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Zamia orinoquiensis (Zamiaceae, Cycadales), a new species from the western Orinoquía region of Colombia

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Abstract

Zamia orinoquiensis Calonje, Betancur & A.Lindstr., a new species from the western Orinoquía region of Colombia is described and illustrated. The species is segregated from and compared to *Z. muricata* Willd., the latter which is morphologically recharacterized, illustrated, and recircumscribed to include populations from tropical dry forest and tropical moist forests in the Lara-Falcón Formation and the Cordillera de la Costa natural regions of Venezuela, as well as the Serranía de Macuira in La Guajira, Colombia. *Zamia orinoquiensis* is morphologically distinguished from *Z. muricata* by its leaves bearing fewer, coriaceous (vs. papyraceous) leaflets, eophylls with 2 (vs. 4) leaflets, pollen strobili that are brown to reddish brown (vs. cream to tan) with larger microsporophylls bearing more numerous microsporangia, and ovulate strobili that are dark brown to black (vs. dark olive green to olive brown) at maturity.

Keywords: Llanos Orientales, Orinoquía, Colombian Cordillera Oriental, Gymnosperms

Introduction

Zamia muricata Willdenow (1806: 847) was described by German botanist Carl Ludwig Willdenow, based on a specimen collected in the Venezuelan coastal city of Puerto Cabello by Alexander von Humboldt and Aimé Bonpland during their travels in the country at the turn of the nineteenth century. Although their collection is undated, it likely occurred during their visit to Puerto Cabello on a journey from Caracas they undertook from February to March of 1800 (Sandwith, 1925). The species is relatively widespread in tropical dry forests and moist forests in the Lara-Falcón Formation and the Cordillera de la Costa natural regions of Venezuela (Fig. 1), and based on Stevenson's (2001, 2004) treatment of Colombian cycads, it is currently considered to occur in two different locations in Colombia: the Serranía de Macuira in the Guajira Peninsula, and along the Eastern Cordillera Llanos foothills (ECLF) of the Orinoquía region (Calonje *et al.* 2020). Stevenson (2001, 2004) noted that the Colombian populations of *Z. muricata* remained enigmatic due to the paucity of known localities and their occurrence in remote areas.

The Serranía de Macuira is an isolated mountain range located in the Guajira Peninsula of northern Colombia which is surrounded by the extremely dry and sparsely vegetated Guajira Desert. It is over 235 km distant from the nearest Venezuelan populations of *Zamia muricata* and separated by the Gulf of Venezuela. The remaining Colombian

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collections of *Z. muricata* (*sensu* Stevenson 2001, 2004) are broadly distributed along the ECLF in the Orinoquía natural region of Colombia. These populations, approximately 780 km from the Serranía de Macuira and at least 610 km from Venezuelan populations of *Z. muricata*, have remained enigmatic for decades due to a paucity of fertile collections and a lack of targeted field research. The recent discovery of viable *Zamia* populations in the Orinoquía region in the Colombian department of Cundinamarca provided us with the opportunity to conduct field research to evaluate these long enigmatic ECLF populations and compare them to Venezuelan populations of *Z. muricata*.

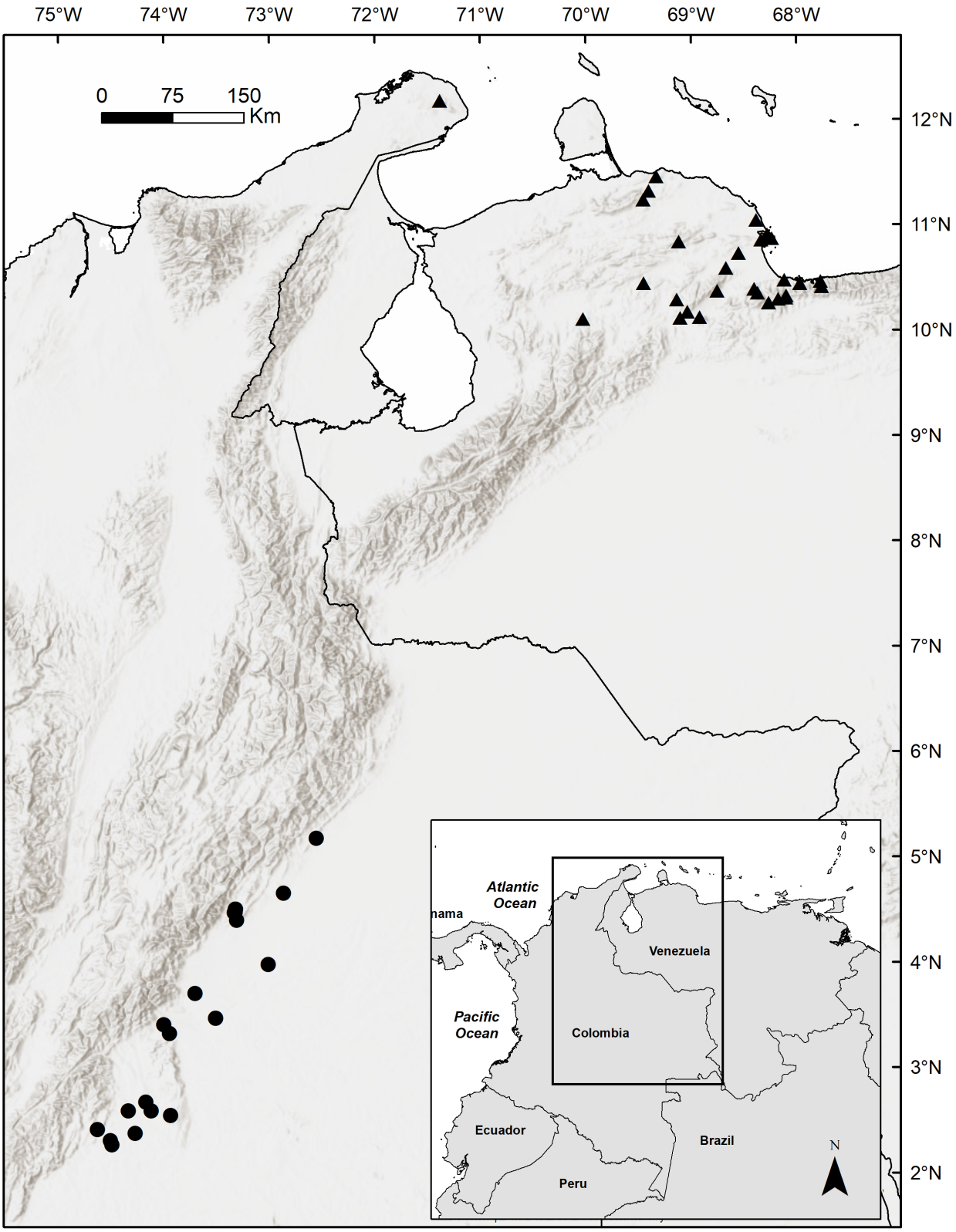

FIGURE 1. Geographic distribution of *Zamia muricata* (triangles) and *Z. orinoquiensis* (circles)

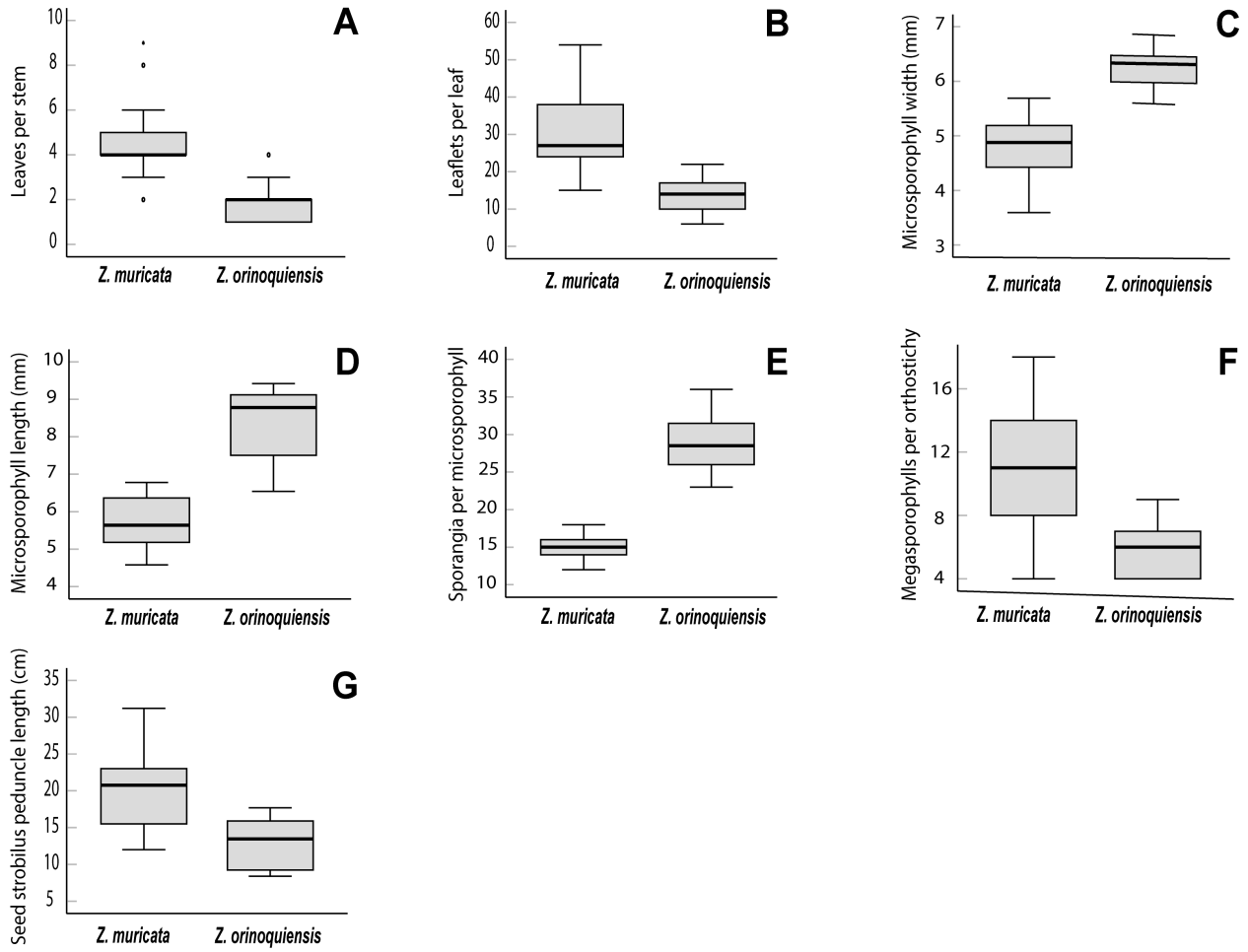

FIGURE 2. Morphometric variation beween *Zamia muricata* and *Z. orinoquiensis*. The plots A–G correspond to the traits listed in Table 3 that had significantly different means ($p \leq .001$). Whiskers indicate standard errors and circles and asterisks represent outliers.

Based on herbarium specimen study coupled with comparative field studies in Cundinamarca and at several *Zamia muricata* populations in Venezuela, we determined that ECLF populations are morphologically distinct from *Z. muricata* and represent a previously undescribed taxon which we describe and illustrate here.

Materials and methods

Herbarium specimens and specimen photographs of *Zamia muricata* (*sensu* Stevenson, 2001) were examined, georeferenced, and mapped in ArcGIS (Version 10.5.1; ESRI, 2018). Specimens and/or specimen images from the following herbaria were consulted: ANDES, COAH, COL, CUVC, F, FHO, FLAS, FMB, HORI, HUA, JAUM, LLANOS, MA, MG, MO, NY, PORT, S, UDBC, UEFS, US, VEN (acronyms according to Thiers 2022), and relevant morphological measurements were recorded from specimen images with the software ImageJ (Schneider *et al.* 2012). Living plants were examined at Montgomery Botanical Center (Florida, USA), Marie Selby Botanical Gardens (Florida, USA), Nong Nooch Tropical Botanic Garden (Chonburi, Thailand), Jardín Botanico Eloy Valenzuela (Santander, Colombia), Jardín Botánico del Quindío (Quindío, Colombia), Jardín Botánico de Cartagena 'Guillermo Piñeres' (Bolívar, Colombia) and the Dolmetsch Arboretum (Valle del Cauca, Colombia). Three separate wild populations of *Zamia* in the ECLF were visited in February of 2020 in the Municipalities of Medina and Paratebueno, Cundinamarca, and a locality in Puerto Lopez, Meta, was previously visited by A. Lindstrom in October of 2002. For the two largest populations we visited in Cundinamarca, we made a preliminary estimation of population structure by locating the largest patch of individuals in their forest-fragment habitats and recorded most adults, juveniles and seedlings. The maximum number of leaflets was used as a proxy for size or developmental stage for the species, and stage-categories were established to obtain the frequency distribution of individuals. Five Venezuelan populations of *Z. muricata* were

visited in October 2021 (Table 1), and another previously visited by S.M. Niño in June of 2006. Specific locality information associated with the visited locations and examined specimens is purposefully withheld in this paper and provided only at the municipality level to minimize the risk of illegal harvesting of these threatened species. Fieldwork at these surveyed localities included the collection of herbarium specimens, morphometric data, and photographs.

TABLE 1. Localities of *Zamia muricata* (*sensu* Stevenson, 2001) studied

Locality, elevation	Representative Specimen(s)	Habitat Type
Medina, Cundinamarca, Colombia, 500–525 m	*J. Castro et al. 1554* (COAH, COL, HUA, LLANOS, JAUM, FMB)	Tropical Moist Forest
Medina, Cundinamarca, Colombia, 520 m	*J. Castro et al. 1555* (COAH, HUA, JAUM)	Tropical Moist Forest
Paratebueno, Cundinamarca, Colombia, 500 m	*J. Castro et al. 1580* (HUA, COL)	Tropical Moist Forest
Puerto López, Meta, Colombia, 231 m	*A. Lindstrom* (observation only)	Tropical Moist Forest
San Felipe, Yaracuy, Venezuela, 360 m.	*S.M. Niño & D. Canelón 6596* (PORT)	Tropical Dry Forest
Bruzual, Yaracuy, Venezuela, 270 m	*S.M. Niño et al. 6597* (PORT)	Tropical Moist Forest
Bruzual, Yaracuy, Venezuela, 254 m	*S.M. Niño et al. 6603* (PORT)	Tropical Moist Forest
San Felipe, Yaracuy, Venezuela, 98–116 m	*S.M. Niño & D. Canelón 6612* & *6613* (PORT)	Tropical Moist Forest
Monseñor Iturriza, Falcón, Venezuela, 44–195 m.	*S.M. Niño & D. Canelón 6614* & *6615* (PORT)	Tropical Dry Forest
Zamora, Falcón, Venezuela, 400–450 m.	*S.M. Niño* (observation only)	Tropical Dry Forest

Morphological data gathered from living plants in habitat and in cultivation as well as from herbarium specimens and specimen images was utilized to compare samples derived from different populations, elaborate species descriptions and determine which characters may be diagnostic. The utility of 17 different quantitative morphological characters was evaluated by comparing the means of each trait between the two species using an independent-samples t-test as implemented by IBM SPSS Statistics for Windows, Version 28.0.1.1. As the sources of the measurements were varied, the number of measurements used for each analysis varied by species and character. The number of samples and relevant statistics for each species-character combination analyzed as well as the significance determined by the t-test is reported in table 3.

Specimen and field occurrence data were entered into GeoCAT geospatial conservation assessment tool (Bachman *et al.* 2011) to estimate the area of occupancy (AOO) and extent of occurrence (EOO) of the species for use in our conservation assessment for the IUCN Red List. Climate within the EOO according to the Koppen-Geiger climate classification system (Geiger 1954, Köppen 1918) was visualized in GIS using maps produced by Kottek *et al.* (2006). Estimates for annual temperature and rainfall ranges within the AOO were obtained by extracting values at occurrence points using CHELSA bioclimatic variables (Karger *et al.* 2017). Monthly precipitation estimates were obtained using Worldclim 2 bioclimatic variables (Fick & Hijmans 2017).

TABLE 2. Qualitative distinctions between *Zamia orinoquiensis* and *Z. muricata.* Measurements taken from adult individuals and mature strobili.

Trait	*Zamia orinoquiensis*	*Zamia muricata*
Leaflet texture	Coriaceous	Papyraceous
Pollen strobilus color	Brown to reddish brown	Cream to tan
Ovulate strobilus color	Dark brown to black	Dark olive green to olive brown

TABLE 3. Number of observations, mean and standard deviation of measures of quantitative traits examined for *Zamia muricata* and *Z. orinoquiensis*. Traits indicated with an asterisk had means that were significantly different ($p \leq .001$) between the two species. The eophyll leaflets trait (marked with double asterisks) had constant values for each species with no standard deviation, so a t-test could not be performed. They are nevertheless considered significantly different and a good diagnostic character as the values don't overlap between the two species.

	Species	N	Mean	Std. Deviation
Eophyll leaflets**	*Z. muricata*	10	4	0
	Z. orinoquiensis	14	2	0
Leaf length (cm)	*Z. muricata*	12	146.3	40.5
	Z. orinoquiensis	4	101.8	41.6
Leaves per stem *	*Z. muricata*	22	4.6	1.7
	Z. orinoquiensis	49	1.9	0.8
Leaflets per leaf *	*Z. muricata*	30	31.8	10.0
	Z. orinoquiensis	29	13.9	4.1
Distance between median leaflets (cm)	*Z. muricata*	14	4.1	1.0
	Z. orinoquiensis	21	4.3	1.6
Median leaflet length (cm)	*Z. muricata*	14	22.1	5.9
	Z. orinoquiensis	21	24.7	4.2
Median leaflet width (cm)	*Z. muricata*	14	3.4	0.6
	Z. orinoquiensis	21	4.7	2.0
Median leaflet teeth number	*Z. muricata*	14	21.5	8.3
	Z. orinoquiensis	21	25.7	6.9
Median leaflet vein number	*Z. muricata*	14	33.2	6.0
	Z. orinoquiensis	21	37.6	7.7
Microsporangia per microsporophyll *	*Z. muricata*	18	14.8	1.7
	Z. orinoquiensis	28	28.6	3.1
Microsporophyll length (mm) *	*Z. muricata*	16	5.7	0.7
	Z. orinoquiensis	14	8.4	1.0
Microsporophyll width (mm) *	*Z. muricata*	16	4.8	0.5
	Z. orinoquiensis	14	6.3	0.4
Microsporophylls per orthostichy	*Z. muricata*	8	19.1	1.5
	Z. orinoquiensis	6	19.7	1.6
Ovulate strobilus peduncle length (cm) *	*Z. muricata*	18	20.5	5.3
	Z. orinoquiensis	8	12.9	3.7
Ovulate strobilus length (cm)	*Z. muricata*	8	15.7	4.4
	Z. orinoquiensis	4	8.4	2.3
Ovulate strobilus width (cm)	*Z. muricata*	8	4.1	0.5
	Z. orinoquiensis	4	4.3	0.6
Megasporophylls per orthostichy *	*Z. muricata*	18	11.3	4.5
	Z. orinoquiensis	9	5.9	1.8

Results

The analysis of morphological characters of *Zamia muricata* (*sensu* Stevenson 2001) allowed us to determine that the plants from the ECLF of Colombia represent a taxon that is distinct from *Z. muricata* and diagnosable by several qualitative and quantitative morphological characters. The most diagnostic qualitative characters to discriminate between the two species are leaflet texture and strobilus color (Table 2). In terms of quantitative characters, the evaluated leaflet traits were not diagnostic, with no significant differences found in median leaflet distance, teeth number, vein number, length or width (Table 3). Similarly, although the leaves of *Z. muricata* may attain a larger size, the difference between their averages lengths was not significant. The number of leaflets on the eophylls appears to be a good character to distinguish between the species, with all observed seedlings of *Z. orinoquiensis* having two leaflets per eophyll, and those of *Z. muricata* holding four. Overall, *Z. muricata* is a much larger plant, holding significantly more leaves per stem and more leaflets per leaves than *Z. orinoquiensis* (Fig. 2A & 2B). The two species are easily distinguished by reproductive morphological traits with *Z. muricata* producing smaller microsporophyll bearing a smaller number of microsporangia, and *Z. muricata* producing ovulate strobili with significantly longer peduncles and bearing a larger number of megasporophyll per orthostichy (Table 3, Fig. 2). No significant differences were found in ovulate strobilus length or width. Based on the above results, we describe this taxon as a new species below, outlining the differences between it and *Z. muricata* in tables 2 and 3, figure 2 and in the 'morphological affinities' section of the description.

Taxonomic treatment

Zamia orinoquiensis Calonje, Betancur & A.Lindstr. *sp. nov.* (Figs 3–5)

Diagnosis:—*Zamia orinoquiensis* is distinguished from *Z. muricata* by its leaves bearing leaflets that are coriaceous (vs. papyraceous) in texture, eophylls with 2 (vs. 4) leaflets, pollen strobili that are brown to reddish brown (vs. cream to tan) with microsporophylls bearing more numerous (22–32 vs. 8–18) microsporangia, and ovulate strobili that are dark brown vs. dark olive green at maturity.

Type:—COLOMBIA. Cundinamarca: Medina, 500–525 m, 1 Feb 2020, *Jonatan Castro, Cristina López, Michael Calonje, Cristian Castro & Fredy Parra 1554* (holotype: HUA!, isotypes COAH!, COL!, FMB!, HUA!, JAUM!, LLANOS!)

Additional specimens examined (paratypes):—COLOMBIA. Casanare: Aguazul, 12 Feb 2012, *C. Ruiz et al. 325* (CUVC!); Tauramena, *F.J. Mijares 2257* (HORI!)**;** Villanueva**,** 300 m, 12 Feb 1939. *O. Haught 2601* (COL!, US!); Cultivated in Casanare, *Harry Vaughan s.n.* (FTG!). Cundinamarca**:** Medina**,** 520 m, 2 Feb 2020, *J. Castro et al. 1555* (COAH!, HUA!, JAUM!); 413–514 m, 25 Oct 2017, *M.F. González et al. 4380* (COL!); 500–525 m, 1 Feb 2020, *C. López et al. 98* (COAH!, HUA!). Paratebueno**,** 4 Feb 2020**,** 500 m, *J. Castro et al. 1580* (COL!, HUA!). Meta: La Macarena, 29 Apr 2002, *M. Gaitán et al. 83* (COAH!); 450 m, 6 Feb 1950, *W.R. Phillipson 2368* (BM!); 296 m, 25 Jun 2004, *J.G. Ramírez-Arango et al. 7701* (COAH!, COL!); 300 m, 6 Jul 2004, *J.G. Ramírez-Arango et al. 8514* (COAH!); 402 m, 13 Jul 2004, *J.G. Ramírez-Arango et al. 8536* (COAH!). Mesetas, 360–490 m, 25 Feb 1988, *R. Callejas & O. Marulanda* 5911 (HUA!, MO!); La Uribe, 350–400 m, Jul 1998, *P. Stevenson 2122* (ANDES!). San Juan de Arama, 445 m, 9 Aug 2004. *L. Carvajal et al. 334* (UDBC!); San Martín, 21 Oct 1945, *P.H. Allen 3355* (MO!, US!); 29 May 2011, *G. Téllez & F. Ciri 1650-A & 1650-B* (JAUM!).

Description:—*Stem* hypogeous, tuberous, typically solitary or rarely branching, globose to cylindrical, to 35 cm long and 12 cm diameter. *Cataphylls* papyraceous, narrowly triangular, beige to grey tomentose, with a pair of stipules near the apex, 1.0–2.5 cm wide at base, 4.5–9.0 cm long. *Leaves* 1–3 (4) per stem apex, erect to spreading, 66–160 cm long. *Petiole* 53–102 cm long, with slight groove on adaxial side and abruptly swollen base to 3 cm wide, dark olive green, sparsely to moderately armed with prickles 1–5 mm long or occasionally unarmed. *Rachis* 13–58 cm long, typically unarmed or with few scattered prickles in proximal fourth, ending in a short 0.1–1.5 cm brown tomentose terminal tip. *Leaflets* 6–22, coriaceous, suboppositely to subalternately arranged, articulate insertion on rachis 1–6 mm wide, spaced 4–8 cm apart at leaf center. Median leaflets lanceolate to obovate, abruptly acuminate distally, straight to slightly falcate, with 20 to 45 spreading teeth 0.2–2.0 mm long restricted to distal one half to one quarter of leaflets, new leaflets emerging light reddish brown covered with white and orange tomentum at emergence, becoming green and glabrous at maturity. Basal leaflets 18.5–36.0 cm × 3.9–9.7 cm, median leaflets 18.0–35.0 cm

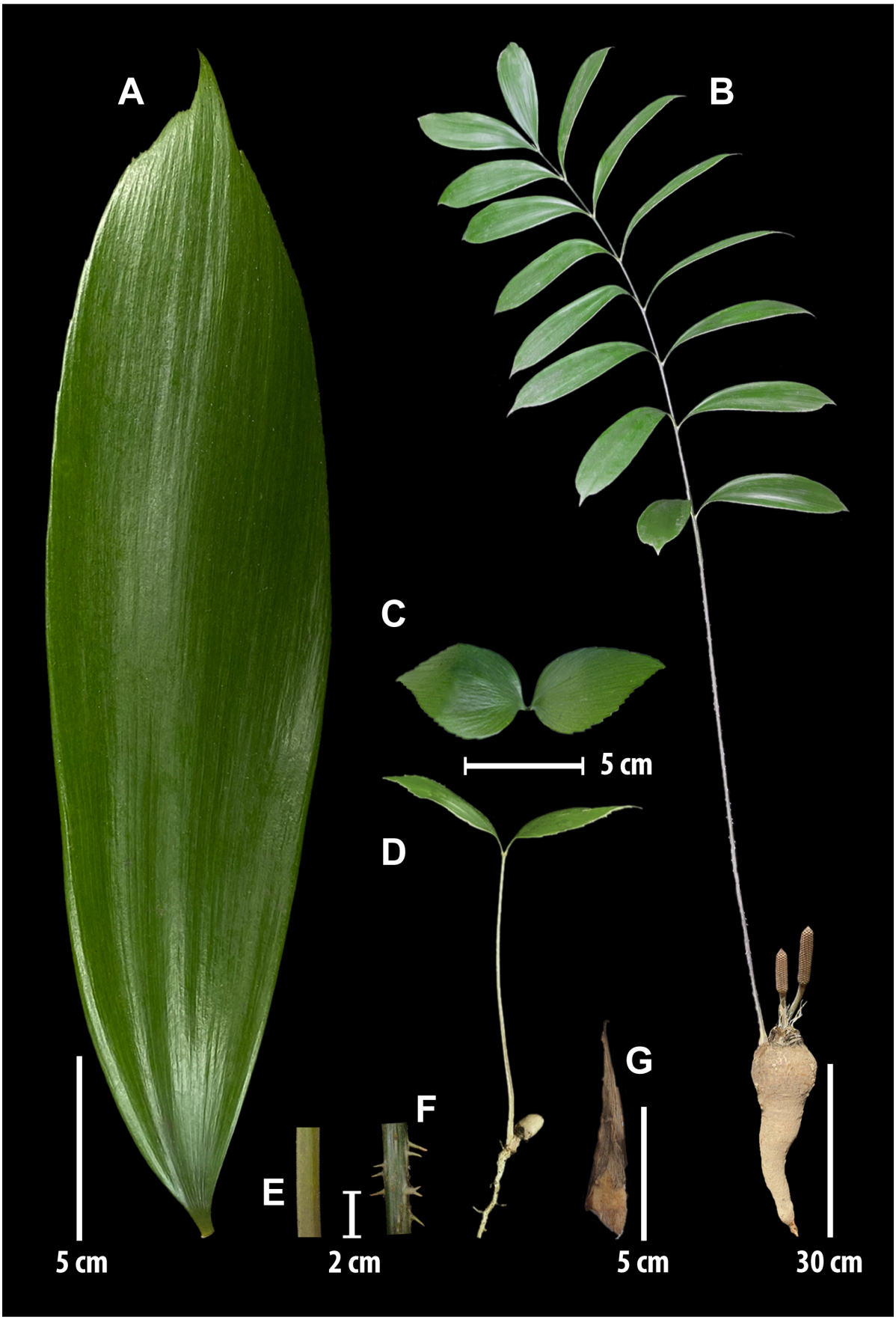

FIGURE 3. Vegetative characteristics of *Zamia orinoquiensis* from Medina and Paratebueno Municipalities in Cundinamarca, Colombia. A. Median leaflet, B. Adult individual with pollen strobili, C. Eophyll leaflets, top view, D. Seedling with eophyll, E. Petiole, unarmed, F. Petiole, armed with robust prickles, G. Cataphyll.

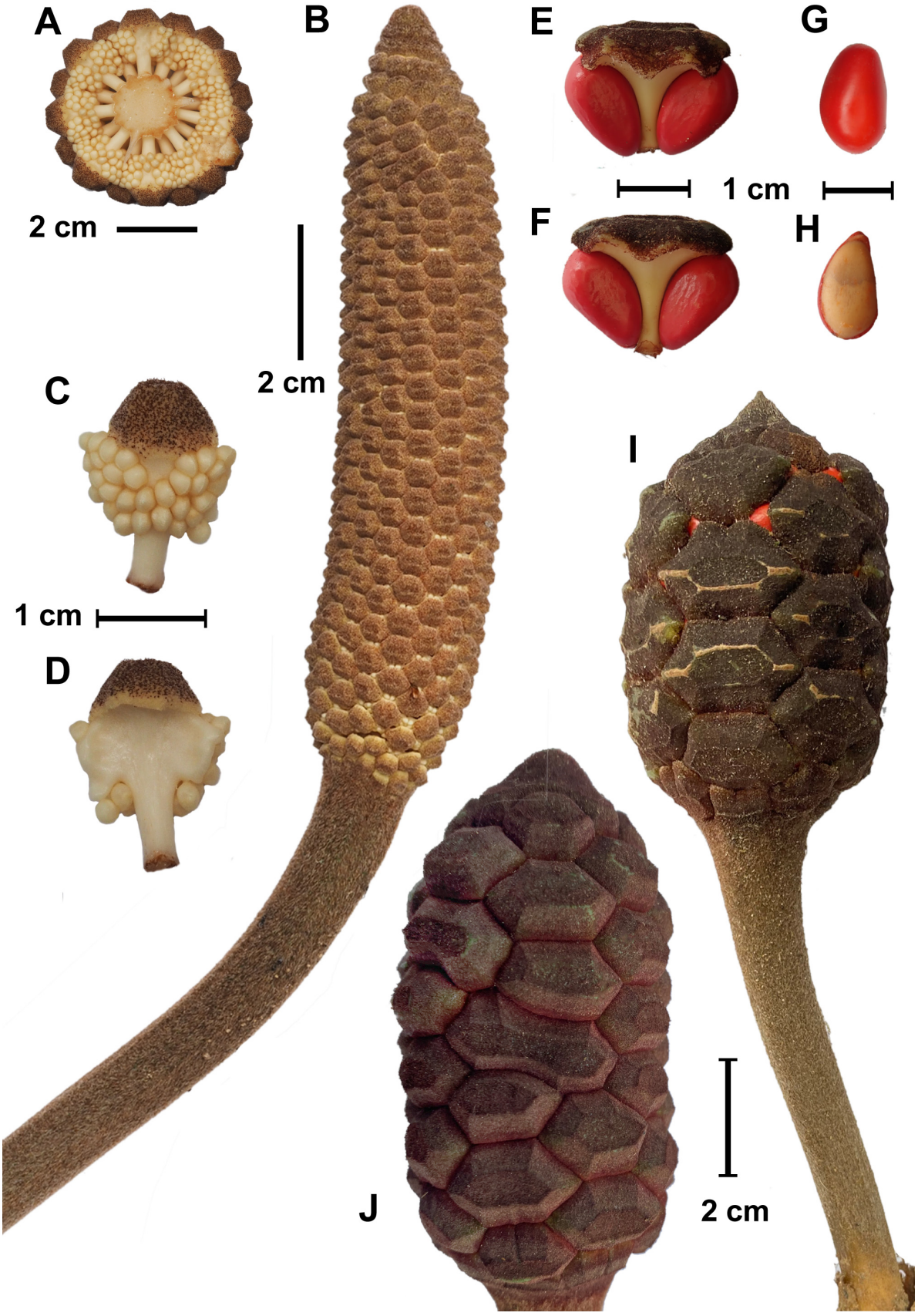

FIGURE 4. Reproductive characteristics of *Zamia orinoquiensis*. A. Pollen strobilus cross section, abaxial view, B. Pollen strobilus near pollen release phase, C. Microsporophyll abaxial view, D. Microsporophyll adaxial view, E. Megasporophyll abaxial view, F. Megasporophyll adaxial view, G. Seed with ripe sarcotesta, H. Seed sclerotesta with half of sarcotesta removed to show thickness. I. Ovulate strobilus at maturity, J. Ovulate strobilus, immature. All images from type locality.

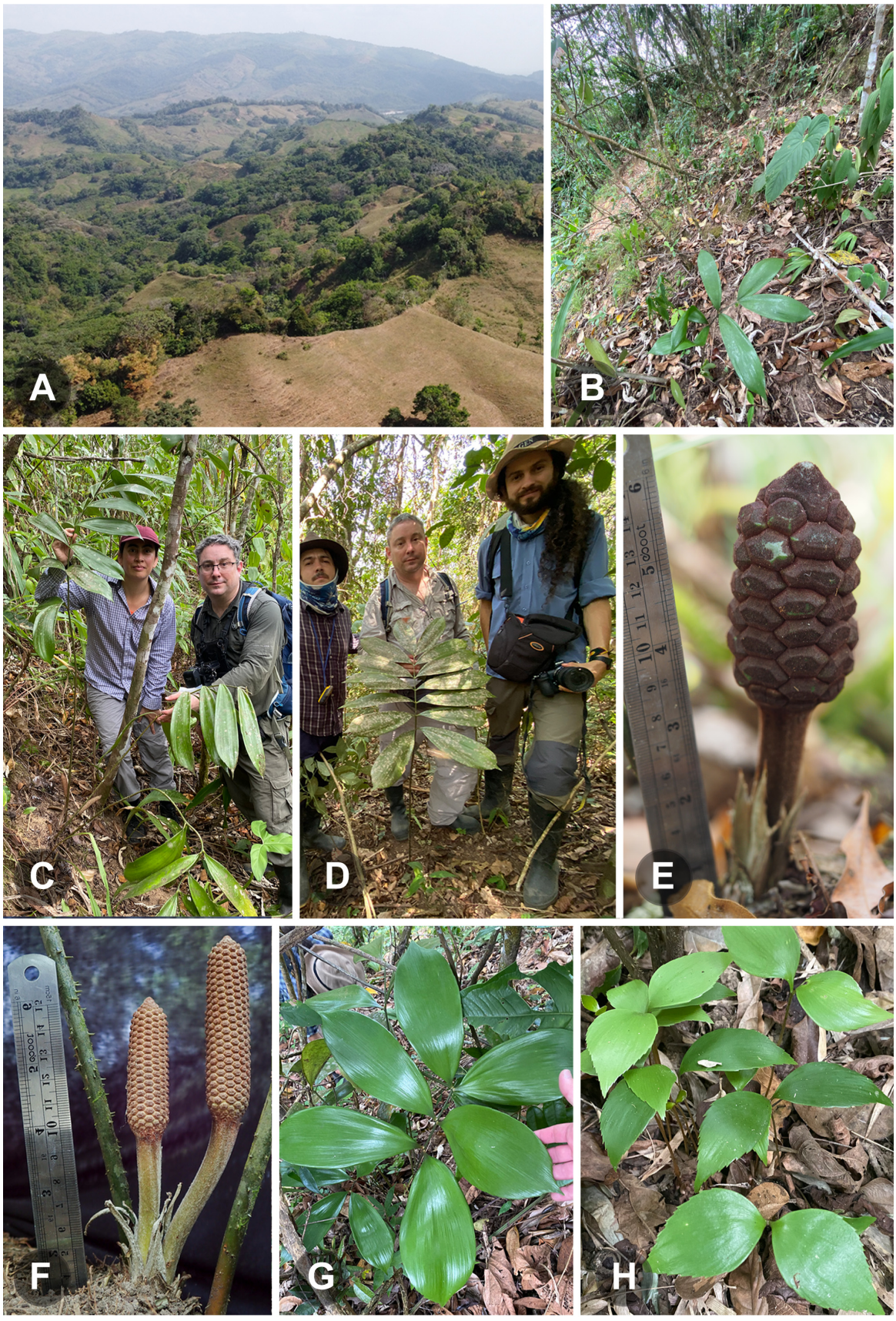

FIGURE 5. *Zamia orinoquiensis* in habitat in Cundinamarca, Colombia. A. Aerial view of type locality showing tropical moist forest fragments surrounded by cattle pasture. B. Tropical moist forest understory habitat. C. Large adult male plant with C. Lopez-Gallego and M. Calonje. D. Adult male plant with J. Castro, M. Calonje, and C. Castro. E. Immature ovulate strobilus, F. Pollen strobili, G. Leaf on a juvenile. H. Seedlings with 2-leaflet eophylls. All photographs taken at type locality in Medina except D and F, which were taken in Paratebueno.

× 3.8–11.0 cm, apical leaflets 17.0–29.0 cm × 3.7–9.5 cm. *Eophylls* with unarmed petioles 10–20 cm long, rachis 1 mm long, carrying two lanceolate leaflets 4.4–6.5 × 1.8–4.0 cm. *Pollen strobili* 1–3 per stem apex, brown to reddish brown tomentose, cylindrical, 7.2–12.0 × 1.6–2.2 cm at pollen shedding, peduncle brown to reddish brown tomentose, 8.0–17.0 × 0.6–1.3 cm, strobilar axis and inner surfaces of microsporophylls glabrous. *Microsporophylls* spirally arranged in 14–19 orthostichies of 15–24 fertile sporophylls each, 6.5–9.4 × 5.6–6.9 mm, pedicel distinct, 1.8–2.0 mm long, sterile shield encompassing 1/4 to 1/3 of sporophyll length. Margins of fertile area of microsporophylls with distinct narrow wings that are falcate and angled towards proximal end. *Microsporangia* spherical to slightly ovate 0.9–1.0 × 0.65–0.8 mm, present only on abaxial side, aggregated into two distinct marginal groups of 12–16 each or a single group of 23–36 microsporangia. Sterile shield a distinctly extruded hexagonal prism 3.1–3.8 mm tall, 5.0–5.6 × 4.1–4.3 mm at the base, the distal facet distinctly indented and reduced to approximately ¼ of the area of the base, mostly reddish-brown tomentose with a narrow cream-yellow strip at proximal section where it comes in contact with other microsporophylls. *Ovulate strobili* one per stem apex, cylindrical, burgundy-tomentose at emergence and receptivity, maturing to black tomentose with green undertones, 7.3–14.0 × 4.7–5.0 cm at maturity, apex pungent and 2–5 mm long, peduncle similar in color to strobilus, 6.0–18 × 0.8–1.2 cm diameter at center, strobilar axes and megasporophyll pedicels glabrous. *Megasporophylls* spirally arranged in 5–7 orthostichies of 4–9 sporophylls each, 19.0–21.5 × 21.2–23.0 mm, sterile shield a shallowly extruded hexagonal prism 14.0–16.0 mm tall, 21.2–23.0 wide at the base, the distal facet shallowly indented and reduced to approximately ¼ of the area of the base. *Seeds* ovoid to ovoid-pyramidal, sarcotesta red-orange at maturity, 15–17 × 0.8–1.0 mm, sclerotesta glabrous, brown-yellow but abruptly and distinctly darker at distal end, 11.0–15.0 × 7.0–10.0 mm.

Etymology:—The specific epithet refers to the Orinoquía natural region in Colombia where this species occurs.

Common name:—Known as 'Quiripia' in the Serranía de La Macarena mountain range (per label on specimen *Gaitan et al. 83* [COAH!]).

Distribution, habitat, and climate:—*Zamia orinoquiensis* is endemic to the Orinoquía natural region of Colombia, also known as the Eastern Plains, or 'Llanos Orientales'. This region, best known for its extensive savannas, consists of three major landscapes: an area of high plains known as the altillanura, extensive flood plains, and the piedmont areas of the Eastern Cordillera of the Andes (Ospina, 2005). The species occurs primarily in the foothills of the piedmont of the Eastern Cordillera as well as in foothills of the isolated Serranía de La Macarena mountain range, extending slightly into the adjacent dissected or flat altillanura landscapes of both regions (Fig. 1). *Zamia orinoquiensis* occurs in the shaded understory of tropical wet and tropical moist forests (*sensu* Holdridge, 1977) at elevations ranging from 230 to 730 m in the departments of Casanare, Cundinamarca, and Meta. The annual mean temperature within its area of occupancy ranges from 24.8–26.8° C and the annual precipitation between 2200–4200 mm. The rainfall pattern is bimodal, with the highest monthly peaks in rainfall within the area of occupancy ocurring in May through June (270–580 mm) and a smaller peak in October (260–441 mm), and the driest month being January (9–95 mm).

Ecology and phenology:—Individuals are distributed in patches in the forest understory, usually on moderate slopes. The three populations visited in February 2020 all occurred in small forest fragments, but all with presence of seedlings and juveniles (see Figure 6 for a stage-based distribution of individuals of the two largest populations). There are no detailed studies on the population dynamics or the vegetative/reproductive phenology of the species, and very few fertile collections exist in herbaria. We observed mature and near-receptive ovulate strobili as well as pollen strobili at or near dehiscence during our fieldwork in February 2020. Mature ovulate strobili of this species have previously been collected in August 1998 and July 2004. In Medina we observed colonies of an unidentified species of *Pharaxonotha* Reitter (Coleoptera: Erotylidae), a potential pollinating agent, within a dehiscent pollen strobilus. A good proportion of viable seeds was observed in ovulate strobili at the three localities visited, indicating the presence of healthy populations of pollinators at these locations. The typical herbivores associated with *Zamia* species, *Eumaeus* (Lycenidae: Lepidoptera), were not observed in the three surveyed locations in Cundinamarca but have been reported in Casanare (Díaz-Pérez & Morales-Puentes, 2018). Most seed dispersal in *Zamia* is by gravity, but small vertebrates could be involved in rare long-distance dispersal events.

Conservation status:—The species has a relatively large geographic distribution with a large number of populations (16 known so far), compared to other endemic *Zamia* species in Colombia. Nevertheless, most of the populations are within highly degraded landscapes with high rates of deforestation, and no conservation actions are known for the species. The estimated extent of occurrence (EOO) is 18,148 km^2. Five of the populations (or subpopulations *sensu* IUCN Standards and Petitions Committee 2019) occur within national-level protected areas with large tracts of viable habitat (Tinigua, Serranía de La Macarena and Cordillera de los Picachos national parks). However, the remaining 11 populations are not within protected areas and persist in small forest fragments (less than 100 hectares) in landscapes highly modified by urbanization and agricultural activities (mostly cattle ranching). The species can be considered as

severely fragmented (10 subpopulations are small and isolated) and with continuing decline in habitat quantity/quality (*sensu* IUCN Standards and Petitions Committee 2019). Therefore, the species should be classified as Vulnerable (VU) using criteria B1ab(iii). Colombia has a national conservation action plan for cycads (López-Gallego, 2015), and the species will be included in this conservation plan to ensure the long-term protection of some populations and their habitats.

Morphological affinities:—*Zamia orinoquiensis* is vegetatively similar to *Z. muricata* in that both species have subterranean stems and leaflets that are markedly toothed in the distal half to two-thirds. However, the two species are readily distinguishable utilizing vegetative and reproductive morphological characters (Tables 2 & 3). *Z. muricata* is generally a more robust plant than *Z. orinoquiensis*, typically bearing more leaves per stem (2–9 vs 1–4), more leaflets per leaf (15–54 vs. 6–22), and ultimately attaining a larger maximum leaf length (2.5 vs 1.6 m). It also appears to branch more frequently, as several branched plants of *Z. muricata* were observed in the field, whereas all plants of *Z. orinoquiensis* observed were single-stemmed. The leaflets of *Z. orinoquiensis* are coriaceous and are held rigidly, whereas the leaflets of *Z. muricata* are papyraceous to chartaceous and slightly pendulous. The leaflet shape generally differs between the two species, albeit with some overlap. *Zamia orinoquiensis* leaflets are typically obovate with abruptly acuminate apices, whereas those of *Z. muricata* are typically lanceolate with acute to long-acuminate apices. The eophylls of *Z. orinoquiensis* carry two leaflets whereas those of *Z. muricata* carry four. In terms of reproductive morphology, the pollen strobili of both species are readily distinguishable. The pollen strobili of *Z. orinoquiensis* are brown to reddish-brown tomentose externally, whereas those of *Z. muricata* are cream to tan tomentose. The microsporophylls of *Z. orinoquiensis* are much larger (6.5–9.4 × 5.6–6.9 mm vs. 4.6–6.8 × 3.6–5.7 mm) and bear more numerous microsporangia (23–36 vs. 12–18) than those of *Z. muricata*. Finally, the ovulate strobili of *Z. orinoquiensis* are brown to black tomentose at maturity, and those of *Z. muricata* are dark olive green to olive brown and tend to be more glabrous. The habitats where the species occur also differ, with *Z. orinoquiensis* occurring in tropical wet and tropical moist forests (*sensu* Holdridge, 1977) with an annual precipitation of 2200–4200 mm, whereas *Z. muricata* in Venezuela occur in dry forests and tropical moist forests with 600–1600 mm of rain per year. The populations *of Z. muricata* in Serranía de Macuira occur in cloud forests at the summits of hills where precipitation is very low (< 1000 mm) but plants get their water primarily from cloud interception (Sugden 1982).

A revised description and taxonomic treatment for *Z. muricata* is provided below to further clarify geographic distribution and morphological characters differentiating these two species.

Taxonomic treatment

Zamia muricata Willd. Sp. Pl., ed. 4, 4: 847–848. 1806. (Figs. 7 & 8)

≡*Palmifolium muricatum* (Willd.) Kuntze, Revis. Gen. Pl. 2: 803. 1891.

Holotype:—VENEZUELA. Carabobo**:** Prope Porto Cabello, *Humboldt & Bonpland s.n.* (B–W No. 18536–010!).

=*Zamia gutierrezii* Sauv., Anales Acad. Ci. Med. Habana. 5: 54. 1868. Type: CUBA. PINAR DEL RIO: Hacienda de Rangel, Cordillera de los Organos, 1200 ft, *F.A. Sauvalle 2362* (HOLOTYPE: HAC!; ISOTYPES: F, NY!).

≡*Zamia media* Jacq. var. *gutierrezi* (Sauv.) J. Schust., in Engl., Pflanzenr. 4(1): 154. 1932.

=*Zamia muricata* var. *angustifolia* Miq., Monogr. Cycad.: 66. 1842. Type: ex Horto Spaarberg, *Miquel s.n.* (HOLOTYPE: U!).

Description:—*Stem* hypogeous, tuberous, solitary or typically branching on adult plants, globose to cylindrical, to 25 cm long and 12 cm diameter. *Cataphylls* papyraceous, narrowly triangular, light brown with sparse whitish-light brown tomentum, with a pair of stipules near the apex, 1.2–1.8 cm wide at base, 6.0–9.0 cm long. *Leaves* 2–9per stem apex, erect to slightly spreading, 134–189 cm long. *Petiole* 57–92 cm long, with a slight groove on the adaxial side and abruptly swollen base to 2 cm wide, dark brown to dark green with sparse dark brown shedding tomentum, sparsely to densely armed with prickles 1–2 mm long for 100% of length. *Rachis* 80–116 cm long, sparsely brown tomentose on new leaves, becoming glabrous at maturity, armed with a few scattered prickles in proximal half, ending in short 0.8–1.0 cm brown tomentose terminal tip. *Leaflets* 15–54, typically light green but occasionally reddish-brown emerging, dark green at maturity, papyraceous, slightly keeled, suboppositely to subalternately arranged, articulate insertion on rachis 3–5 mm wide, spaced 2.5–3.5 cm apart at leaf center. Median leaflets oblong-lanceolate to lanceolate, acute to long-acuminate distally, straight to slightly falcate, with 20–45 spreading teeth 0.2–2.0 mm long restricted to distal one third to one quarter. Basal leaflets 15.0–29.0 cm × 2.0–4.0 cm, median leaflets 21.0–32.0 cm × 2–4 cm, apical

leaflets 14.0–21.0 cm × 1.5–3.7 cm. *Eophylls* with unarmed petioles 9–10 cm, rachis 0.8–0.9 cm carrying 4 obovate to lanceolate leaflets 3.8–5.0 × 1.6–1.9 cm. *Pollen strobili* 1–6 per stem apex, cream tomentose with greenish undertones, cylindrical, 6.4–9.7 × 1.3–1.8 cm at pollen shedding, sterile apex blunt, less than 2 mm tall; peduncle light brown-tomentose, 9.0–16.0 × 0.6–0.8 cm, strobilar axes and inner surfaces of microsporophylls glabrous. *Microsporophylls* spirally arranged in 10–17 orthostiches of 15–25 sporophylls each, 4.6–6.8 × 3.6–5.7 mm, pedicel distinct, 2.2–2.8 mm long, sterile shield encompassing approximately 1/3 of sporophyll length. Margins of fertile area of microsporophylls with distinct narrow wings that are straight or slightly falcate and angled towards proximal end. *Microsporangia* spherical to slightly ovate, 0.9–1.1 × 0.8–0.9 mm, present only on abaxial side of microsporophyll bearing 12–18 sporangia aggregated into two widely separated marginal groups of 6–9 each. *Ovulate strobili* 1–2 per stem apex (up to 5 in cultivated individuals), brown-grey tomentose with green undertones, cylindrical, 7.6–22.0 × 3.8–4.5 cm at maturity, sterile apex acute and 1.5–2.0 cm long, peduncle faintly brown tomentose, 12.4–27.0 × 0.9–1.2 cm, strobilar axes and megasporophyll pedicels glabrous. *Megasporophylls* spirally arranged in 5–9 orthostichies of 4–18 sporophylls each, sterile shield a shallowly extruded hexagonal prism 8.0–12.0 mm tall, 16.5–19.7 mm wide, and 14–15 mm thick, the distal facet shallowly indented and reduced to 10 mm wide or approximately 1/8 of the area of the base. Seeds with red sarcotesta at maturity, ovoid to ovoid-pyramidal, 14.0–17.0 × 8.0–10.0 mm, sclerotesta 13.0–15.5 × 7.0–9.0 mm.

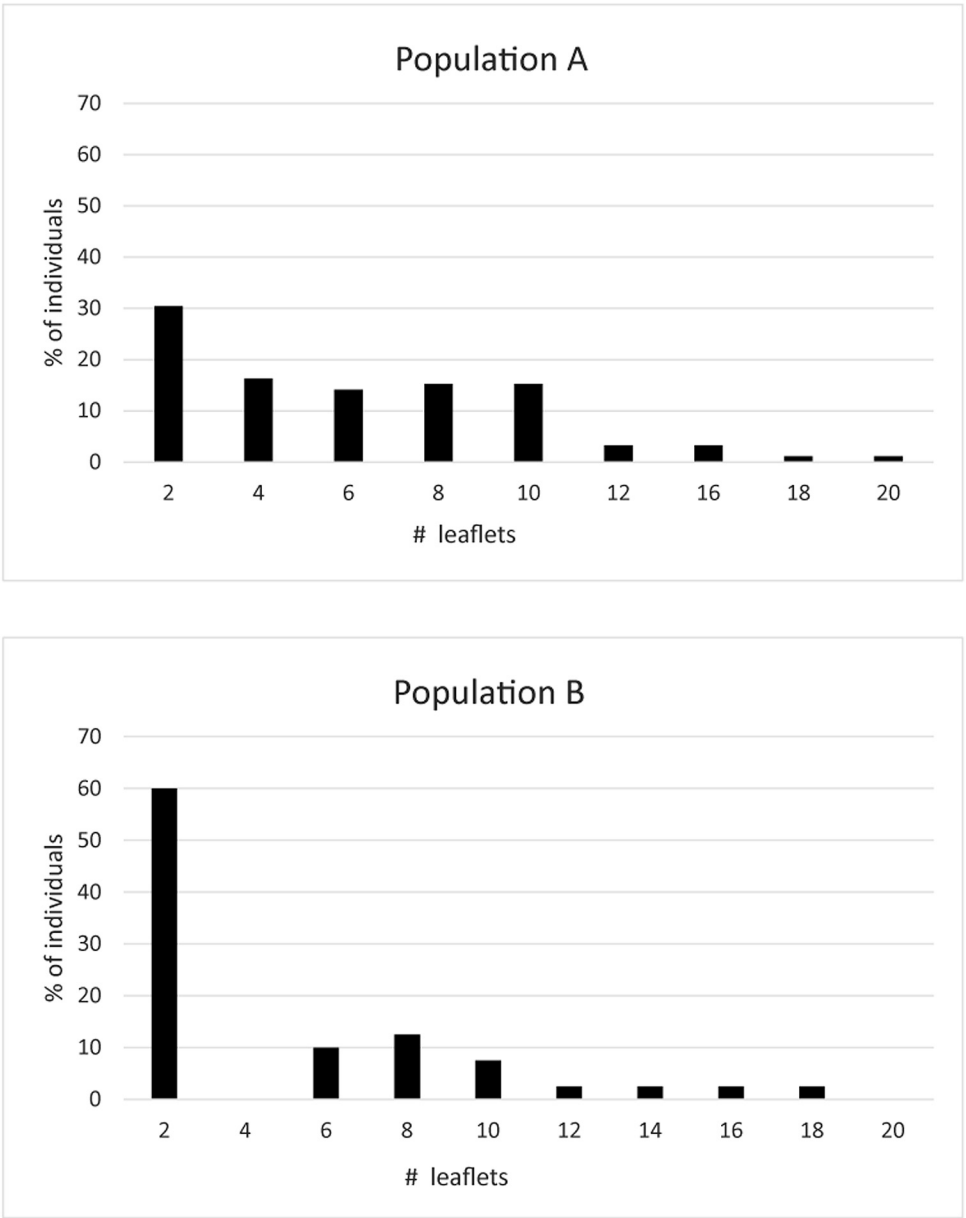

FIGURE 6. Stage population structure of two *Zamia orinoquiensis* populations in Medina, Cundinamarca. Population A is the type locality, identified by the specimen Castro *et al.* 1554 (HUA). Population B is represented by the collection Castro *et al.* 1555 (HUA).

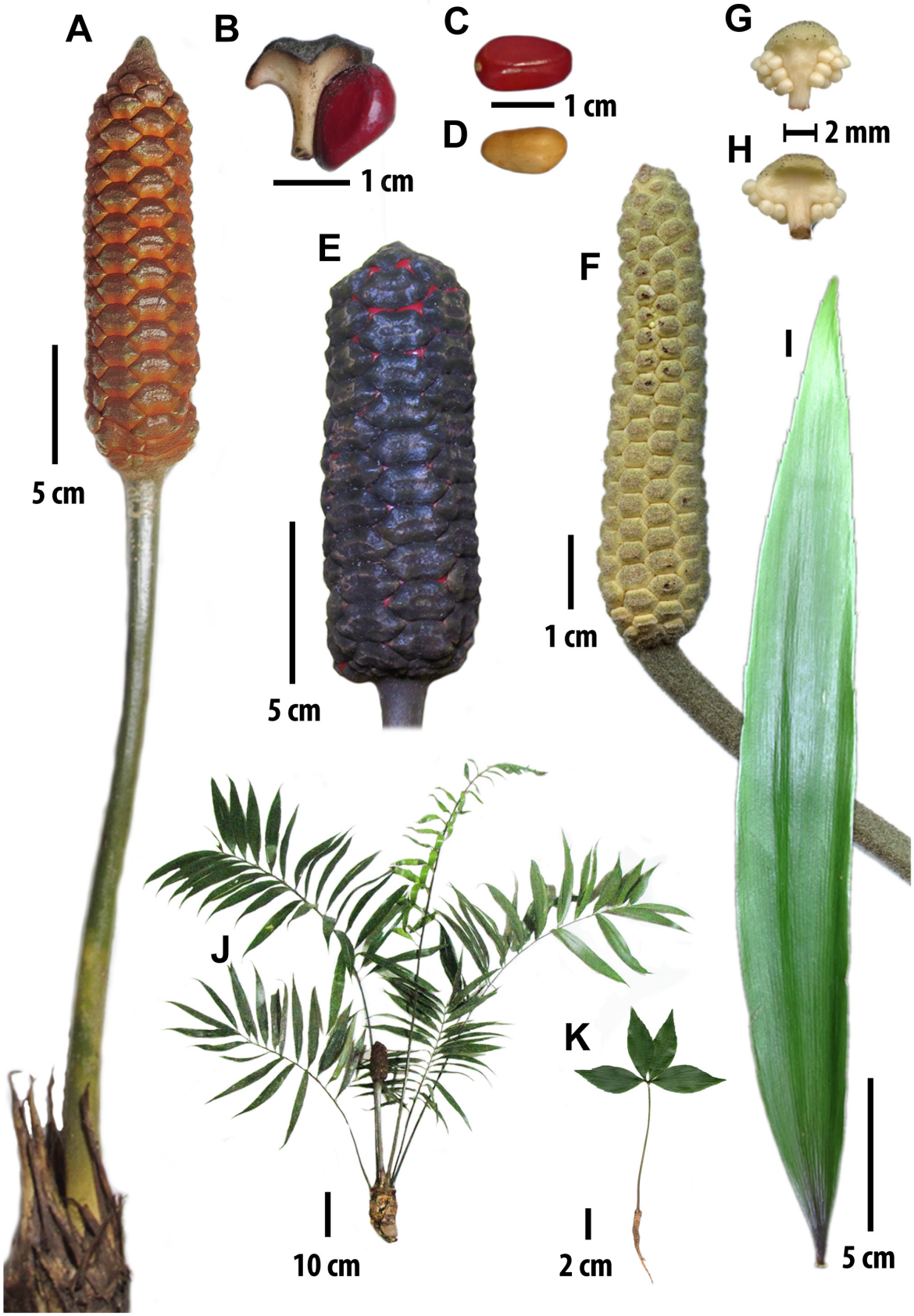

FIGURE 7. *Zamia muricata*. A. Immature ovulate strobilus showing characteristically long peduncle, B. Megasporophyll, abaxial side with mature seed, C. Mature seed with sarcotesta, D. Mature seed sclerotesta, E. Mature ovulate strobilus with ripe seeds, F. Immature pollen strobilus, G. Microsporophyll abaxial side, H. Microsporophyll adaxial side, I. Median leaflet, J. Adult plant with ovulate strobilus, K. Seedling with eophyll.

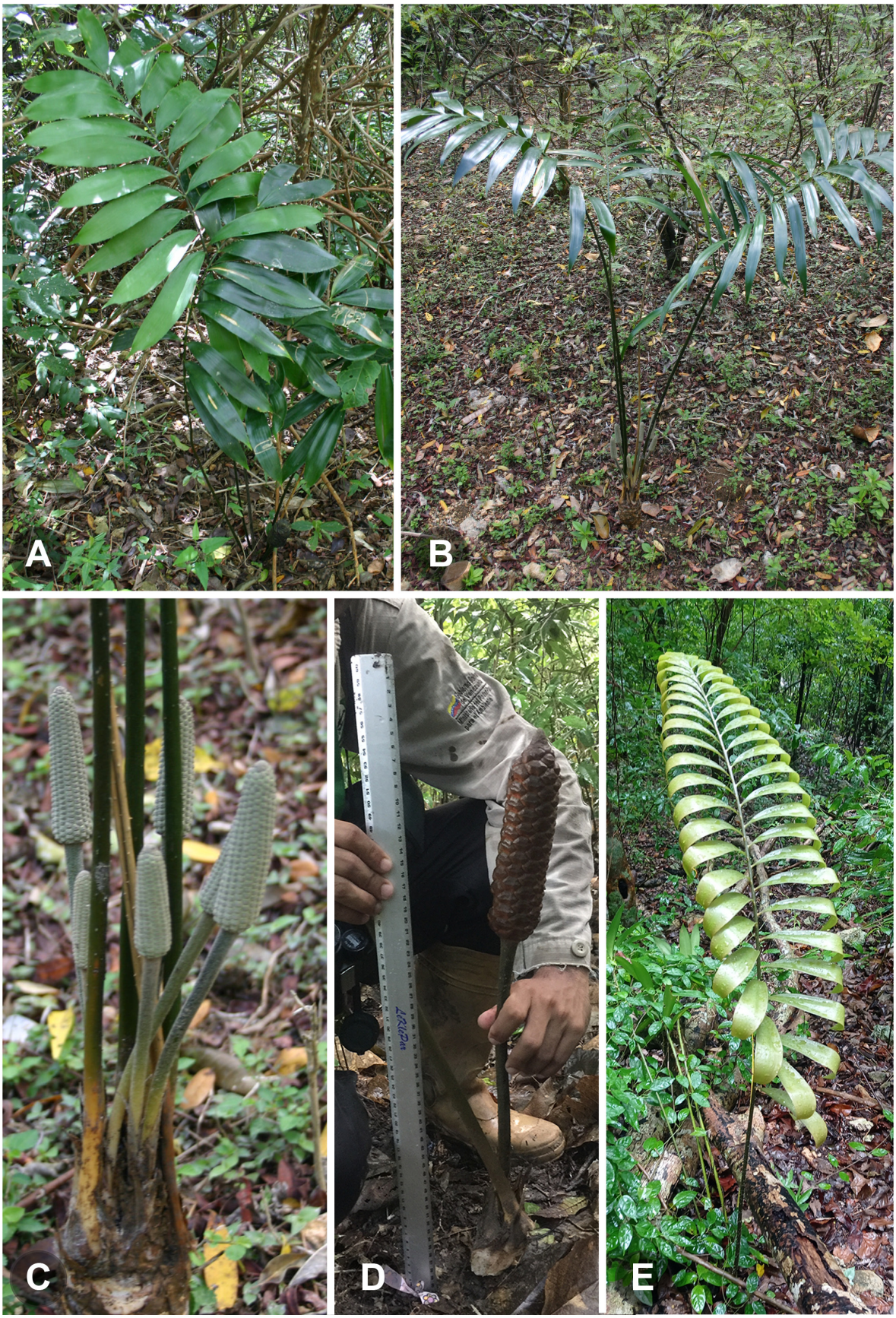

FIGURE 8. *Zamia muricata* in habitat in Venezuela. A. Adult plant in Puerto Cumarebo, Falcón. B. Mature plant in Puerto Cumarebo, Falcón. C. Pollen strobili in Puerto Cumarebo, Falcón. D. Ovulate strobilus with characteristic long peduncle, San Felipe, Yaracuy [*Niño et al. 6597* (PORT)]. E. New leaf in Chichirivichi, Falcón.

Specimens examined:—VENEZUELA**.** Aragua**:** 11 Dec 1921, *H.F. Pittier 9947* (US No. 1186989!, VEN No.

19249!); 150 m, 11 Apr 1937, *H.F. Pittier 13965* (F Nos. 895314! & 895326!, NY!, US No. 1740852!); Carabobo**:**14 Feb 1978, *G. Bunting & C. Bowles* 6149 (VEN No. 199373!); 220–650 m**,** 18 May 1991, *W.A. Díaz 357* (MO Nos. 6346569!, 6346570!, 6346571!); 350–400 m, 1 Jan 1999, *W. Meier & M. Speckmaier 4340* (VEN Nos. 304666!, 3046667!, 3046669!); 300–350 m, 16 Apr 2000, *W. Meier & N. Flauger 6882* (VEN No. 307192!); 830 m, *G. Morales s.n.* (L barcode L.3933349!); 200 m, 31 Dec 1917, *H.F. Pittier 7685* (US Nos. 987782!, 987783!, 987784!); 150 m, 8 Sep 1988, *D.W. Stevenson et al. 1141* (FLAS barcode 237699!, INPA 238335!, MG, MO No. 6242929 barcode MO-2322685!, NY 1197628!, PORT!, U barcode U.1044625!, UEFS); 100 m, 26 Mar 1966, *J.A. Steyermark & C. Steyermark 95146* (VEN!). Falcón**:** 23 Mar 1989, *A. González 1995* (VEN No. 370402!); 600–900 m, 22 Jun 1979, *R.L. Liesner et al. 7823* (MO No. 2776840 barcode MO-1916294!); 75 m, 2 Sep 1993, *M.A. Martín Ballesteros MB13* (MA No. 540991!); 45 m, 6 Oct 1993, *M.A. Martín Ballesteros MB180* (MA No. 541247!, VEN!); 195 m, 30 Oct 2021, *S.M. Niño & D. Canelón 6614* (PORT!); 195 m, 30 Oct 2021, *S.M. Niño & D. Canelón 6615* (PORT); 10 Sep 1923, *H.F. Pittier 11138* (US No. 1186151!, VEN No. 19251!); 5 Mar 1978, B. Stergios 1039 (PORT!); 10 m, 22 Jan 1966, *J.A. Steyermark & A. Braun 94489* (S No. 84082!, VEN No. 70041!); 10–100 m, 30 Aug 1974, *J.A. Steyermark & B.J. Manara 110435* (MO No. 2684141 barcode MO-1916296!); 10–25 m, 4 Sep 1974, *J.A. Steyermark & B.J. Manara 110702* (VEN No. 105229!); 200 m, 11 Feb 1977, *J.A. Steyermark & A. Gonzales 113651* (MO No. 2772884 barcode MO-1916295!); 300 m, 12 Feb 1977, *J.A. Steyermark & A. Gonzales 113724* (IAN No. 157820!, MO No. 2777033 barcode MO-1916292!); Lara**:** 30 Mar 1980, *N. Ramírez 335* (VEN No. 339799!, MO No. 5029621!); 820 m, 29 Jun 1985, *R. Rivero 972A* (PORT!); 27 Jan 1967, *R.F. Smith V879* (VEN!); Yaracuy**:** 200–450 m, 11 Jul 1973, *G. Agostini et al. 1749* (VEN No. 395129!) & *1760* (VEN No. 395130!); 100 m, 7 Feb 1959, *A.L. Bernardi 6931* (VEN No. 47720!); Jan 1947, *H. Brito 34* (VEN 98538!); 12 Apr 1946, *A. Burkart 16501* (VEN No. 98537!); 25 Jul 1985, *G. Colonello 944* (MO No. 5702959! barcode MO-1916291); 500–700 m, 6 Apr. 1980, *R.L. Liesner & A. González 10120* (MO Nos. 2777172! & 2777173!, VEN!); 360 m, 15 Oct 2021, *S.M. Niño & D. Canelón 6596* (PORT**!);** 270 m, 16 Oct 2021, *S.M. Niño, D. Canelón & M. Torres 6597* (PORT**!);** 254 m, 16 Oct 2021, *S.M. Niño, D. Canelón & M. Torres 6603* (PORT!);98 m, 29 Oct 2021, *S.M. Niño & D. Canelón 6612* (PORT!)**;** 116 m, 29 Oct 2021, *S.M. Niño & D. Canelón 6613* (PORT!); 150 m, 27 Nov 1971, *J.A. Steyermark & G. Bunting 105344* (COL 252799!, MO No. 2676495 barcode MO-1916297!); 50 m, 28 Feb 1981, *J.A. Steyermark et al. 124692* (VEN No. 167603!); 250–260 m, 12 Mar 1981, *J.A. Steyermark et al. 124895* (VEN Nos. 167601!, 167602!, 169211!,); 400 m, 12 Feb 1983, *B. Trujillo et al. 18244* (MO No. 6065634 barcode MO-2112795!, NY No. 990953!). COLOMBIA**.** La Guajira: 600–700 m, 14 Jan 2004, *J. Aguirre et al. 05* (COL No. 495118!); 24 May 2007, *B.H. Rey-C. et al. BHRC-434* (COL No. 527473 barcode COL000377140!); 1800 ft., 11–12 Apr 1964, *C. Saravia & M.E. de Saravia 3584* (COL Nos. 117582!, 117583!, US No. 2470668!); 650 m, 13 Aug 1975, *A. Sugden 62* (COL No. 169580!); 650 m, 8 Apr 1977, *A. Sugden 211* (COL No. 173548!, MO No. 2540725 barcode MO-1916290!); 650 m, 11 Apr 1977, *A. Sugden 238* (COL!, FHO No. 149418!, MO No. 2540724!).

Etymology:—Derived from the Latin word *muricatus*, meaning rough with short, hard points and referring to the prickles on the petiole.

Common names:—'Acesiva', 'Achichive' (Steyermark 1994).

Distribution, habitat, and climate:—*Zamia muricata* occurs in tropical very dry forests, tropical dry forests, and tropical moist forests (*sensu* Holdridge 1977) in the Lara-Falcón Formation and the Cordillera de la Costa Natural Regions of Venezuela at an elevational range of 10–900 m in the States of Aragua, Carabobo, Falcón, Lara, and Yaracuy. In Colombia, it occurs in cloud forests of the Serranía de Macuira in La Guajira at elevations of 550–700 m (Sugden, 1982). The annual mean temperature within the area of occupancy of *Z. muricata* ranges from 21.5–27.3° C and the annual precipitation is 550–1430 mm in Venezuela, and 400 mm at the Serranía de Macuira. The rainfall pattern within the area of occupancy in Venezuela is bimodal, with the highest peaks occurring in July (140 mm) and November (126 mm), and the driest month being March (27 mm). In the Serranía de Macuira, there is very little precipitation and plants get their water primarily from cloud interception. The rainiest month is October (109 mm) the driest month March (3 mm).

Ecology and phenology:—The vegetative and reproductive phenology of *Zamia muricata* remains poorly understood. In October 2021, we observed near-receptive and mature ovulate strobili as well as immature and dehiscent pollen strobili at two populations of *Z. muricata* in Yaracuy, Venezuela. Mature ovulate strobili are represented in specimens collected in January through March and in September through November. Immature pollen strobili have been collected in April and November, and dehiscent strobili in October.

Conservation status:—The species is currently classified as Near Threatened according to the IUCN Red List (Stevenson, 2010). It is relatively widespread and locally abundant at several locations in Venezuela, and present in several protected areas. Our Geocat analysis based on 39 georeferenced locations shows the species has an extent of occurrence of approximately 42,000 km^2 and an area of occupancy of 140 km^2.

Discussion

Collections of *Zamia* from the Serranía de Macuira in the Guajira Peninsula of Colombia were also included in Stevenson's (2001, 2004) concept of *Z. muricata*. The Serranía de Macuira is an isolated mountain range in the middle of the Guajira Desert, and the nearest populations of *Z. muricata* in Venezuela are 240 km distant and separated by the Gulf of Venezuela. Even so, the Serranía de Macuira populations are geographically closer to Venezuelan populations of *Z. muricata* than to Colombian populations of *Z. orinoquiensis*. Furthermore, although the pollen strobili of plants from Serranía de Macuira have not been collected or studied, the ovulate strobili most closely resemble those of Venezuelan *Z. muricata*, being narrower than those of *Z. orinoquiensis* and dark olive green in color. Therefore, we tentatively follow Stevenson's (2001, 2004) circumscription here, noting that the *Zamia* populations from Serranía de Macuira will require future field studies including the examination of fresh reproductive material to ascertain their taxonomic affinity with confidence.

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