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Two new species of *Zamia* (Zamiaceae, Cycadales) from the Magdalena-Urabá moist forests ecoregion of northern Colombia

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Abstract

We describe and illustrate *Zamia imbricata* and *Z. sinuensis*, two new species (Zamiaceae, Cycadales) from the Magdalena-Urabá moist forests ecoregion of northern Colombia. The new species appear to belong to the manicata clade, an assemblage of species strongly supported by recent molecular phylogenetic analyses and which shares a set of morphological characters such as hypogeous to semi-hypogeous stems, distinctly toothed leaflets, long peduncles, megasporophylls with relatively flat shields, and diminutive pollen cones containing microsporophylls with a much-reduced fertile section of the lamina. *Zamia imbricata,* a species from the Middle Magdalena Valley Basin of Caldas, is distinguished from other members of the clade by its planar leaves comprised of diminutive, highly imbricate papyraceous leaflets. *Zamia sinuensis*, a species from the Sinú River Basin of Córdoba is similar to *Z. manicata*, from which it is distinguished by the absence of the petiolule and gland-like collar that characterize the latter, and by its strongly undulate leaflets. The two new species are discussed within the context of the manicata clade, and a vegetative key to the clade is provided.

Keywords: manicata clade, *Zamia disodon, Zamia manicata, Zamia melanorrhachis, Zamia restrepoi*

Introduction

The manicata clade of the genus *Zamia* Linnaeus (1763: 1659) (Zamiaceae, Cycadales) is a group of four currently accepted species (Calonje *et al.* 2020) whose monophyly is strongly supported in recently published phylogenetic analyses (Calonje *et al.* 2019). Its constituent species—*Z. disodon* D.W.Stev. & Sabato in Stevenson (2001: 38), *Z. manicata* Linden ex Regel (1876: 310), *Z. melanorrhachis* Stevenson (2001: 55), and *Z. restrepoi* (Stevenson 1990: 170) Lindstrom (2009: 268)—have perhaps the most widely variable leaflet morphology of any closely related group within the Cycadales, as evidenced by the distinctly channeled petiolule with a gland-like collar of *Z. manicata*, the membranaceous and prominently veined broad leaflets of *Z. disodon*, and the unique midrib found in the leaflets of *Z. restrepoi* (Fig. 1). Due to the extremely variable leaflet morphology found in the manicata clade, the close relationship between these species is not readily apparent. However, species in the manicata clade do share a suite of morphological similarities that help distinguish them from the rest of the genus. These include hypogeous to semi-hypogeous stems, leaflets with strongly toothed margins, strobili with extremely long peduncles (typically > 20 cm) and relatively flat sporophyll shields, small seeds with an extremely thin sarcotesta, and diminutive pollen cones containing microsporophylls with a very narrow fertile section of lamina.

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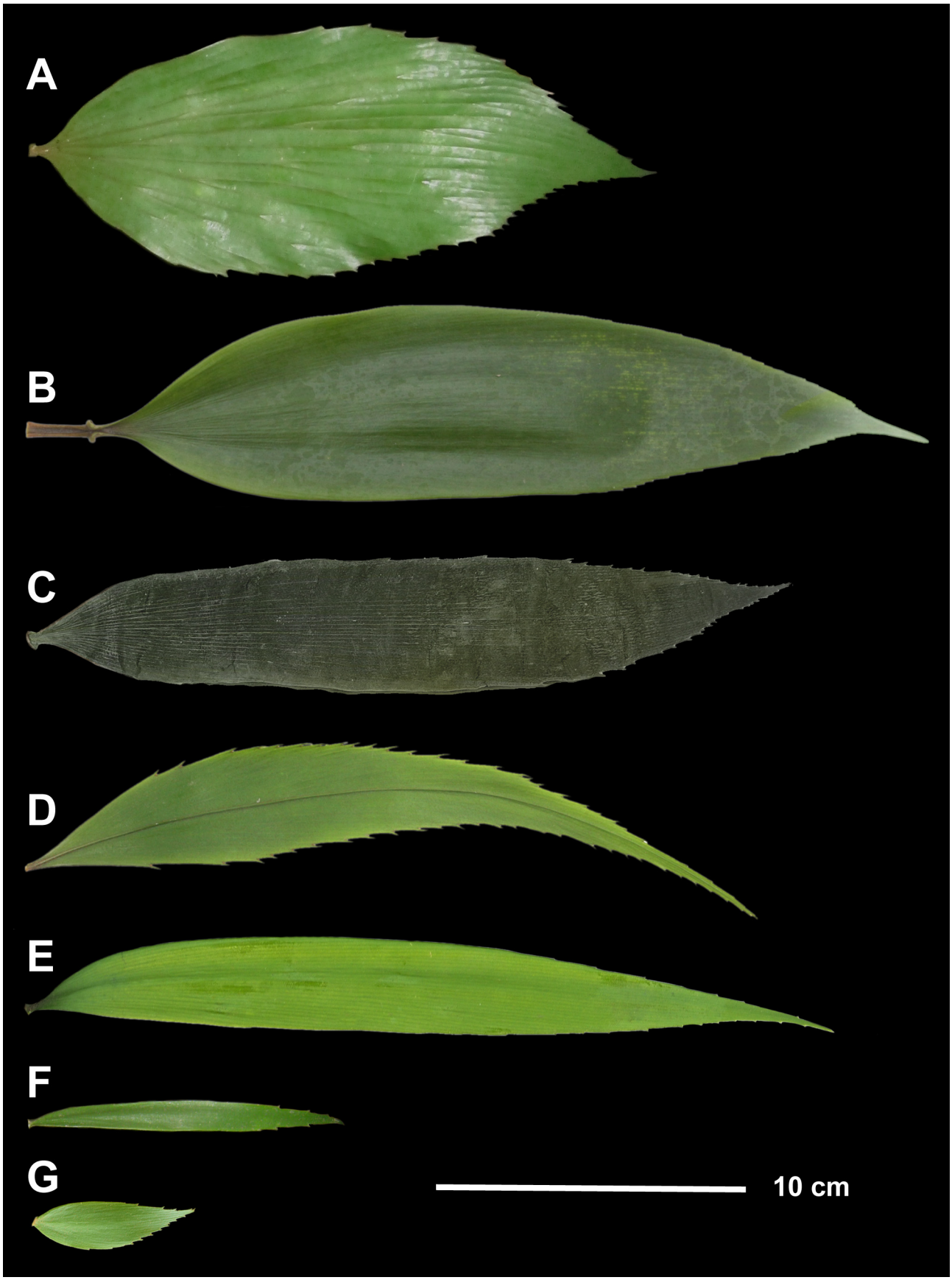

FIGURE 1. Leaflet morphology of members of the manicata clade. **A.** *Zamia disodon*: *Castro 508* (HUA). **B.** *Z. manicata*: cult. ex Antioquia. **C.** *Z. sinuensis: Castro et al. 1146* (HUA), **D.** *Z. restrepoi:* cult. ex Córdoba, **E.** *Z. melanorrhachis*: *Castro et al. 1581* (HUA), **F.** *Zamia* "Cogollo": *Tuberquia et al. 3251* (HUA), **G.** *Z. imbricata: Castro et al. 1601* (HUA).

Except for *Zamia manicata*, which is primarily distributed in the Chocó-Darién moist forests ecoregion of Colombia and adjacent Panama, the manicata clade occurs mostly within the Magdalena-Urabá moist forests ecoregion (MUMFE) of northern Colombia (Fig. 2; Olson *et al*. 2001). This region, including the lower course of the Magdalena River and extending west over the coastal plain to the Gulf of Urabá, has a high degree of endemism and species diversity and serves as a bridge between the northern ecoregions of Mesoamerica and the Chocó and the Andean and Amazonian ecoregion (Constantino 2020). Although incredibly biodiverse, the region has nevertheless remained biologically underexplored in recent decades due to the violence and social unrest that have plagued it for over half a century (Romero-Medina 1994). Recent exploration in the MUMFE has revealed the presence of three taxa that appear to belong to the manicata clade but do not appear to match any of the currently described species. Here we describe and illustrate two of these species, and discuss them within the broader context of the manicata clade.

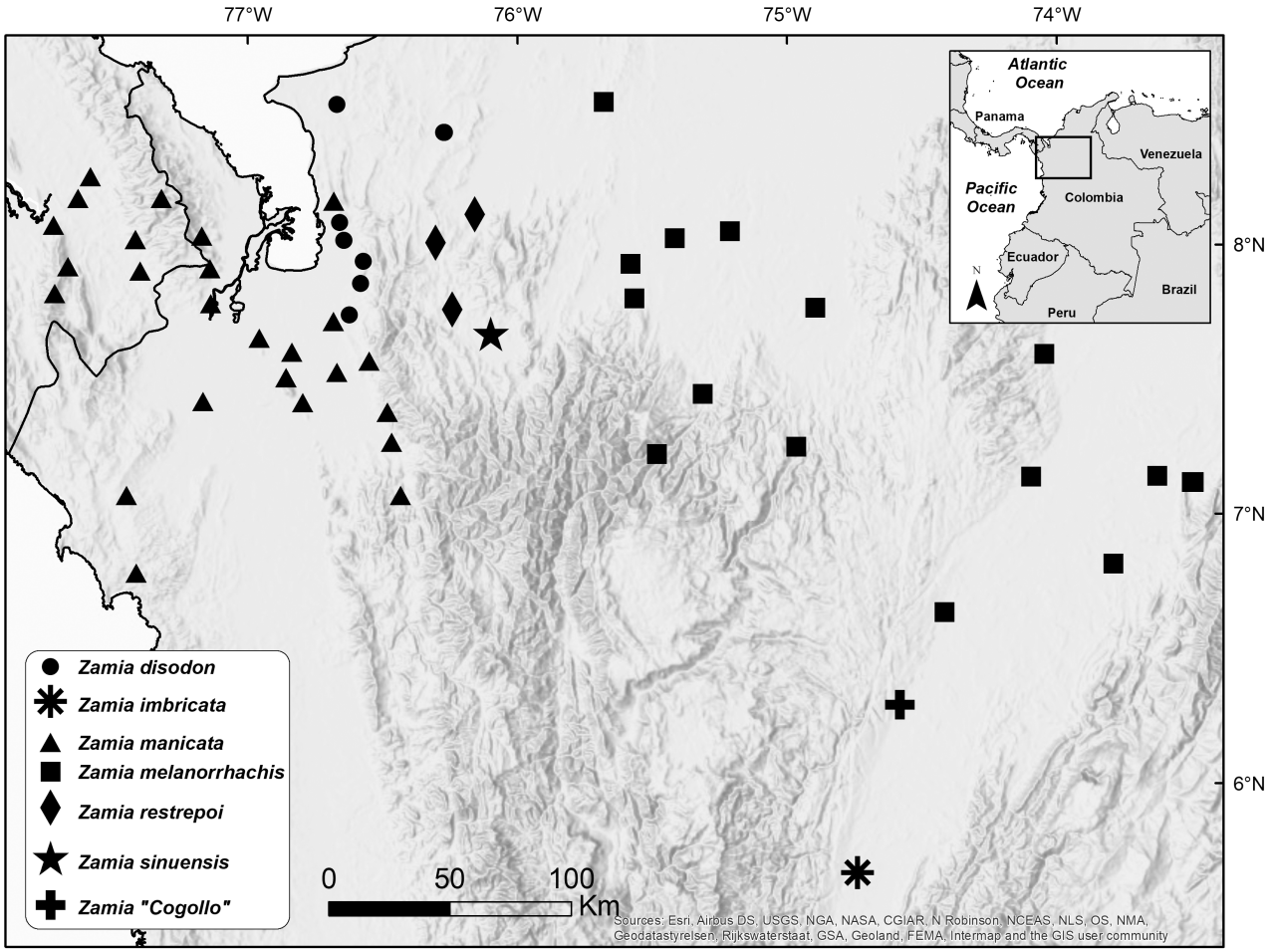

FIGURE 2. Distribution of manicata clade in northern Colombia and adjacent Panama.

Materials and Methods

We conducted field research focused on documenting the two potential new species in the municipalities of Tierralta, Córdoba, in October 2017, and La Dorada, Caldas, in February 2020.

Both taxa are only known to occur at a single locality and appear to be locally rare, with only fifteen individual plants located in La Dorada, and five in Tierralta. As part of ongoing ecological and taxonomic research conducted by the Colombian Cycad Society in furtherance of the goals of the Conservation Action Plan of Colombian Cycads (López-Gallego 2015), populations of the other species in the manicata clade were also studied and documented in recent years. This included visits to populations of the following species within the respective municipalities: *Zamia disodon* (Necoclí and San Pedro de Urabá, Antioquia), *Z. manicata* (Chigorodó, Antioquia), *Z. melanorrhachis* (Barracanbermeja and Betulia, Santander; Montelíbano, Córdoba), and *Z. restrepoi* (Tierralta, Córdoba). Fieldwork also included visits to the single known population of another undescribed species in the Municipality of Puerto Berrío,

Antioquia. This species, currently in the process of being described by another team of researchers, was referred to in the Red List of Colombian Plants (Cogollo & Idárraga 2005) as *Zamia* sp. (Cogollo 11843), the parenthetical referencing the collector and collection number of the first known collection of this species. We discuss this species here for comparative purposes and refer to it in the text as *Zamia* "Cogollo". Fieldwork at the surveyed localities included the collection of herbarium specimens, morphometric data and photographs. We evaluated quantitative and qualitative morphological characters obtained during our fieldwork as well as from specimens and specimen photographs comprising approximately 130 collections of the manicata clade from the following herbaria: COL, FAUC, FMB, FTG, GH, HUA, JAUM, L, MEDEL, MO, NY, P, PMA, SCZ, TOLI and US (acronyms according to Thiers 2021 onwards). Herbarium specimen data and field observations were recorded in BRAHMS database (Version 7.9.14; Filer, 2019), and mapped and analyzed in ArcGIS (Version 10.5.1; ESRI, 2018). Georeferenced locations were used to estimate the area of occupancy (AOO) and extent of occurrence (EOO) to prepare IUCN Red List assessment recommendations for both new species.

Specific locality information associated with 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. A list of specimens examined is provided in the protologues of the two newly published names, and in Appendix I for the remaining species of the manicata clade.

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).

Results

Our review of qualitative and quantitative morphological characters of members of the manicata clade revealed that the plants from the municipalities of Tierralta, Córdoba, and La Dorada, Caldas, correspond to new taxa that can be readily distinguished from the other species in the clade based on multiple qualitative morphological characters. These are outlined in comparative tables (Tables 1 & 2), discussed in the 'morphological and taxonomic affinities' section for each species, and utilized to produce a vegetative diagnostic key to the manicata clade which we provide following species protologues.

TABLE 1. Comparison of diagnostic qualitative morphological characters distinguishing *Zamia imbricata* and *Zamia* "Cogollo"

Characters	*Zamia imbricata*	*Z*amia "Cogollo"
Leaflet shape	Lanceolate (length-to-width ratio < 7:1)	Linear-lanceolate (length-to-width ratio > 7:1)
Leaflet separation	Strongly imbricate	Separate
Leaflet disposition	Leaflets flat and arranged mostly in a single plane, making the upper leaf zone appear planar	Leaflets slightly deflexed, not held in a single plane
Presence of adaxially raised longitudinal crease on leaflet	Absent	Present
Petiole and rachis angle	Rachis abruptly curved away from petiole, held at near horizontal disposition on older leaves	Leaf slightly spreading outwards with petiole and rachis at continuous angle
Ovulate strobilus apex length	Short (< 1 cm)	Elongate (> 1 cm)

TABLE 2. Comparison of diagnostic qualitative morphological characters distinguishing *Zamia manicata* and *Z. sinuensis*

Characters	*Zamia manicata*	*Zamia sinuensis*
Petiolule and gland-like collar at base of leaflet	Present	Absent
Leaflet undulation	Flat to slightly undulate	Strongly undulate
Leaflet base concavity	Strongly concave adaxially due to constriction of gland-like color at leaflet base	Planar
Leaflet base color	Petiolule, collar, and leaflet base reddish-purple and distinctly different from the rest of leaflet	Green and indistinct from rest of leaflet
Pollen cone color	Dark reddish brown	Cream colored with reddish-brown speckled tomentum

Taxonomic Treatment

Zamia imbricata Calonje & J.Castro *sp. nov.* (Figs. 3A–E, 4A–J, 5A–G)

Diagnosis:—Distinguished within the genus by its subterranean stem, its petioles which are typically unarmed or rarely armed with minute scattered prickles, its rachis which is straight and horizontally disposed bearing highly imbricate leaflets held in a planar disposition, its leaflets which are lanceolate, papyraceous, and diminutive (3.9–11.6 × 1.2–1.9 cm) with strongly toothed margins, and its strobili which are held on extremely long peduncles (20+ cm) and which bear relatively flat and unornamented sporophylls.

Type:—COLOMBIA. Caldas: La Dorada, 244 m, 17 Feb 2020, *J. Castro, M. Calonje, L.F. Coca & D. Jaramillo 1601* (holotype HUA!, isotype FAUC!).

Additional specimens examined (paratypes):—COLOMBIA. Caldas: La Dorada: 200–245 m, 17 Feb 2020, *J. Castro, M. Calonje, L.F. Coca & D. Jaramillo 1594* (FMB!), *1595* (COL!), *1602* (HUA!), 9 Mar 2019, *L.F. Coca & D. Jaramillo 13012* (FAUC!), 17 Dec 2018, *S.H. Gómez et al. SHG 3628* (HUA!), 21 Dic 2018, *D. Sanín et al. 7251* (FAUC!, CUVC!).

Description:—*Stem* hypogeous, typically solitary, cylindrical, 10–30 × 1–15 cm. *Cataphylls* caducous, chartaceous, triangular to narrowly triangular, 3.2–5.2 cm long and 1.0–2.3 cm wide at the base, tan tomentose with cream-colored base, losing tomentum and base turning brown at maturity. *Leaves* 1–5 per apex, 13–200 cm long (58+ cm on adults), 10–19 cm wide, covered with white to beige tomentum at emergence and becoming glabrous at maturity, petiole erect to slightly spreading to 45° from the stem apex, rachis relatively straight and horizontally disposed in older leaves. *Petiole* 14–141 cm long (34+ cm on adults), ochre to olive green, typically unarmed but rarely with a few translucent scattered minute prickles 0.5–0.8 mm long, abruptly swollen base to 15 mm wide. *Rachis* 20–73 cm long (24+ cm on adults), ochre to olive green, unarmed. *Leaflets* 6–110 (40+ on adults), suboppositely to subalternately arranged, strongly imbricate, succubously or incubously arranged and forming a mostly planar leaf surface, with a pinna-to-pinna angle (pp-angle *sensu* Grobbelaar 2002: 23) of approximately 180° throughout most of the leaf except for the basalmost pair which have a pp-angle of approximately 120°, articulate insertion on rachis 3.6–4.8 mm wide, spaced 1.2–1.4 cm at leaf center, membranaceous, lanceolate, acute distally, symmetrical to slightly falcate, discolorous, dark green and dull to semi-glossy adaxially, light green and dull abaxially with 13–18 veins visible, margins revolute and bearing 5–25 marginal teeth 1.0–2.5 mm long restricted to distal half, basal leaflets 4.0–8.7 cm × 1.2–1.9 cm, middle leaflets 4.9–11.6 × 1.5–1.8 cm, apical leaflets 3.9–6.3 cm × 1.2–1.7 cm. *Eophylls* to 16.2 cm long, petiole 14.0 cm, rachis 2.2 cm, carrying 6 leaflets 45–48 × 13.4–14.4 mm. *Pollen strobili* 1–2, light reddish-brown, conical-cylindrical, at pollen shedding 2.8–3.0 × 0.7–0.8 cm, sterile apex obtuse and 2.0–2.2 mm long, strobilar axis glabrous, peduncle olive brown and lightly covered with villous white tomentum, 20–25 × 0.30–0.35 cm. *Microsporophylls* spirally arranged in 6 orthostichies of 9–11 sporophylls each, obtrullate, 6.0–6.2 × 6.2–6.5 mm at pollen shedding, distal shield rounded and encompassing 30–50 % of microsporophyll length, hexagonal, external face light orange-brown tomentose, 3.0–4.0 mm tall × 3.0–4.2 mm wide, abaxial surface of microsporophyll with 9–11 microsporangia aggregated into a single group along margins and extending beyond surface of lamina, adaxial surface glabrous and lacking microsporangia. *Ovulate strobili* 5.2–8.8 × 2.8–4.0 cm, solitary, reddish-brown to brown, cylindrical with short acute apex 20–40 mm long. Strobilar axes and megasporophyll pedicels glabrous on mature strobili, peduncle 25.0–31.5 × 0.60 to 0.75 cm, olive green with short white tomentum at maturity. *Megasporophylls* spirally arranged in 4 to 5 orthostichies of 5 to 6 sporophylls each, pedicel 8–10 mm long, sterile shield flat (not extruded), 5–6 mm thick with oblong-hexagonal distal face 9–13 mm tall and 18–22 mm wide and terminal face shallowly depressed. *Seeds* ovoid, at maturity 13.0–13.6 × 9.2–9.6 mm with orange-red sarcotesta 0.4–1.1 mm thick, sclerotesta 12.2–12.3 × 7.7–7.9 mm.

Etymology :—From the Latin ‘imbricatus’ meaning ‘covered with tiles’, referring to the strongly overlapping leaflets.

Distribution, habitat and climate:—The species occurs on steep slopes in tropical moist forest at an elevational range of 200–245 m. The soils are sandy and well drained, with abundant organic material and leaf litter. The pH in the region is acid (4.5–5.0) and the soils are high in aluminum, iron, and manganese, and low in phosphorus, calcium, potassium, and sodium (Ramírez Guapacha & Bohórquez Osorio 2013). The canopy ranges from 9–35 m with a partially open understory with moderate solar exposure. The most species-rich plant families in the region are Rubiaceae, Fabaceae, Araceae, Piperaceae, and Melastomataceae (Ramírez Guapacha & Bohórquez Osorio 2013).

The climate within the area of occupancy of *Zamia imbricata* is classified as tropical rainforest (Af) by the Koppen-Geiger classification system (Geiger 1954, Köppen 1918, Kottek *et al*. 2006). The tropical rainforest climate is hot, humid, and wet, with no pronounced dry season. The annual mean temperature within the area of occupancy is

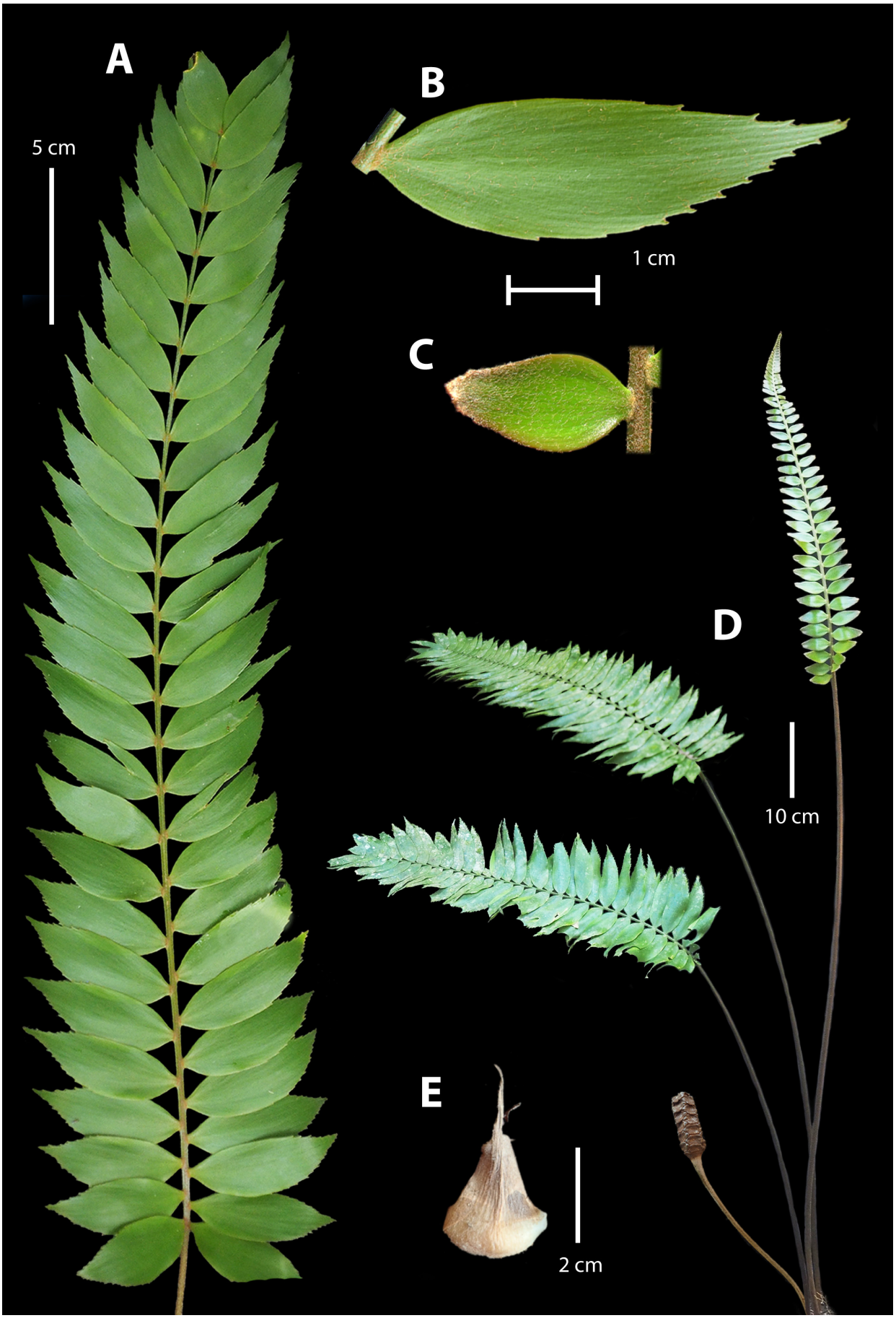

FIGURE 3. Vegetative characteristics of *Zamia imbricata*. **A.** Leaf. **B.** Median leaflet, adaxial side. **C.** Immature, expanding leaflet **D.** Adult plant with ovulate strobilus. **E.** Cataphyll. Photographs from type locality, illustration by Michael Calonje.

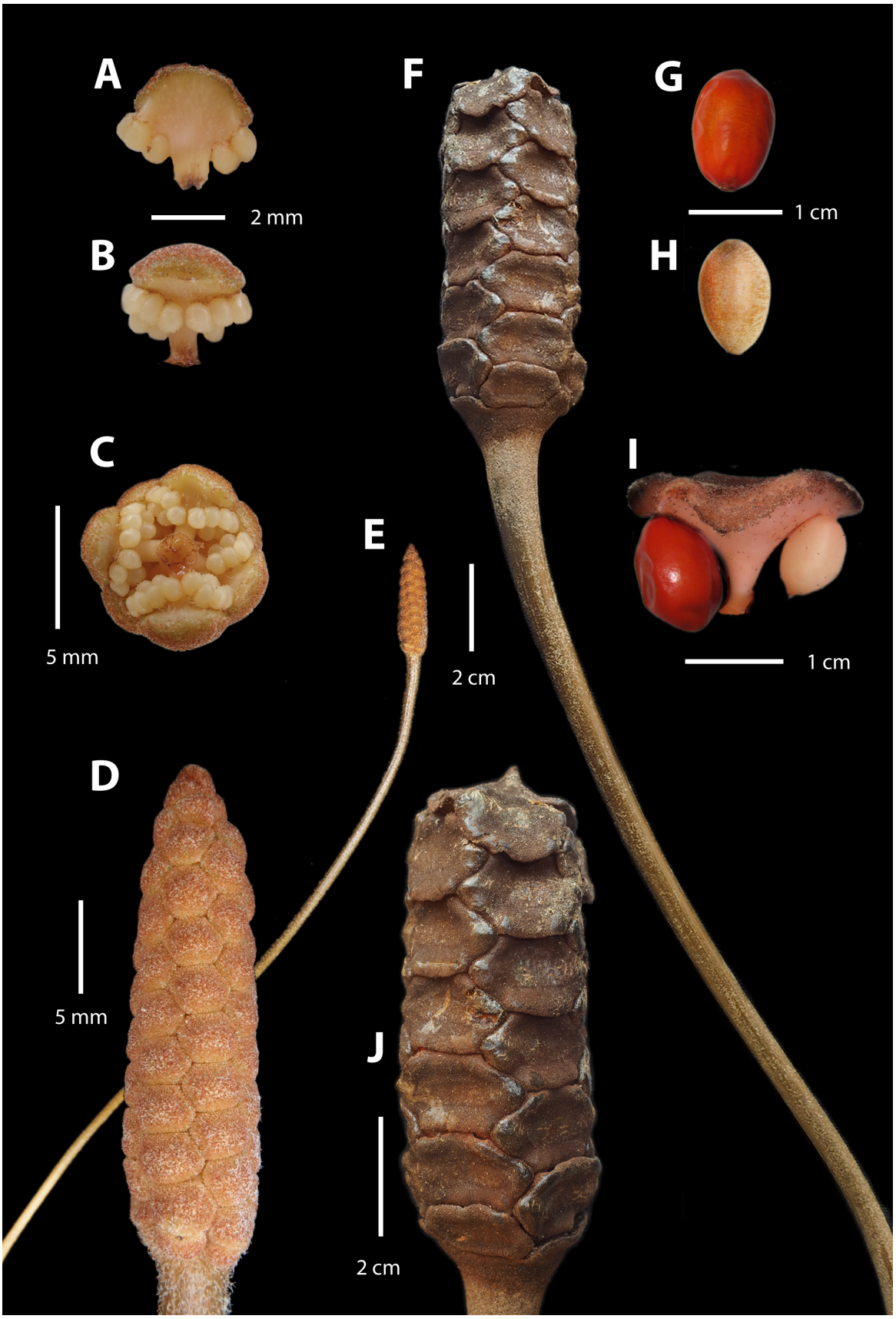

FIGURE 4. Reproductive characteristics of *Zamia imbricata*. **A.** Microsporophyll adaxial side. **B.** Microsporophyll abaxial side. **C.** Pollen strobilus cross-section, abaxial side. **D.** Pollen strobilus near pollen dehiscence. **E.** Pollen strobilus with characteristically long peduncle. **F.** Ovulate strobilus, near maturity. **G.** Mature seed with ripe sarcotesta. H. Mature seed sclerotesta. **I.** Megasporophyll with mature seed and unpollinated ovule, abaxial side. **J.** Ovulate strobilus with peduncle, near maturity. Photographs from type locality, illustration by Michael Calonje.

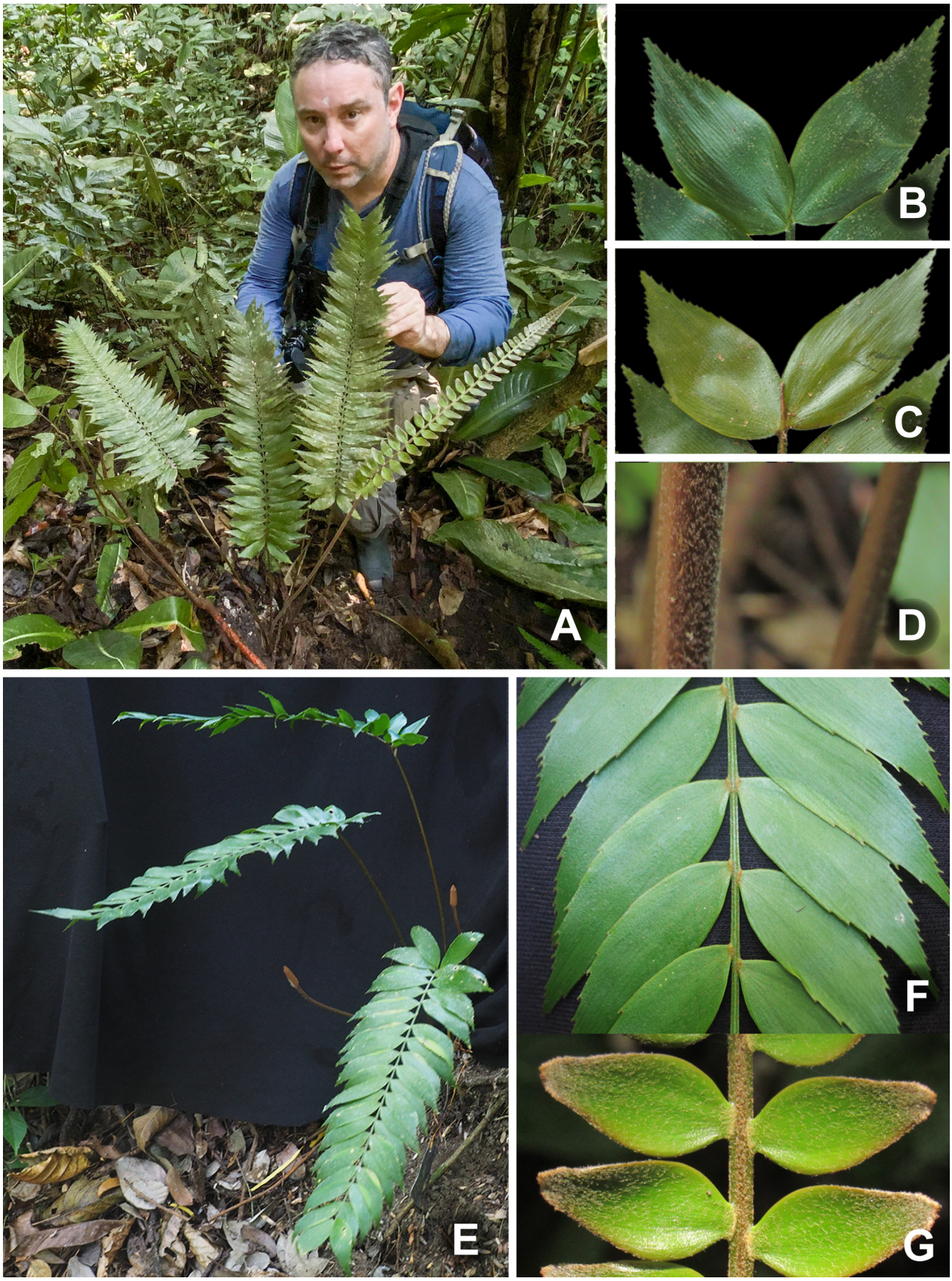

FIGURE 5. *Zamia imbricata* in habitat. **A.** Adult plant, with Michael Calonje. **B.** Distal leaflets, adaxial side. **C.** Distal leaflets, abaxial side. **D.** Close-up of unarmed petioles. The petiole on the left is newly emergent and still covered with tomentum. **E.** Adult microsporangiate plant, showing horizontal disposition of rachis and leaflets. **F.** Median leaflets showing imbrication with alternate succubous and incubous orientation. **G.** Immature leaflets in the process of expanding. Photographs A–C by Jonatan Castro, D–G by Michael Calonje.

27° C and the annual precipitation 2500 mm. The rainfall pattern is bimodal, with peaks in rainfall ocurring in April and October, and troughs ocurring in January and July. The driest month is January, with 50 mm of rain and the wettest month is October, with 314 mm.

Ecology:—The species occurs in sympatry with *Zamia incognita*, but no evidence of hybridization was detected, as all individuals observed of both species were morphologically consistent with no intermediate forms observed. While the pollination of *Zamia incognita* has been studied in great detail and its pollinators have been identified as beetles belonging to the genus *Pharaxonotha* Reitter (Valencia-Montoya *et al.* 2017), the pollinating agent of *Z. imbricata* has not been determined and it is unclear whether differences in pollinating agents could be one of the reasons for the apparent lack of hybridization between the two species. Other possible reasons include sexual incompatibility between the two species since *Z. incognita* does not belong in the manicata clade (Calonje *et al*. 2017), or differences in their reproductive phenology. Unfortunately, the phenology for *Z. imbricata* remains largely unknown and will require additional field studies to better understand. Pollen cones approximately 1 to 2 weeks from pollen release were observed in mid-February of 2020 as well as near mature, mostly unpollinated ovulate cones. A single full-sized seed with a fully formed sclerotesta and a light pink sarcotesta was found in an ovulate cone and fully matured in the excised cone two months later. Other biological interactions involving *Z. imbricata* also remain unrevealed. A few leaves were observed with damage consistent with herbivory, but no insects were observed feeding on the leaves.

Conservation:—The species is known from a single location within a forest fragment of approximately 1 km^2 in La Dorada municipality of Caldas. Despite occurring in a healthy forest fragment, the plant was very rare at the surveyed location, with only 15 plants observed after four days of vigorous searching, and no live seedlings observed, only the remains of a single recently deceased seedling. Seed set was extremely poor, with only a single pollinated ovule observed in two separate seed cones. The above suggests that there are too few and/or too widely separated individuals to sustain a healthy population, and that no seedling recruitment is occurring at its only known location. Based on the above, we recommend this species be listed as Critically Endangered (CR) based on IUCN Red List criteria B1ab(iii,v)+2ab(iii,v); C2a(i,ii); D (IUCN Standards and Petitions Sub-committee, 2017).

Morphological and taxonomic affinities:—*Z. imbricata* appears most closely related to the currently undescribed species of *Zamia* "Cogollo" (Fig. 6). The two species are the southernmost species of the manicata clade and occur in the Magdalena River valley along the eastern foothills of the Cordillera Central, approximately 75 km distant from each other (Fig. 2). Both have small membranaceous leaflets and petioles that are unarmed or rarely with minute scattered prickles, but the species can readily be distinguished based on qualitative characters (Table 1). The leaflets of *Z. imbricata* are lanceolate (length-to-width ratio < 7:1), imbricate, and flatter than those of *Zamia.* "Cogollo" which are linear-lanceolate (length-to-width ratio > 7:1), not imbricate, and with a distinct adaxially raised longitudinal crease. Furthermore, *Z. imbricata* generally attains smaller dimensions with shorter leaf length (to 2.0 m vs. 2.5 m) and shorter leaflet length (to 10 cm vs. 25 cm). Lastly, the sterile cone apex in ovulate strobili of *Z. imbricata* are shorter, typically less than 1 cm long vs. those of *Zamia* "Cogollo" which typically exceed 1.5 cm. The short, broad, membranaceous leaflets of *Z. imbricata* somewhat resemble those of the Mexican species *Z. vazquezii* D.W.Stev., Sabato & De Luca in Stevenson *et al*. (1998: 14). However, the leaflets of *Z. vazquezii* are not held in a planar disposition as they are in *Z. imbricata*, the peduncles are much shorter (< 10 cm vs. > 15 cm), and the microsporophylls bear more numerous microsporangia (18–22 vs. 9–11).

Zamia sinuensis Calonje & J.Castro *sp. nov*. (Figs. 7A–G, 8A–I, 9A–F)

Diagnosis:—The species is similar to *Zamia manicata* from which it is distinguished in having leaflets that are strongly undulate and lacking a distinct petiolule and gland-like collar at the junction of the lamina and the petiolule.

Type:—COLOMBIA. Córdoba: Municipio de Tierralta, Parque Nacional Natural Paramillo: 187 m, 3 Oct. 2017, *J. Castro, D. Taborda & P. Hernández 1146* (holotype HUA!).

Additional specimens examined (paratypes):—COLOMBIA. Córdoba: Municipio de Tierralta, Parque Nacional Paramillo: 180 m, 3 Oct. 2017, *J. Castro, D. Taborda, P. Hernández 1147* (HUA!).

Description:—*Stem* hypogeous or semihypogeous, tuberous, solitary or clumping with up to three apices, cylindrical, 10–30 × 5–20 cm. *Cataphylls* chartaceous, triangular to narrowly triangular, pale tomentum covering from the base, pale brown-colored, losing tomentum and turning dry and brown at maturity, 5.3–14.5 cm long and 2.0–5.0 cm wide at the base. *Leaves* 3–6 per apex, erect to slightly spreading, 1.8–3.1 m long, 24.1–52.4 cm wide. *Petiole* 20–175 cm long and 0.7–1.0 cm thick at the middle, entire length strongly to moderately armed with prickles 0.4–3.6 mm long, abruptly swollen base 2–3 cm thick. *Rachis* 20–135 cm long, lightly armed with prickles in the proximal third. *Leaflets*

FIGURE 6. *Zamia* "Cogollo" in habitat. **A.** Large plant with Arturo Aristizábal holding two leaves. **B.** Leaf. **C.** Median leaflets showing adaxially raised longitudinal crease. **D.** Immature ovulate strobilus showing elongated sterile apex. Photographs by Arturo Aristizábal.

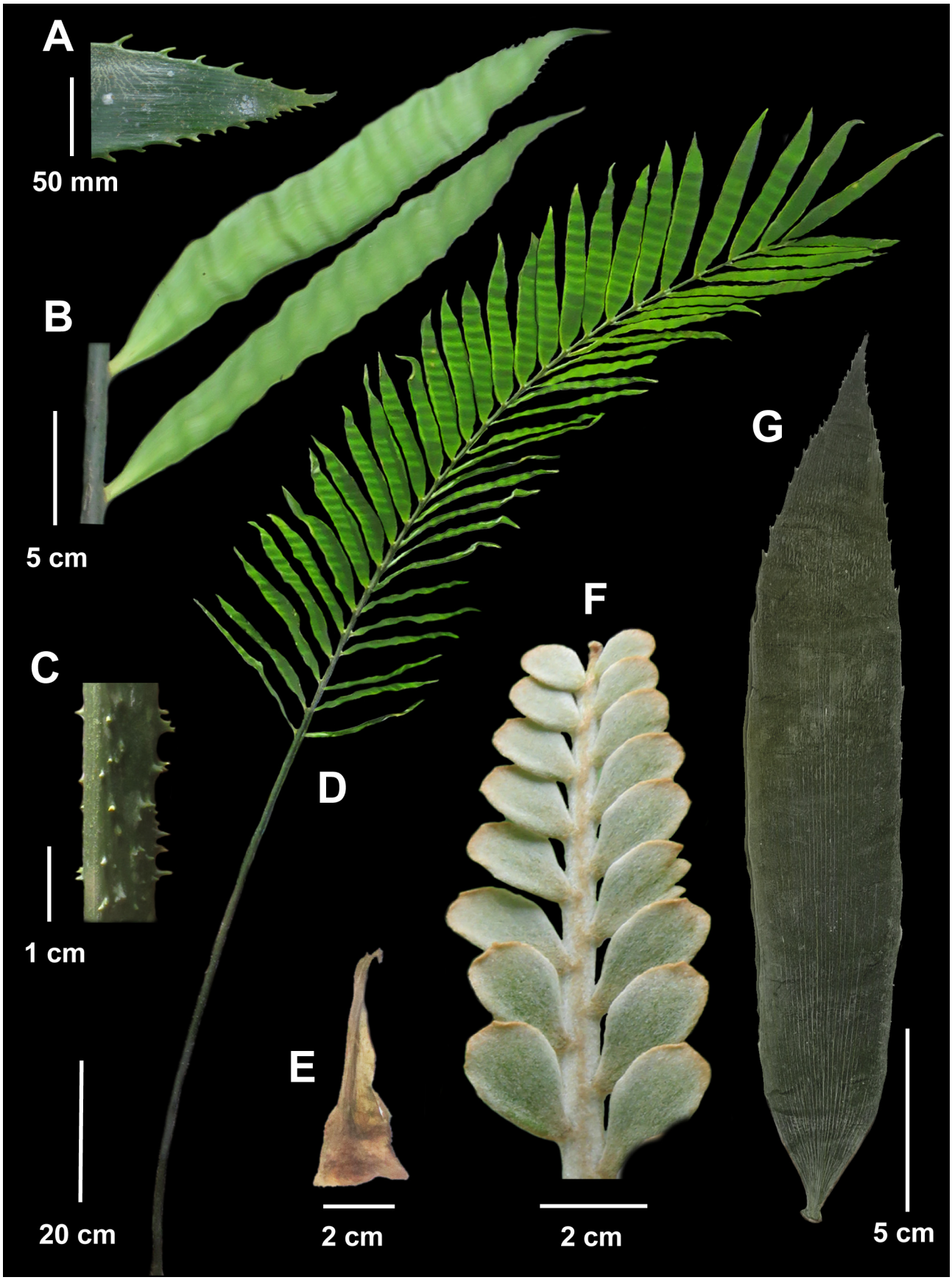

FIGURE 7. Vegetative characteristics of *Zamia sinuensis*. **A.** Leaflet tip showing dentation. **B.** Median leaflets illustrating strong undulation, abaxial side. **C.** Median section of petiole armed with prickles. **D.** Leaf, abaxial side. **E.** Cataphyll. **F.** Apex of new leaf in the process of expansion showing white tomentum. **G.** Median leaflet (dry). Photographs taken at type locality by Jonatan Castro, illustration by Michael Calonje.

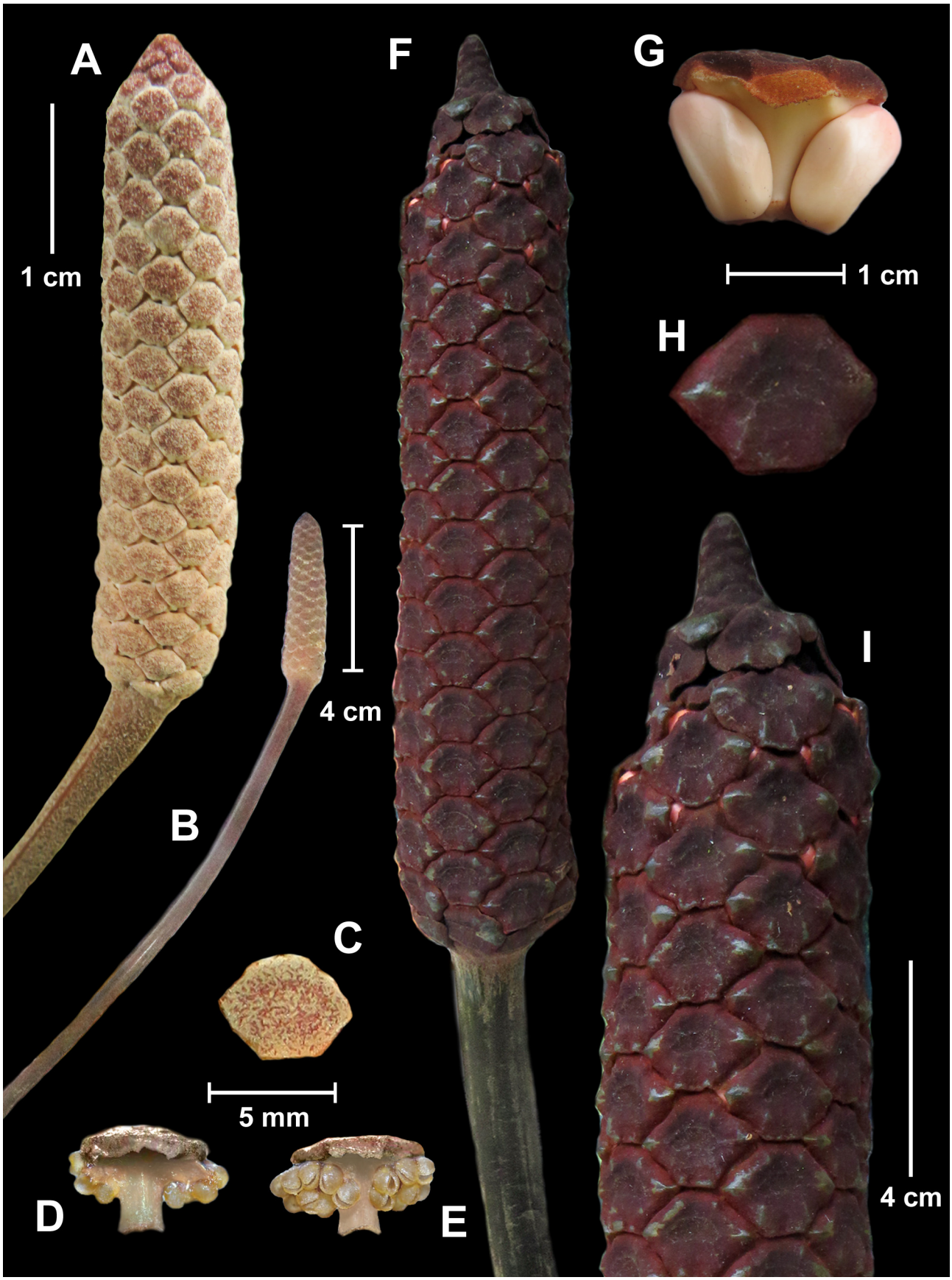

FIGURE 8. Reproductive characteristics of *Zamia sinuensis*. **A.** Pollen strobilus near pollen dehiscence. **B.** Pollen strobilus with peduncle. **C.** Microsporophyll shield. **D.** Microsporophyll adaxial side. **E.** Microsporophyll abaxial side. **F.** Ovulate strobilus, fully developed but slightly immature. **G.** Megasporophyll, abaxial side. **H.** Megasporophyll shield. **I.** Close-up of distal half of ovulate strobilus. Photographs taken at type locality by Jonatan Castro, illustration by Michael Calonje.

FIGURE 9. *Zamia sinuensis* in habitat. **A.** Large megasporangiate plant with three apices and three ovulate strobili, with David Taborda for scale. **B.** Immature and near-mature ovulate strobili. **C.** Close-up of stem and petiole bases. **D.** Microsporangiate plant. **E.** Leaf apex displaying strongly undulate leaflets. **F.** Pollen strobilus near dehiscence stage. All photographs taken at type locality. Photograph E by David Taborda, all others by Jonatan Castro.

11–54, subopposite to subalternately arranged, spaced 3.0–3.5 cm apart at leaf center, articulate insertion on rachis 4.3–6.9 mm wide, chartaceous to subcoriaceous, strongly discolorous, adaxially dark green and lustrous, abaxially light green and dull, new leaflets emerging densely white tomentose, gradually becoming glabrous, lanceolate, symmetrical to slightly falcate, strongly undulate longitudinally, margins revolute and bearing 32–39 marginal teeth 0.6–2.3 mm long restricted to distal half, basal leaflets 24.5–26.2 × 4.2–4.5 cm, middle leaflets 23.5–25.8 × 3.7–3.9 cm, apical leaflets 17.9–21.6 × 3.1–3.5 cm. *Pollen strobili* 1–5 per crown, at pollen shedding 4.9–5.1 × 1.0–1.2 cm, peduncle 23–24 cm long, 0.38–0.40 cm diameter at base, strobilar axis and inner surfaces of microsporophylls glabrous. *Microsporophylls* spirally arranged in 15 orthostichies of 12–13 fertile sporophylls each, 5.0–5.6 × 5.3–5.4 mm, distal shield encompassing 1/4 to 1/3 of sporophyll length, external face hexagonal relatively flat with rounded edges, cream colored with reddish-brown speckled tomentum, abaxial surface with 14–16 microsporangia aggregated into two separate groups along margins and extending beyond surface of lamina, adaxial surface glabrous and lacking microsporangia. *Ovulate strobili* typically one per stem apex, 27.5 × 5.0 cm, reddish-brown, cylindrical with elongated sterile apex 170 mm long. Strobilar axes and megasporophyll pedicels glabrous on mature strobili, peduncle 40.0 × 1.5–2.1 cm, dark olive green with fine tan tomentum. *Megasporophylls* spirally arranged in 8 orthostichies of 13–14 sporophylls each, pedicel 11–14 mm long, sterile shield flat (not extruded), 3–5 mm thick with oblong-hexagonal distal face 15–17 mm tall and 23–24 mm wide and terminal face shallowly depressed. *Seeds* ovoid to ovoid-pyramidal, at maturity 13.0–14.0 × 7.5–8.5 mm with sarcotesta 1 mm thick, sclerotesta 11.0–12.0 × 6.5–7.5 mm.

Etymology :—The epithet refers to the Sinú River basin in which this species occurs.

Distribution, habitat and climate:—*Zamia sinuensis* is only known from two simultaneous collections within the same population occurring 3 km distant from each other in disturbed tropical moist forest in the Sinú River basin. The known elevational range is 180–187 m. The climate within the area of occupancy of *Z. sinuensis* is classified as tropical monsoon (Am) by the Koppen-Geiger classification system (Geiger, 1954; Köppen, 1918; Kottek *et al.*, 2006). It is characterized by having monthly mean temperatures above 18 °C and a distinct dry season. The annual mean temperature within its area of occupancy ranges between 25.4° C and 25.5° C, and the annual precipitation ranges between 2200–2900 mm/yr. The rainfall pattern is relatively unimodal, with the dry season occurring December through March, and the rainy season in April through November. The rainiest month is May with 420–430 mm, and the driest month is February, with 56–58 mm.

Ecology:—This species remains poorly understood and understudied due to the logistical difficulties and security concerns impeding long-term access to its habitat. Little is known about its demography, population viability, or biological interactions (e.g. pollination and seed dispersal agents, herbivory, etc.). During our October 2017 visit, we observed pollen strobili at near pollen release, immature and near-mature ovulate strobili, and newly emerging leaves. Additional observations at different times of the year will be necessary to better understand the phenology of this species.

Conservation:—The only known collections of this species are from within a protected area, Paramillo National Park. Nevertheless, the distribution, abundance, demography, and threats facing this species remain unknown, so the species should be considered Data Deficient (DD) in the IUCN Red List until enough information is obtained to adequately assess its risk of extinction.

Morphological and taxonomic affinities:—*Zamia sinuensis* most closely resembles *Z. manicata* but the species can readily be distinguished from each other based on several qualitative morphological characters (Table 2). *Zamia sinuensis* is readily distinguished from *Z. manicata* by its strongly undulate leaflets lacking a petiolule and gland-like collar at the base. It is separated from populations of Z. *manicata* by the Serranía de Abibe, a northward extension of the Andean Cordillera Occidental, but it shares the Sinú River basin with *Z. restrepoi* and occurs only 20 km distant from historic collections of this species. However, the two species do not resemble each other at all vegetatively (Fig. 1) and do not appear to be sympatric.

Key to the manicata clade

Species of the genus *Zamia* may exhibit drastic ontogenetic changes in morphological traits such as the prevalence of petiolar prickles, as well as the shape, texture and dentition of leaflets (M. Calonje, personal observation). For example, the very distinct petiolule and gland-like collar of *Z. manicata* is not present in seedlings and young juvenile plants. Consequently, the following vegetative key is primarily intended for use with material derived from mature or larger juvenile plants.

1 Petioles moderately to strongly armed with prickles 2
- Petioles unarmed or rarely with scattered minute prickles 3
2 Leaflets with distinct petiolule and gland-like collar ..... *Z. manicata*
- Leaflets sessile and without gland-like collar 4
3 Leaflets separated, linear-lanceolate with length-to-width ratio > 7:1, and an adaxially raised longitudinal crease ..... *Zamia* "Cogollo"
- Leaflets imbricate, lanceolate with length-to-width ratio < 7:1, and lacking an adaxially raised longitudinal crease ..... *Z. imbricata*
4 Leaflets with conspicuous midrib ..... *Z. restrepoi*
- Leaflets without conspicuous midrib 5
5 Leaflets elliptical, membranaceous, with adaxially raised veins ..... *Z. disodon*
- Leaflets lanceolate to linear lanceolate, chartaceaous to papyraceous 6
6 Leaflets planar, forwardly falcate, with adaxially raised longitudinal crease ..... *Z. melanorrhachis*
- Leaflets strongly undulate, relatively symmetrical, without adaxially raised longitudinal crease ..... *Z. sinuensis*

Discussion

With the addition of the two new species herein described and the recognition of the currently undescribed *Zamia* "Cogollo" as distinct, we recognize seven taxa belonging to the manicata clade, all of which are readily identifiable based on qualitative morphological characters discussed here. Although *Z. manicata* was described nearly a century and a half ago and has been extensively collected (Appendix I), the other members of the clade have only become known to science in the last couple of decades and the group as a whole has been generally understudied, with only a handful of published studies shedding light into this still relatively obscure clade. These include research into the genetic (Aristizábal *et al*. 2018) and demographic variation of *Z. melanorrhachis* (Lopez-Gallego 2007), a clarification of the taxonomy of *Z. restrepoi* (Lindstrom, 2009), and a single study examining the leaflet anatomy of *Z. disodon* and *Z. restrepoi* (Acuña-Castillo & Marín-Mendez 2013). The paucity of research into the manicata clade is due in part to the logistical and security concerns of the region, but also due to intense deforestation in the region (Sanchez-Cuervo & Aide 2013) that has greatly reduced the suitable habitat available for exploration. The two new species described here, as well as the undescribed *Z.* "Cogollo", remain poorly collected and understudied, with only a single population known for each species and a small number of plants known to occur in the wild. Future research into these species should focus on locating new populations of these taxa in the field and gaining a better understanding of their demography, population viability, phenology, and biological interactions (e.g. pollination and seed dispersal agents, herbivory, etc.). Although the monophyly of the previously described species of the clade is strongly supported in recently published phylogenetic analyses utilizing Sanger sequencing technologies, the fine-scale genetic relationships within the clade remain unresolved (Calonje *et al*. 2019) and will likely require the utilization of next-generation sequencing technologies to fully resolve.

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Appendix 1. Additional specimens examined for other members of the manicata clade:—

Zamia disodon. Type:—COLOMBIA. Antioquia: Dabeiba. 200m, 26 Sep 1986, *D. Restrepo et al. s.n.* (Holotype COL nos. 297003!, 297004!, 297005!, 411107!; Isotype NY 658401!).

COLOMBIA. Antioquia: Apartadó. 70 m, *A. Idárraga-Piedrahita 1199* (HUA!), 200–300 m, 22 Oct 2017, *J.P Tobón & M. Restrepo 2556* (HUA nos. 212191!, 121192!, 212193!), 28 Sep 1986, *I. Turner 1* (FTG 60082!); Carepa. 30 m, 13 Dec 2011, *A. Rivera Duque & J.J. Granada Botero 113* (HUA 180989!); Dabeiba. 10 Oct 2002, *A.J. Lindstrom AL-1168A* (L L.3933357!); Necoclí. 50 m, 17 Mar 2014, *J. Castro 508* (HUA!); San Pedro de Urabá. 116 m, 2 Feb 2014, *J.P. Tobón et al. 851* (JAUM nos. 64458!, 64476!, 64480!, 64481!, 64498!) & *857* (JAUM nos. 64486!, 64524!); 200 m, 2 Apr. 1946, *O. Haught 4782* (COL 37411!, US nos. 1903612!, 1903613!).

Zamia manicata. Neotype (designated by Stevenson & Sabato 1986):—t. 926, fig. e in Gartenflora 27, 1878 = *Zamia madida* Schultes (1958: 114). Holotype:—COLOMBIA. Antioquia: 150 ft, 16–20 Feb 1953, *R.E. Schultes & I. Cabrera 18694* (GH!).

COLOMBIA. Antioquia: Chigorodó: 60 m, 18 Dec 1990, *Callejas et al. 9749* (HUA 83763!), 100 m, 20 Mar 2014, *J. Castro 520* (HUA), 40 m, 4 Mar 2000, *Estudiantes de Botánica Taxonómica Medel 20* (MEDEL 42742!), 50 m, 10 Jun 2012, *V.M. Montoya et al. 1* (HUA nos. 181922!, 181923!), 50 m, 15 Jun 2012, *V.M. Montoya et al. 2* (HUA nos. 181923!, 181924!), 0–100 m, 14 Jun 2012, *D. Silva Sierra 5* (HUA 185189!), 100 m, 18 Mar 1948, *E. Yepes et al. 18c293* (MEDEL 4237!); Dabeiba: 50 m, 26 Jun 1998, *J.A. Perez-Zabala 359* (MEDEL nos. 45668!, 45669!, 45670!); Mutatá: 150 m, 14 May 1983, *R. Bernal & O.I. Delvalle 601* (COL nos. 291017!, 291024!, 291552!, 292810!), 75 m, 28 Jan 1995, *J. Betancur et al. 5999* (COL 400681!, HUA nos. 101912!, 102007!, MO 4982025!, US 3337959!), 19 Nov 1987, *R. Callejas et al. 5665* (HUA 51238!), 30–80 m, 21 Nov 1987, *R. Callejas et al. 5772* (HUA!, MO 3598817!, NY!), 150 m, 4–8 Aug 1947, *W.H. Hodge 7041* (MEDEL 37249!, US 1950712!), 25 Apr 1985, *E. Rentería A. 3943* (HUA nos. 27984!, 28049!, JAUM 11958!), 150 ft, 16–20 Feb 1953, *R.E. Schultes & I. Cabrera 18640* (GH!), 150 ft, 16–20 Feb 1953, *R.E. Schultes & I. Cabrera 18679* (GH!), 150 m, 24 Aug 1984, *D.W. Stevenson et al. 604* (FTG nos. 55794!, 87170!, 87171!, 87172!, HUA 48342!), *J.P Tobón & I. Mendoza 840* (JAUM nos. 64467!, 64475!); Turbo: 30 m, Nov 2001, *F. Alzate & F. Cardona 1265-A* (HUA 130219!, MO 5767332!), 10–20 m, 10 Dec 1982, *R. Bernal & G. Galeano 447* (COL 291656!), 20m, 25 Dec 1983, *J. Brand & M. Escobar 747* (JAUM 10137!), 20 m, 27 Jun 1983, *J. Brand & E. Ascanio 363* (JAUM 10138!, 10139!), 50 m, 2 May 1946, *O. Haught 4820* (COL nos. 91920!, 91921!, US 1903628!, 1903629!), *E. Rentería A. 5292* (HUA 48456!), 70 m, 13 Jul 1983, *J. Santa & J. Brand 835* (COL 264646!, HUA 19375!); Chocó: Acandí: 100 m, 10 Jul 1976, *L.E. Forero 614* (COL 173728!); Riosucio: 17 Jul 1979, *C. Barbosa 1094* (FMB 2610), 24 Oct 1979, *C. Barbosa 1304* (FMB 2611!), 10–540 m, 15 Aug 1987, *D. Cárdenas 347* (JAUM nos. 16863!, 19808!, 19810!, 19811!, MO nos. 3915532!, 3915533!), 10–520 m, 11 Sep 1987, *D. Cárdenas 437* (JAUM nos. 16843!, 19809!, MO 4007821!), 10–50 m, 9 Nov 1987, *D. Cárdenas 715* (JAUM 16815!, MO 4007822!), 50–500 m, 20 Jan 1988, *D. Cárdenas 1116* (JAUM 16814!, MO 4007793!), 20–200 m, 13 Apr 1988, *D. Cárdenas 1576* (JAUM 16875!, MO 4007794!), 100 m, 15 May 1988, *D. Cárdenas 1885* (JAUM 16859!, MO 4007795!), 50 m, 10 Feb 2002, *F. Cardona 1069* (HUA 125005!), 13 Jul 13 1996, *R. Fonnegra 6128* (HUA 105848!), 30 m, 26 Mar 1999, *R. Fonnegra 6841* (COL 442816!, HUA 114252!), 250 m, 28 May 1976, *E. Forero & R. Jaramillo 1577* (COL nos. 177048!, 177049!, 177050!, 177051!, 177052!, , MO 2765773!), 230–260 m, 26 Feb 1976, *H. León 572* (COL nos. 256082!, 256106!, MO 2595270!), 25 Jan 1983, *S. Zuluaga R.* 1033 (COL 293313!); Sautatá: 50 m, 12 Oct 1994, *E. Rentería A. 10669* (HUA 99037!), 100 m, 23 Mar 1995, *E. Rentería A. et al. 10929* (CHOCO 9683!, HUA 99664!), 24 Mar 1995, *E. Rentería A. 10981* (HUA 99795!); Unguía, 300 m, 16 Jun 1975, *A.H. Gentry & L.E. Aguirre 15190* (COL 153271!, MO 2588482!), PANAMA: Darién: 15 m, 17 Mar 1937, *P.H. Allen 248* (MO nos. 1256596!, 1256597!), 750 ft, 12–13 Jun 1947, *P.H. Allen 4553* (MO 1572071!), 19 Dec 1966, *D. Burch et al. 1112* (MO!, US 2589521!), 200–450 m, 27 Jul 1994, *T.B. Croat & G. Zhu 77132* (MO nos. 4621515!, 4621516!), 10–11 Aug 1962, *J.A. Duke 5432* (MO 1892977!), 29 Aug 1967, *J.A. Duke & J.D. Kirkbride 14000* (MO 2588472!), 700–1000 m, 25 Jan 1975, *A.H. Gentry & S.A. Mori 13909* (MO 2300634!, SCZ 609!), 375 m, 21 Dec 1980, *W. Hahn 155* (MO 2937749!), 5 Apr 1975, *S.A. Mori & J. Kallunki 5427* (MO 2588483!), 200 m, 13 Oct 1987, *G.C. de Nevers et al. 8279* (MO 3592866!).

***Zamia melanorrhachis*.** Type:—COLOMBIA. Córdoba: Montelíbano. *Stevenson et al. 695* (holo-: COL, iso-: HUA, MO 2195522!, NY nos. 951595!, 951596!, U)

COLOMBIA: Antioquia: Anorí: 450 m, 24 Sep 2002, *D. Tuberquia & C. Gutierrez 1891* (JAUM nos. 42730!, 42731!, 42732!); Briceño: 338 m, 13 Oct 2013, *L. Ríos M. & E. Garcés 8* (HUA 195732!), 338 m, 13 Oct 2013, *L. Ríos M. & E. Garcés 9* (HUA 195733!); El Bagre: 80–100 m, 20 Nov 2016, *Tobón et al. 2116* (JAUM 75800!); Tarazá: 400 m, 15 May 1987, *R. Callejas & J. Betancur 3512* (42694!); Bolívar: Cantagallo: 100 m, 23 Oct 2016, B. *Villanueva & L.F. Henao* 3255 (TOLI), San Pablo: 110 m, 15 Sep 2010, *A. Cogollo et al. 12634* (FMB 100161!, JAUM nos. 52599!,

52601!, 52603!, 52609!); Córdoba: Montelíbano: 50–65 m, 10 Feb 2020, *J. Castro et al. 1581* (HUA!)*, 1582* (JAUM!)*, 1582-A* (HUA!)*, 1582-B* (COL!)*, 1583* (COL!)*, 1584* (HUA!, HUC!)*, 1585* (MEDEL!), *1586* (HUA!), 86 m, 27 Aug 2002, *R. Fonnegra et al. 7473* (HUA 133857!), 70 m, 31 Aug 1997, *C. Gutiérrez et al. 406* (JAUM 76054!), 16 Aug 1998, *C. López-Gallego & A. Gil 63* (HUA nos. 111447!, 111448!), 29 Sep 1998, *C. López Gallego & J.C. Benavides 64* (HUA nos. 111754!, 111755!, 111756!), 29 Nov 1998, *C. López-Gallego & J.D. Gonzáles 65* (HUA 112418!), 30 m, 24–25 Oct 1990, *F.J. Roldán et al. 1478* (HUA 79938!, 79939!), 30–60 m, 24–25 Oct 1990, *F.J. Roldán et al. 1491* (COL 428380!, NY 278465!), 120 m, 27 Oct 1990, *F.J. Roldán et al. 1523* (COL 428379!, MO 4263015!, NY 278464!), 70 m, 10 Aug 2016, *K. Zamora 23* (MEDEL 65254!), 89 m, 11 Aug 2016, *K. Zamora 25* (MEDEL nos. 65255!, 65257!); Planeta Rica: 22 Jun 1991, *U. Troncoso 15* (HUC 1391!); San José de Uré: 89 m, 11 Aug 2016, *K. Zamora 26* (MEDEL 65258!), 100 m, 12 Aug 2016, *K. Zamora 27* (MEDEL 65259!); Santander: Barrancabermeja: 100–500 m, 9 Dec 1934, *O. Haught 1447* (COL 1242!, F 861946!, GH!, NY!, US 1662464!), 100–500 m, 26 Feb 1935, *O. Haught 1578* (P!, US 1662474!), 100 m, 8 Dec 1936, *O. Haught 2101* (US 1740604!); Betulia: 215 m, Sep 2015, *A. Rojas et al. 732* (CDMB, HUA nos. 210774!, 210775!); Simacota: 110 m, 19 Apr 2018, *C. Cacua Toledo Cyca 17* (COL 606597!).

Zamia restrepoi. (≡ *Chigua restrepoi* Stevenson: 170). Type:—COLOMBIA. Córdoba: Tierralta: 100 m, 14 Mar 1987*, D. Stevenson et al. 693* (holo-: HUA nos. 73394!, 77395!, 77396!), iso-: FTG, NY nos. 1174!, 1175!, 1176!, 1177!, U 10941!)

= *Chigua bernalii* Stevenson (1990: 170). Type:—COLOMBIA: Córdoba: Tierralta: 150 m, 27 Jul 1986, *R. Bernal et al. 1189* (holo-: COL nos. 343380!, 343381!, 343382!, 343383!, iso-: FTG 60432!, HUA nos. 51605!, 51606!, 51607!, US nos. 3197584!, 3197584!)

COLOMBIA: Córdoba: Tierralta: 120 m, 24 Jul 1986, *R. Bernal et al. 1138* (FTG 60431!, COL 343384!), 100-200 m, Feb 2015, *J. Castro et al. 498* (HUA nos. 205141!, 205142!), 84 m, 4 Oct 2017, *J. Castro & Taborda 1148* (HUA nos. 219610!, 219611!, 219612!, 219613!), 0–100 m, 1 Dec 1999, *A. López & F. Solano Manco 4679* (JAUM 39075!), 90–120 m, Mar 5–6 1918, *F.W. Pennell 4608*, 28 Sep 1986, *I. Turner 3* (FTG 60081!).

***Zamia* "Cogollo"**

COLOMBIA. Antioquia: Puerto Berrío: 240 m, 27 Jan 2008, *Idárraga et al. 3456* (HUA nos. 179778!, 179779!), 240 m, 23 Jan 2001, *Idárraga et al. 1946* (JAUM 34588), 14 Feb. 2011, *Tuberquia et al. 3251* (HUA 181780!).