 12 Apr 1991, *J.J. Pipoly III et al. 15203* (MO No. 5670169!), *15233* (COL No. 405452!, FMB No. 53344!, MO No. 5670168!); 110–120 m 28 Oct 1991, *J.J. Pipoly III 15619* (FMB No. 23733!, MO No. 4224377!), *15629* (FMB No. 23732!, MO Nos. 5310319!, 5310320!); 200–220 m 15 Nov 1991, *J.J. Pipoly III 16228* (FMB No. 23736!, MO 4228243!); Puerto Nariño, 118 m, 26 Aug 2001, *R. Bernal & M. Grussmacher 2927* (COL Nos. 470292!, 470293!, HUA No. 163972!); 12 Apr 1975, *I. Cabrera* 3351 (COL No. 184567!); 100 m, Sep 1946, *R.E. Schultes & G.A. Black 8366* (F Nos. 1372847!, 1372848!, 1372876!); 250 m*,* 11 Mar 1999, *R. López et al. 5268* (COAH Nos. 51532!, 51533!), *5275* (COAH No. 51534!), *5279* (COAH Nos. 51527!, 52377!); 100 m, 26 Aug 2004, *R. López et al. 8499* (UDBC 19272!); 90 m, 17 Nov 2004, *R. López et al. 9946* (COAH No. 59169!, COL No. 556824 / barcode COL000375115!), *9958* (FMB No. 92535!); 89 m, 4 Nov 2005, *R. López et al. 10693* (COAH No. 62017!); 250 m, 11 Dec 1998, *C. Marín et al. 827* (COAH No. 51512!); 250 m, 17 Apr 1999, *C. Marín et al. 1678* (COAH No. 51513!); Tarapacá, 102 m, 30 Jul 2016, *A. Barona 3775* (COAH 96298!); 2 Jul 2017, *Rodríguez Castañeda et al. 2997* (COAH No. 96836!); 10 Jul 2017, *Rodríguez Castañeda et al. 3034* (COAH No. 96717!); 11 Jul 2017, *Rodríguez Castañeda et al. 3042* (COAH No. 96858!); PERU. Loreto: Maynas, 115 m, 28 Oct 2010, *I. Huamantupa et al. 14717* (USM Nos. 254419!, 254420!, 254421!); 12 Apr 1977, *T. Plowman et al. 6773* (F No. 1825020!, GH!, K!); 27 Apr 1977, *T. Plowman et al. 7065* (GH!); 4 May 1977, *T. Plowman et al. 7255* (GH!, USM No. 140396!), *7256* (GH!, USM No. 140397!); 150–190 m, 28 Oct 2012, *M. Ríos et al. 2848* (AMAZ!); 90–145 m, 4 Feb 2016, *M. Ríos et al. 5184* (AMAZ!); 90–145 m, 6 Feb 2016, *M. Ríos et al. 5301* (AMAZ!); 20 Aug 2001, *J. Ruiz 5003* (AMAZ No. 27674!, USM Nos. 215148!, 241760!); 140 m, 21 Dec 1990, *R. Vásquez 15836* (MO No. 4398435!); Mariscal Ramón Castilla, 93 m, 3 Mar 2002, *A.J. Lindstrom et al. 955* (AMAZ 37415!). USA. Illinois: Cultivated *ex* Leticia, Amazonas, Colombia, *T.C. Plowman 11800* (NY Barcode 278468!).

Note: There appears to be no record of the isotype cited in the protologue description being deposited at NY.

Z. urep Type: PERU. Huánuco: Pachitea, 660 m, 15 Jul 1988, *B. Wallnöfer* 112-15788 (holo-: W No. 1997-0004271 / barcode W0215386!, iso-: LZ, USM)

PERU: Huánuco: Pachitea, 275 m, 25 Feb 2002, *A.J. Lindstrom AL-930* (USM No. 215150!); 335 m, 25 Feb 2002, *A.J. Lindstrom AL-934* (AMAZ No. 27677!); 24 Feb 2002, *A.J. Lindstrom AL-936* (FTG!, W Nos. 2012-0010011 / barcode W0215388!, 2012-0010012 / barcode W0215389!),

Note: There are no records of the following specimens cited in the protologue description as being deposited at USM,W, or LZ: PERU: Huánuco: Pachitea, 260 m, 11 May 1989, *C. Listabarth 11-11589* (USM, W), *12-11589* (USM, W), *12-15789* (W No. 1997-0004270! / barcode W0215387!); 260 m, 1 Feb 1993, *C. Listabarth 14-1293* (USM, W); 15 July 1988, *B. Wallnöfer* 15-241188 (LZ, USM, W), 660 m, 15 Jul 1988, *B. Wallnöfer* 112-15788 (iso-: LZ, USM).