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Zamia urarinorum (Cycadales, Zamiaceae), a new cycad species from wetland forests of Loreto, Peru

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Abstract

We describe and illustrate *Zamia urarinorum*, a new species of arborescent cycad from wetland forests in the Tigrillo and Urituyacu river basins of Loreto, Peru. It is the only cycad known to inhabit permanently waterlogged wetland forests, a unique and ecologically challenging environment. Morphologically, the species most closely resembles *Zamia multidentata*, but differs in both vegetative and reproductive traits. Vegetative distinctions include fewer leaves per stem and longer, more narrowly shaped leaflets with marginal teeth confined to the distal portion. Reproductive differences include significantly smaller pollen strobili with a tomentose rachis, and ovulate strobili with shorter peduncles and smaller seeds. We also document a range extension of *Z. multidentata* into Peru, expanding its known distribution beyond Acre, Brazil. These findings highlight the underexplored diversity of Amazonian *Zamia* and contribute to a growing understanding of its biogeographic and ecological complexity.

Key words: Amazon Rainforest, endemic species, gymnosperm, Urarina people, taxonomy

Introduction

The genus *Zamia* Linnaeus (1763: 1659) is the most species-rich and broadly distributed lineage of New World cycads, comprising over 85 species ranging from Florida (United States) to Bolivia (Calonje et al., 2025). In the Amazon basin, ten species are currently recognized (Calonje et al., 2025): *Zamia 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. multidentata* Calonje *et al.* in Segalla *et al.* (2023: 22), *Z. poeppigiana* Martius & Eichler in Eichler (1863: 414), *Z. ulei* Dammer (1907: 117), and *Zamia urep* Wallnöfer (1996: 1056).

Despite recent advances in understanding the taxonomy (i.e. Calonje *et al.*, 2011; Segalla & Calonje, 2019; Segalla *et al.*, 2023; Stevenson *et al.*, 2018), reproductive biology (Segalla *et al.*, 2021), ecological interactions (Segalla & Morelato, 2019) and genetic relationships (i.e. Calonje *et al.*, 2019; Lindström *et al.*, 2024) of *Zamia* species in the Amazon basin, much of the region has been poorly surveyed for cycad diversity, and the taxa occurring here remain insufficiently studied and in need of taxonomic clarification.

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During a biodiversity inventory conducted along the Tigrillo River in Urarinas District of Loreto, Peru, an unusual arborescent species of *Zamia* was observed growing in waterlogged wetland environments, a physiologically challenging habitat previously unreported for any cycad species. Close morphological analysis and extensive field observations support its recognition as a new species, herein described as *Zamia urarinorum*. This new taxon adds to the growing body of evidence that the Amazon basin may harbor a greater diversity of cycads than currently recognized.

Materials and methods

Fieldwork for this study was Conducted in March and April of 2025 as part of a research expedition led by the Instituto de Investigaciones de la Amazonía Peruana (IIAP) along the Tigrillo River in the department of Loreto, Peru. The expedition aimed to investigate biodiversity and social dimensions of the biocultural landscape within the Indigenous territory of the Urarina people. During this expedition, individuals of the putative new species were located and documented in the Urarina communities of Raya Yacu, Nuevo Horizonte, and Puerto Rico. Morphometric data, photographic documentation, georeferenced observations, and habitat characterizations were recorded in situ, and herbarium specimens were prepared for formal study. Specimens of other Amazonian *Zamia* species from various herbaria were examined for comparative and mapping purposes (Appendix 1). Distribution maps were generated in QGIS v3.40.2 (QGIS Development Team, 2023) and Extent of Occurrence (EOO) and Area of Occupancy (AOO) were calculated using Geocat (Bachman *et al.*, 2011).

To minimize subjectivity in color descriptions, we identified colors using the RHS Colour Chart (Royal Horticultural Society [Great Britain], 2015), referencing both official RHS numbers (e.g., RHS 173C) and the corresponding color names from Color Names for the RHS Colour Chart (UPOV, 2019). Color identification was performed using the R package ColorNameR (Sánchez Beeckman, 2021) in R v4.2.2 (R Core Team, 2022). RGB values were extracted from high-resolution photographs by sampling average CIELAB color values from 31 × 31 pixel areas using the eyedropper tool in Adobe Photoshop v24.0 (Adobe Inc., 2025). When possible, specimens were photographed alongside a calibrated 18% grey card (Pixel Perfect brand) to assist with color correction and improve consistency across lighting conditions. Final RHS color matches were determined with ColorNameR (Sánchez Beeckman, 2021) and used in the species description.

Taxonomic treatment

Zamia urarinorum Calonje, R. Zárate & M.Asa Jones *sp. nov.* (Figs. 1–4)

Diagnosis. *Zamia urarinorum* is most similar to *Z. multidentata* but differs by having fewer leaves per stem (2–5 vs. 8–14), longer leaflets (up to 45.6 cm vs. 21.7 cm) that are narrowly elliptic to lanceolate in shape (vs. ovate to elliptic in *Z. multidentata*), and marginal teeth restricted to the distal third to fourth of the leaflet margin (vs. more extensive serration beyond the proximal fourth). It also differs in reproductive structures, with significantly smaller pollen strobili (5.1–5.2 × 1.1–1.2 cm vs. 8.2–8.3 × 1.4–1.5 cm), with a tomentose rachis (vs. glabrous), ovulate strobili with shorter peduncles (5.5–11.5 cm vs. 12.0–17.5 cm), and smaller seeds (sclerotesta 10.0–14.0 × 6.8–8.3 mm vs. 13.0–16.4 × 8.6–9.8 mm).

Type:—PERU. Loreto Department: Loreto Province, Urarinas District, Raya Yacu, 135 m, 12 Apr 2025, *R. Zárate, M. Calonje & M. Jones 24417* (holotype USM!; isotypes HH!, FTG!).

Additional specimens examined:—PERU. Loreto Department: Loreto Province, Urarinas District, Curuinsi, 115 m, 12 Sep 2025, S. Portalanza & *G. Hidalgo SPR87* (HH!); Juan Velasco Alvarado, 180 m, 8 Aug 2003, *H. Balslev, C. Grández & G. Criollo 6580* (AAU!); Nuevo Horizonte, 136 m, 17 Apr 2025, *R. Zárate, C. Angulo & J. Valles 24419* (HH!); Puerto Rico, 149 m, 21 Apr 2025, *R. Zárate & C. Angulo 24421* (AMAZ!); Reforma, 130 m, 16 Aug 2003, *J. Vormisto et al. 776* (AAU!); Raya Yacu, 145m, 13 Mar 2025, *R. Zárate, C. Angulo & J. Valles 24399* (HH!), *24400* (HH!), *24401*(HH!), *24402* (AMAZ!), *24403* (AMAZ!), *24404* (AMAZ!); 135 m, 11 Apr 2025, *R. Zárate, M. Calonje & M. Jones 24415* (USM!), *24416* (HH!), *24418* (HH!).

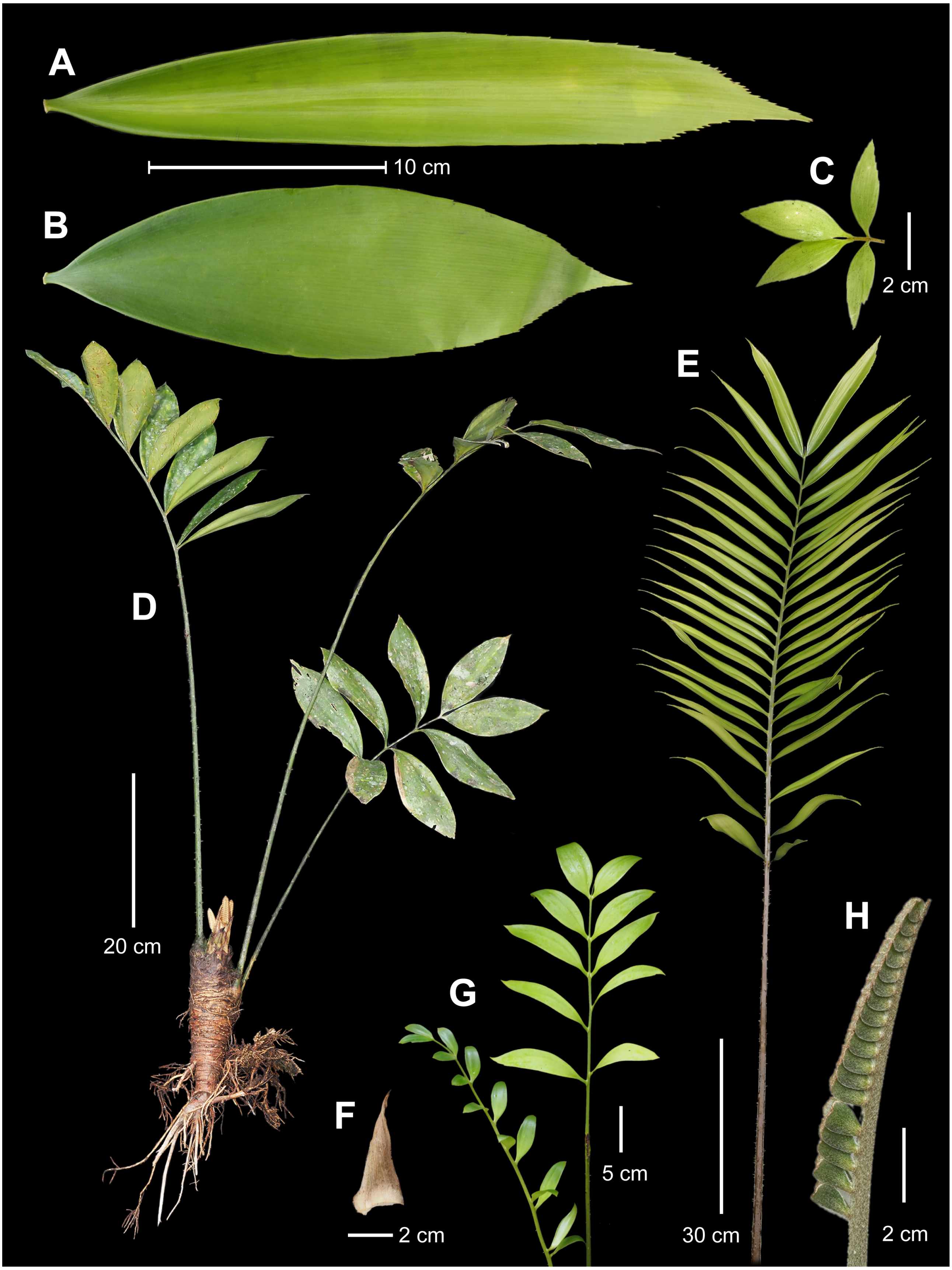

FIGURE 1. Vegetative characteristics of *Zamia urarinorum*. A. Median leaflet from peatland pole forest habitat, adaxial side, B. Median leaflet from shebonal forest habitat, adaxial side, C. Eophyll, D. Habit of adult individual from shebonal forest with pollen strobili. E. Leaf from peatland pole forest, F. Cataphyll, G. Emerging leaves H. Newly emerging leaf showing slightly reflexed ptyxis. All photographs used for the preparation of this illustration were taken at the type locality of Raya Yacu.

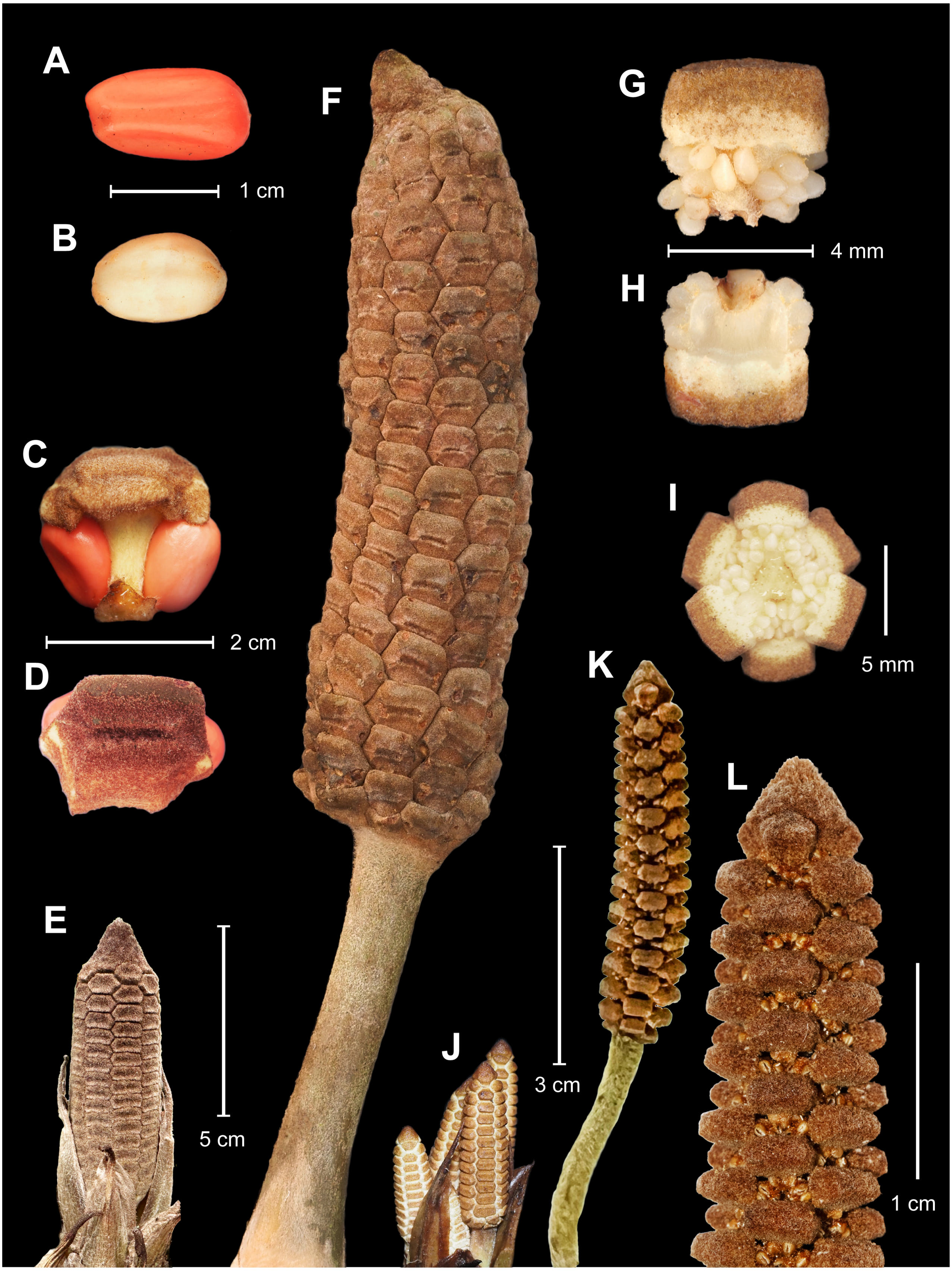

FIGURE 2. Reproductive characteristics of *Zamia urarinorum*. A. Seed sarcotesta, B. Seed sclerotesta, C. Megasporophyll with two mature seeds, D. Megasporophyll shield, E. Immature ovulate strobilus, F. Mature ovulate strobilus, irregularly pollinated, G. Microsporophyll abaxial view, H. Microsporophyll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

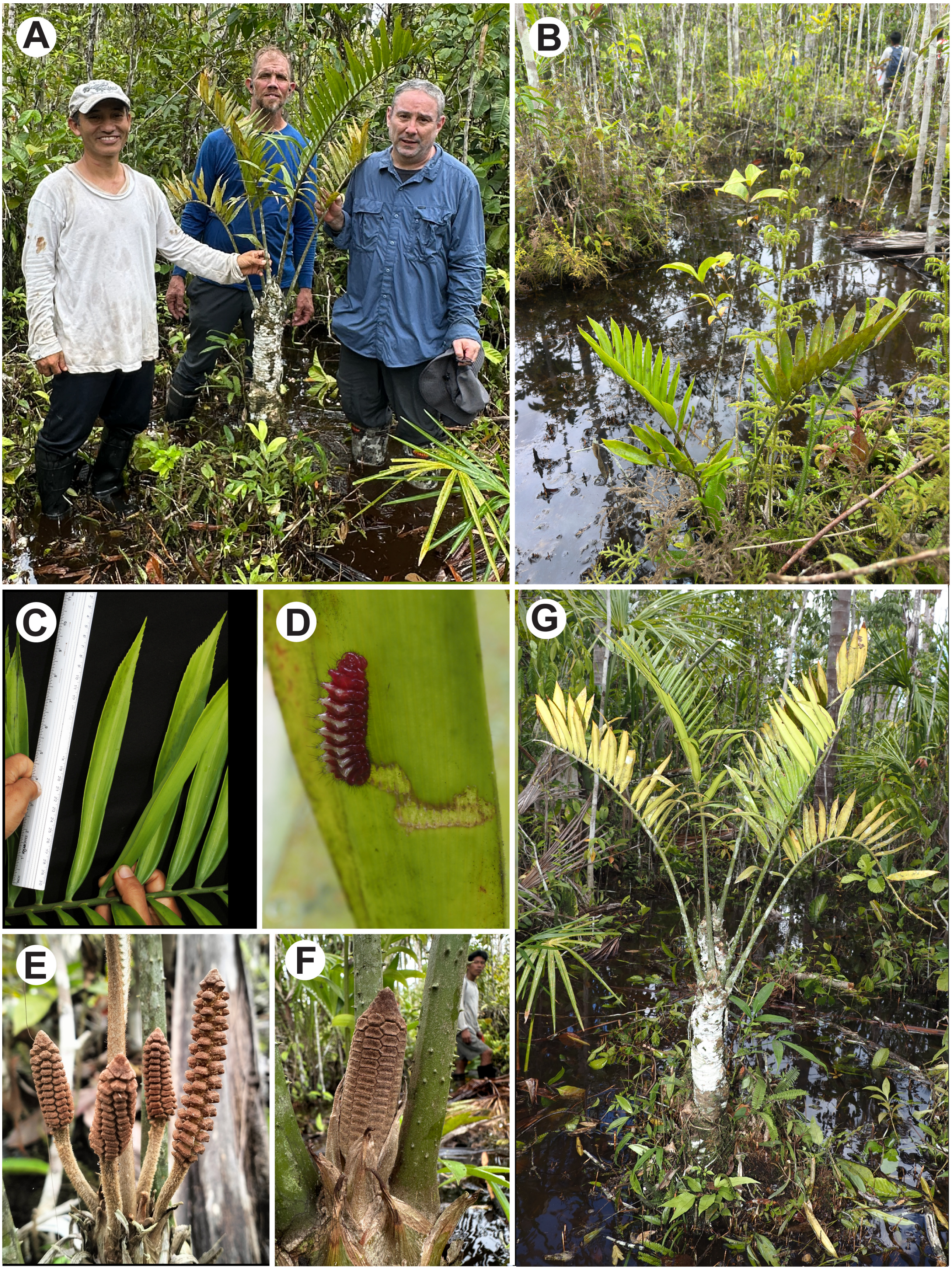

FIGURE 3. *Zamia urarinorum* in open-canopy peatland pole forest habitat. A. Tall arborescent plant with Ricardo Zárate Gómez, Malcolm Jones, and Michael Calonje. B. Juvenile plant in waterlogged habitat, C. Lanceolate leaflets with inwardly curved margins typical of this open, solar exposed habitat, D. Tall arborescent plant surrounded by water, E. *Eumaeus toxana* larva, F. Immature ovulate strobilus.

FIGURE 4. *Zamia urarinorum* in shebonal forest habitat. A. Small mature plants in inundated habitat, B. Large plant with Malcolm Jones, Michael Calonje, and Ricardo Zárate-Gómez, C. Juvenile plant, D. Narrowly elliptic leaflets typical of shaded environment, E. Plant with multiple juvenile pollen cones emerging from two separate stem apexes.

Description:—*Stem* epigeous, cylindrical, typically solitary but occasionally branching with up to two stem apices, 14.0–150.0 × 4.5–12.0 cm. *Cataphylls* caducous, triangular to narrowly triangular, 4.5–5.5 cm long and 2.0–3.2 cm wide at base, abaxial surface densely covered with grey brown (RHS 199B–199D, N199D) to light yellow brown (RHS 161A, 161C) felted indumentum, aging to medium yellow brown (RHS 163B) after loss of indumentum. *Ptyxis* slightly reflexed. *Leaves* 2–6 per stem, erect to slightly spreading, 68–300 cm long and 20–90 cm wide. *Petiole* 28–136 cm long with abruptly swollen base 2.0–4.5 cm wide, moderately to strongly armed with 2–5 mm long, generally upturned prickles, petiole and rachis densely covered with white (RHS 155A–C) felt-like indumentum on new leaves, gradually shedding it to reveal grey brown (RHS N199A–N199B) epidermis aging to dark brown green (RHS 146B). *Rachis* 27–166 cm long, unarmed or lightly armed with prickles mostly in the proximal fourth, with occasional solitary prickles occurring beyond. *Leaflets* 10–52, chartaceous to coriaceous, oppositely to sub-oppositely arranged, with articulate insertion on rachis 3.8–8 mm wide, spaced 1.4–6.6 cm apart at leaf center, narrowly elliptic to lanceolate with attenuate base and long acuminate to abruptly acuminate apex, adaxial surface with a distinctly raised longitudinal crease, margins finely serrulate in the distal third to fourth bearing 10–41 teeth, median section traversed by 24–46 parallel veins, on new leaf flushes light yellow green (RHS 2C) to light green (RHS N144A) in full sun, light green (RHS 149A–C) to light yellow green (RHS 154D) in shade, maturing to medium green (RHS 144A) in full sun and dark brown green (RHS 146A) in shade, slightly discolorous with the abaxial surface lighter than the adaxial, basal leaflets 9.0–45.4 cm × 1.4–7.1 cm, median leaflets 10.7–45.6 cm × 2.5–7.8 cm, apical leaflets 9.6–30.1 cm × 2.0–8.2 cm. *Eophylls* 8.5–10.5 cm long, petiole 7.5–9.5 cm long, rachis 0.5–0.7 cm long bearing 4 leaflets 3.2–4.0 × 0.8–1.1 cm. *Pollen strobili* 4–8 per stem apex, fertile portion conical-cylindrical, at pollen-shedding stage (excluding peduncle) 5.1 – 5.2 × 1.1 – 1.2 cm, covered with medium orange pink (RHS 173D) to medium brown (RHS 166B–C) felted indumentum, strobilus apex acute, 0.3 – 0.4 mm long and 0.4 – 0.5 mm wide at base, peduncle 4.8 – 9.0 × 0.4 – 0.6 cm, densely covered with a thick layer of short, matted light yellow brown (RHS 161C–D) trichomes, giving the surface a felt-like texture, strobilar axis densely covered with a persistent indumentum of long, crisped, yellowish to reddish brown trichomes. *Microsporophylls* spirally arranged in 5–8 orthostichies of 8–18 fertile sporophylls each, median sporophylls 4.0 – 4.5 mm long and 3.5 – 3.6 mm wide. Microsporophyll shield a distinctly extruded hexagonal prism, 1.8 – 2.0 mm tall and comprising 2/5 to 1/2 of sporophyll length; 3.5 – 3.6 mm wide at the base; distal face slightly indented and only very slightly reduced, measuring approximately 9/10 the size of the base. *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 10–17 sporangia. *Ovulate strobili* one per stem apex, 13.0–19.5 × 3.8–5.3 cm at maturity (excluding peduncle); fertile portion cylindrical, sterile apex broadly conoid and obtuse, 10–17 mm long and 25–27 mm wide at base; surface initially covered with dark greyed brown felted indumentum (RHS N199B) on newly emerging strobili, gradually transitioning to greyed brown (RHS 199C) to light greyed brown (RHS 199D) at maturity; peduncle 5.5–11.5 × 1.2–1.7 cm, at maturity with indumentum persisting in pale yellow brown (RHS 161C) to greyed brown (RHS 199C) patches or shedding to reveal glabrous dark greyed brown (RHS 199A) epidermis. *Megasporophylls* spirally arranged in 9–11 orthostichies of 11–19 sporophylls each, median sporophylls 16.8–19.0 wide and 8.0–18.5 mm deep, megasporophyll shield relatively flat, only slightly extruded, 2.0–2.5 mm thick, 16.8–19.0 mm wide, and 12.0–15.0 mm tall, the distal facet shallowly indented, narrow and elongated. Seeds ovoid-pyramidal, sarcotesta light red (RHS N30A) to orange red (RHS 169A) at maturity, 11.6–15.6 × 7.8–9.3 mm, sclerotesta ovoid, glabrous, light yellow (RHS 150D, 10D) to medium yellow brown (RHS 164C), 10.0–14.0 × 6.8–8.3 mm.

Etymology:—The specific epithet honors the Urarina Indigenous people, in recognition of their long-standing presence and stewardship of the flooded lowlands of the Peruvian Amazon where this species occurs.

The Urarina, whose population was estimated at approximately 5,812 in the 2017 national census (Ministerio de Cultura del Perú, 2025), inhabit the *Abanico del Pastaza*, a vast and ecologically important wetland complex (Ramsar Convention Secretariat, 2002) within the *Pastaza–Marañón Foreland Basin* (PMFB). The Urarina maintain a deep cultural relationship with these floodplain ecosystems (Schulz *et al.*, 2019). Their territory—spanning the basins of the Chambira and Corrientes rivers (Ministerio de Cultura del Perú, 2025), in the department of Loreto, in the Peruvian Amazon—constitutes a biocultural landscape of exceptional regional significance (Martín Brañas *et al.*, 2023).

Habitat, geology and soils—*Zamia urarinorum* occurs in wetland forests (Flores-Llampazo *et al.*, 2022) within the Pastaza–Marañón Foreland Basin of northeastern Peru (Draper *et al.*, 2014). Known populations lie near the southern margin of the Pastaza Fan, the largest humid tropical alluvial fan in the world (Räsänen *et al.*, 1992) and one of the most extensive wetland landscapes in the Amazon basin. Covering more than four million hectares, it encompasses the largest known Amazonian peatland complex and plays a key role in regional hydrology and ecosystem function (Álvarez Alonso, 2020). This depositional system formed at the base of the Eastern Cordillera of Ecuador, where it is undergoing uplift due to active crustal deformation, and receives volcaniclastic sediment and nutrient inputs from several Ecuadorian stratovolcanoes—including Cotopaxi, Sangay, Tungurahua, Altar, Chimborazo, and Carihuairazo—that lie within the upper Pastaza River watershed (Bès de Berc *et al.*, 2005). *Zamia urarinorum* is currently known from the vicinity of the Tigrillo River, which flows into the Chambira River shortly before it joins the Marañón, and from the Urituyacu River, a direct tributary of the Marañón.

During field surveys conducted along the Tigrillo River, we found the species to be restricted to four wetland forest types: peatland pole forests (varillales hidromórficos) (Honorio Coronado *et al.*, 2021), shebonal forests (Fig. 5), and, to a lesser extent, palm swamp habitats (aguajal). All three habitats are characterized by water-saturated soils, periodic or permanent flooding, and unique hydrological regimes.

Peatland pole forests are structurally distinct ecosystems that develop on deep peat deposits formed under persistently saturated and nutrient-poor conditions. They store exceptionally high quantities of carbon—on average 1391 ± 710 Mg C ha^{-1}—and rank among the most carbon-dense forest types in Amazonia (Draper *et al.*, 2014). This forest type was surveyed in the communities of Nuevo Horizonte and Puerto Rico, where peat deposits were recorded with average depths of 89 cm (maximum 129 cm) and 251 cm (maximum 380 cm), respectively. They are characterized by slender, low-diversity tree assemblages and include species typically found in white-sand forests (Draper *et al.*, 2017). These forests occur on hydromorphic acidic (pH ~4.0) soils, primarily histosols, and are permanently saturated, with the water table consistently close to the soil surface and maximum flood depths rarely exceeding 0.28 m (Flores Llampazo *et al.*, 2022). The canopy may be open or closed. In closed-canopy peatland pole forests, trees range from 10–20 cm DBH, though some individuals reach up to 40 cm DBH and 35 m tall. The five most frequent tree species, listed in order of abundance were *Pachira nitida* Kunth in Humboldt *et al.* (1821: 302), *Mauritia flexuosa* Linnaeus filius (1782: 454), *Platycarpum loretensis* Dávila & Kinoshita-Gouvea (2016: 277), *Hevea guianensis* Aublet (1775: 871), and *Lueheopsis hoehnei* Burret (1926: 841). Open-canopy peatland has a similar species composition but is characterized by a low density of large trees, with the dominant vegetation comprising herbaceous species up to 2 m tall and shrubs reaching 5 m. Emergent vegetation is represented by individuals of *Mauritia flexuosa*, reaching 25–30 m in height. The peat layer is relatively shallow, averaging 34 cm in depth.

Shebonal forests are seasonally flooded palm-dominated forests, typically lacking peat accumulation, and are dominated by *Attalea phalerata* Martius ex Sprengel in Linnaeus (1825: 624). These forests reach up to 25 m in height, with emergents up to 35 m. The five most common tree species were *Attalea phalerata, Euterpe precatoria* Martius (1842: 10), *Mauritia flexuosa* Linnaeus filius (1782: 454), *Socratea exorrhiza* (Martius 1842: 36) Wendland (1860: 103) and *Elaeis oleifera* (Kunth 1816: 306) Cortés (1897: 203).

Palm swamp habitats (aguajal) are permanently or near-permanently waterlogged forests dominated by *Mauritia flexuosa*, often with a dense understory and a canopy reaching 20–30 m, occurring on peat or organic-rich mineral soils (Draper *et al.*, 2014; Flores Llampazo *et al.*, 2022). The five most common tree species were *Mauritia flexuosa*, *Hevea guianensis*, *Attalea phalerata*, *Lonchocarpus sp.*, and *Protium nodulosum* Swart (1942: 197).

Zamia urarinorum was most abundant in open-canopy peatland pole forest, relatively common in adjacent shebonal forest and closed-canopy peatland pole forest, and rare in palm swamp habitats.

Climate.—The known distribution range of *Zamia urarinorum* lies within the Chambira and Urituyacu river basins of northeastern Peru. Roucoux *et al.* (2023) describe the climate of this region as humid tropical, with high annual rainfall, minimal seasonal variation, and consistently warm temperatures. Annual precipitation ranges from 2,040 to 2,830 mm, with a mean of 2,380 mm, and a marked wet season from March to May. Mean maximum temperatures average 34°C, with little variation throughout the year. The combination of high rainfall, poor drainage, and flat topography supports the extensive peatlands and swamp forests that define the landscape.

Ecology.—*Zamia urarinorum* occurs in extremely waterlogged environments, with its highest observed abundance in open-canopy peatland pole forests, where most individuals were found with their stems partially or entirely submerged during fieldwork in April 2025. Field observations suggest that *Z. urarinorum* is not merely surviving under these conditions, but is well adapted to them. Individuals were frequently rooted directly in standing water, not just on elevated tree bases or hummocks, and showed no signs of root or stem rot—even in prolonged inundation. In one notable case, a mature plant was observed on a flooded riverbank with its apical meristem fully submerged, yet it remained healthy, providing striking evidence of its resilience.

A few other *Zamia* species, such as *Z. chigua* Seemann (1854: 201) and *Z. roezlii* Linden (1873: 10) from the Chocó region of South America, grow in areas of extremely high rainfall in moist or periodically saturated soils. The latter grows in very wet, muddy environments adjacent to mangrove systems, where soils are saturated and often unstable, but individuals typically grow on slightly raised ground or natural hummocks which are not inundated, so the plants do not regularly experience submergence of their roots or stems in the same way that *Z. urarinorum* does.

FIGURE 5. Aerial view of shebonal (top) and peatland pole forest (bottom) habitats.

In contrast, *Z. urarinorum* is the only cycad species known to thrive in permanently saturated, anoxic soils. The species occupies a range of light environments, from open-canopy peatland pole forests with high irradiance to more shaded habitats, including closed-canopy pole forests and shebonal forests. Plants were observed growing continuously across this gradient, with no clear gaps in occurrence between habitat types. Individuals in lower light conditions had longer leaves and broader, darker green leaflets (Fig. 4), whereas those in high-light environments displayed shorter leaves with narrower, more yellowish, and often recurved leaflets (Fig. 3). These phenotypic differences suggest a degree of plasticity in vegetative morphology, likely driven primarily by variation in light availability across habitat type. This gradient of morphological variation was initially noted during fieldwork and found to correspond closely with habitat transitions. Reproductive structures were morphologically identical in all observed individuals, regardless of habitat.

Knowledge of the phenology of this species remains limited, as reproductive material has only been documented during fieldwork conducted in March and April 2025. During the April expedition, we observed newly emerging leaves, pre-receptive and near-mature seed cones, and juvenile pollen cones. A plant with a single pollen-dehiscent pollen cone was recorded on March 13th. The pollinator remains unknown, although it is suspected to be a species of *Pharaxonotha* Reitter (1875: 44)—a genus of beetles in the family Erotylidae known to pollinate other *Zamia* species in South America (Skelley & Segalla 2019; Skelley & Tang 2020; Valencia-Montoya *et al.* 2017). In addition, we recorded ample evidence of foliar herbivory, including a larva of *Eumaeus toxana* Boisduval (1870: 13) observed feeding on a *Zamia* leaflet (Fig. 3E). Herbivory by *Eumaeus* larvae represents a common and obligate antagonistic interaction in New World cycads (Segalla & Morelato 2019; Whitaker & Salzman 2020), and this butterfly species has also been reported from white-sand pole forests in the Colombian Amazon (Sierra-Botero *et al.*, 2023).

Distribution and Conservation Status.—*Zamia urarinorum* is currently known from six localities: three along the Tigrillo River, which flows into the Chambira River shortly before it joins the Marañón, two along the Urituyacu River, a direct tributary of the Marañón, and one near the community of Curuinsi. The known extent of -1478743243 occurrence (EOO) is 2,280 km^2 -1478743243 and the area of occupancy (AOO) is 24 km^2.

The three localities along the Tigrillo River surveyed during this study are situated in a particularly remote region with no road access and minimal signs of human disturbance. According to Honorio Coronado *et al.* (2023), low deforestation rates in Urarina territory are largely due to low population density, absence of roads, and cultural traditions that promote forest conservation. However, emerging threats include oil contamination from pipeline spills, economic dependence on oil-related employment, and infrastructure proposals such as highways and transmission lines, all of which pose risks to the ecological integrity of peatland habitats. Additional pressures identified by Martín Brañas *et al.* (2023) include commercial agriculture, unsustainable extraction of forest products for regional markets, and the progressive erosion of traditional ecological knowledge and cultural identity. These factors collectively threaten the biocultural resilience of Urarina territory and increase the vulnerability of its ecosystems to poorly planned external interventions. The species' reliance on persistently waterlogged habitats suggests a high sensitivity to hydrological changes, making it particularly vulnerable to alterations in rainfall patterns, drainage, or broader impacts of climate change. Given this ecological specificity, *Zamia urarinorum* is unlikely to persist under altered hydrological conditions in the wild, underscoring the importance of maintaining the integrity of its natural habitat.

Given its restricted geographic range (EOO of 2,280 km^2, AOO of 22 km^2) and the presence of multiple plausible threats that could affect all known subpopulations, we recommend that *Zamia urarinorum* be listed as Endangered under IUCN Red List criteria B1ab(i,ii,iii,iv,v) + 2ab(i,ii,iii,iv,v) (IUCN Standards and Petitions Committee 2024).

Morphological Affinities.—Arborescent stems were historically considered rare among Amazon basin *Zamia* species, with only *Zamia poeppigiana* recognized as such (Stevenson 2001, 2004). However, the recent description of *Z. multidentata* by Segalla *et al.* (2023) introduced a second arborescent species and further recognized *Z. hymenophyllidia* as arborescent. *Zamia urarinorum* thus becomes the fourth arborescent species among the eleven currently known from the Amazon basin. Of the four arborescent Amazonian species, *Zamia poeppigiana* is readily distinguished from the rest of the arborescent species by its significantly larger size, with thicker and taller stems attaining 25 cm in diameter and 3 m tall compared to the remaining species which have slender, shorter stems never exceeding 10 cm in diameter and 1 m in height.

Zamia hymenophyllidia can be distinguished from *Z. multidentata* and *Z. urarinorum* by its leaflets of a membranaceous texture (vs. papyraceous to chartaceous in *Z. multidentata* and chartaceous to coriaceous in *Z. urarinorum*) and veins that are prominent on the adaxial leaflet surface, especially notable in dry herbarium specimens. In addition to these three arborescent species, *Zamia urep*, a species with subterranean stems and strongly veined leaflets is also thought to be related to the three slender-stemmed species based on similarities in reproductive morphology (Segalla *et al.*, 2023). A comparative summary of key characters among the four species—*Z. urarinorum*, *Z. multidentata*, *Z. hymenophyllidia*, and *Z. urep*—is provided in Table 1. These species occur in widely separated regions within the upper Amazon basin (Fig. 6).

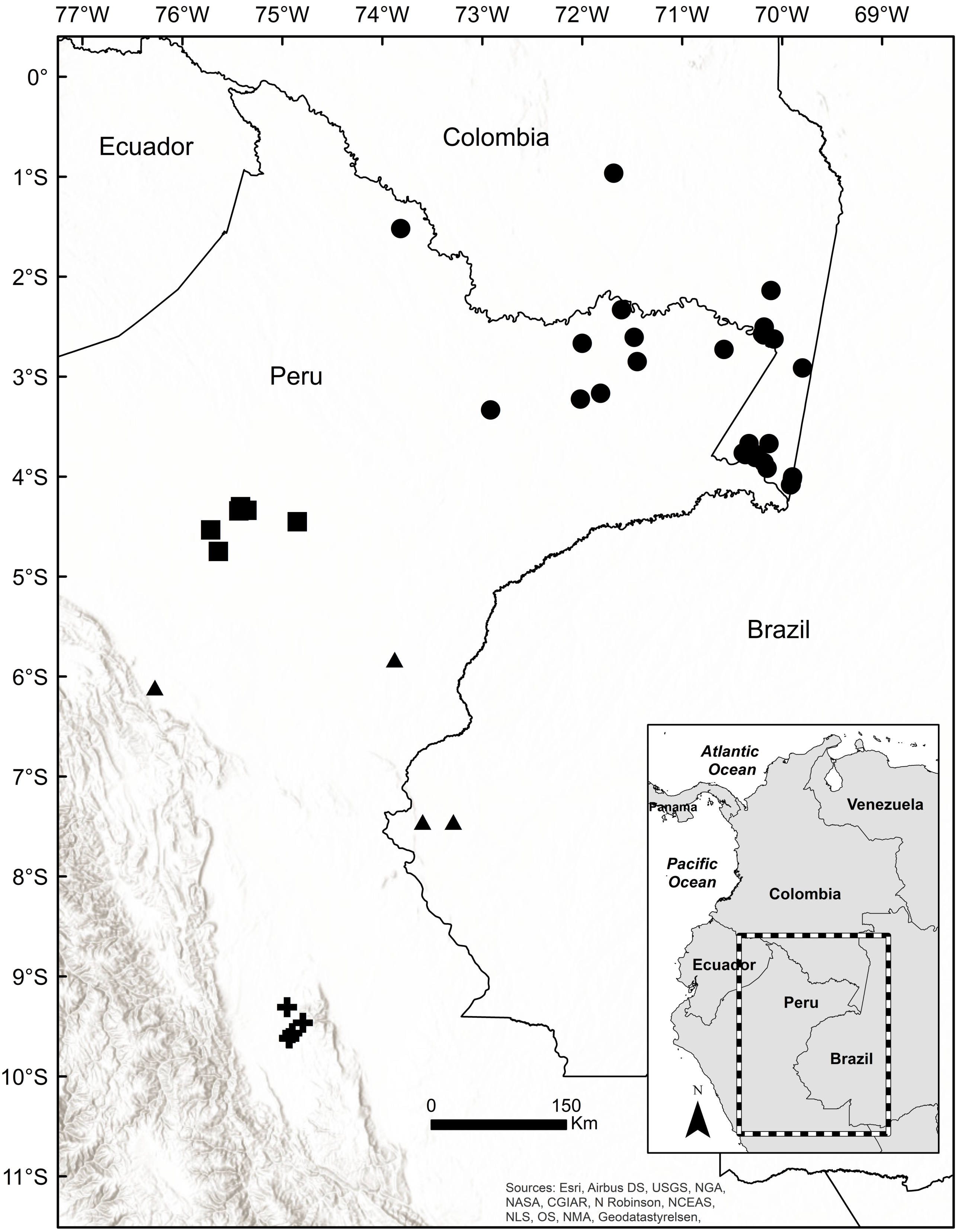

FIGURE 6. Geographic distribution of *Zamia urarinorum* (squares), *Z. multidentata* (triangles), *Z. hymenophyllidia* (circles), and *Z. urep* (crosses). Specimens examined for map preparation listed in Appendix 1.

Zamia urarinorum most closely resembles *Z. multidentata* morphologically, as both species share slender arborescent stems and dentate leaflets. However, the two species differ in several vegetative and reproductive morphological characters (Fig. 7). *Zamia urarinorum* produces fewer leaves per stem (2–6 vs. 8–14), and has leaflets that are finely serrulate, with teeth restricted to the distal third to fourth of the margin, whereas in *Z. multidentata*, they are strongly serrulate and toothed beyond the proximal fourth. Leaflet shape also differs: *Z. urarinorum* has narrowly elliptic to lanceolate leaflets, while those of *Z. multidentata* are ovate to elliptic. In addition, the leaflets of *Z. urarinorum* can exceed twice the length of those in *Z. multidentata* (up to 45.6 cm vs. 21.7 cm).

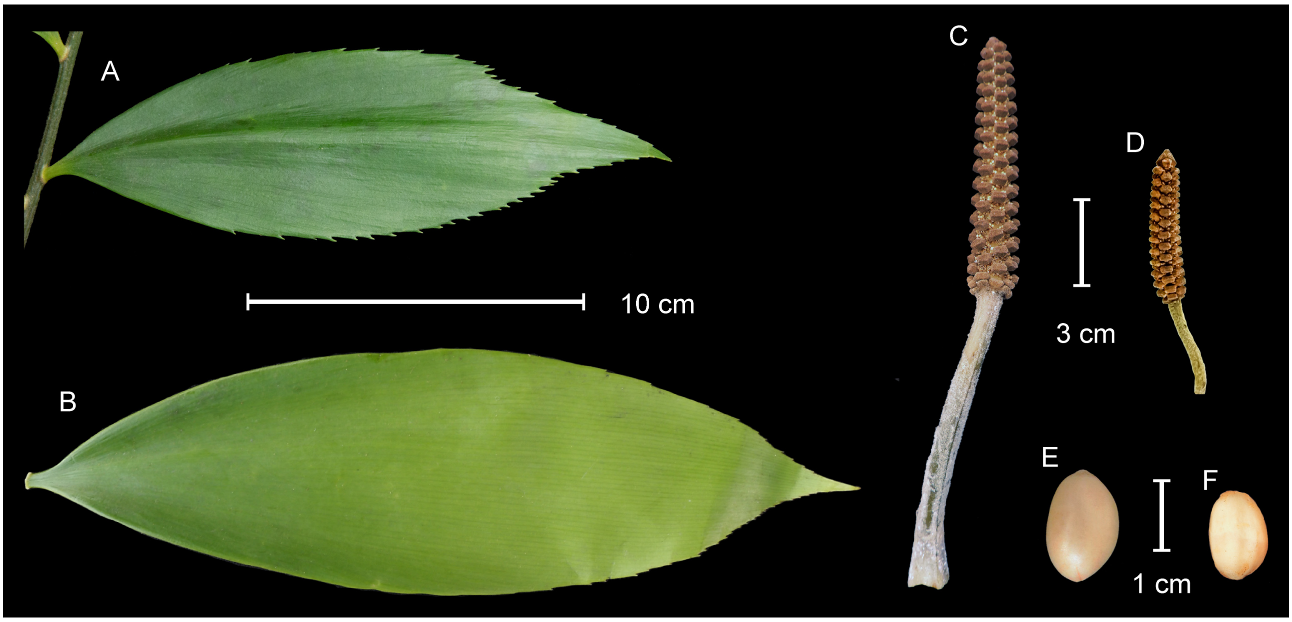

FIGURE 7. Comparison of morphological characteristics of *Zamia multidentata* and *Z. urarinorum*. A. Median leaflet of *Z. multidentata*, adaxial side, B. Median leaflet of *Z. urarinorum*, adaxial side, C. Pollen strobilus of *Z. multidentata*, D. Pollen strobilus of *Z. urarinorum*, E. Sclerotesta of *Z. multidentata* seed, F. Sclerotesta of *Z. urarinorum* seed.

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

	Z. multidentata	*Z. hymenophyllidia*	*Z. urep*	*Z. urarinorum*
Stem habit	Caulescent	Caulescent	Acaulescent	Caulescent
Leaves per stem	8–14	3–15	1–4	2–6
Median leaflet length (cm)	18.2–21.7	16–24	11–20	10.7–45.6
Median leaflet width (cm)	4.3–9.3	4.5–7.2	3–6	2.5–7.8
Median leaflet teeth number	30–49	0–11	18–29	10–41
Leaflet teeth present in proximal half	Yes	No	Yes	Yes
Leaflet adaxially raised longitudinal crease	Present	Present	Absent	Present
Median leaflet veins at center	36–47	21–28	19–24	24–41
Adaxial leaflet vein prominence	Low	Moderate	High	Low
New leaf color	Green	Green	Brown	Green
Microsporangia per microsporophyll	12–17	10–12	9–10	10–17

The species also differ in reproductive morphology: *Z. urarinorum* produces significantly smaller pollen strobili (5.1–5.2 × 1.1–1.2 cm vs. 8.2–8.3 × 1.4–1.5 cm, excluding peduncle), with a tomentose rachis (vs. glabrous in *Z. multidentata*). Its ovulate strobili have shorter peduncles (5.5–11.5 vs. 12.0–17.5 cm) and yield smaller seeds (sclerotesta 10.0–14.0 × 6.8–8.3 mm vs. 13.0–16.4 × 8.6–9.8 mm).

In addition to their morphological differences, the two species also differ markedly in habitat preference and distribution: *Zamia urarinorum* is the only cycad species known to occur in permanently inundated wetland forests, whereas *Z. multidentata* is restricted to well-drained terra firme forests. Their known ranges are geographically distinct and do not overlap. Previously known only from the Serra do Divisor in Brazil (Segalla *et al.*, 2023), *Z. multidentata* is here newly reported for Peru based on recently determined collections from Loreto, representing a significant range extension for the species (Fig. 6, Appendix 1).

Discussion

The genus *Zamia* is the most ecologically diverse in the Cycadales (Nortog & Nicholls 1997: 285), with species occupying a remarkably wide range of environmental niches. These include *Z. pseudoparasitica* Yates in Seemann (1854: 202, 253), the only known obligate epiphytic cycad; several cliff-dwelling species, such as *Z. meermanii* Calonje (2009: 22); and taxa restricted to sandy coastal habitats such as *Z. lucayana* Britton (1907: 311). Some species, such as *Z. encephalartoides* Stevenson (2001: 40) are adapted to arid desert-like environments while others, such as *Z. pyrophylla* Calonje *et al.* (2010: 80), occur in some of the wettest regions of the world. Amid this astounding ecological breadth, Zamia urarinorum stands out as the first known cycad species adapted to permanently waterlogged habitats. This ecological specialization is remarkable given the general intolerance of cycads to saturated soils and may reflect novel physiological adaptations that warrant future study. The ability of this species to persist in these conditions expands our understanding of cycad ecological plasticity and challenges long-held assumptions about the environmental limits of the genus *Zamia*. Our findings contribute to a growing recognition of the genus's ecological and morphological diversity and add to mounting evidence that the Amazon basin harbors an underappreciated diversity of cycads.

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Appendix 1. Specimens examined of Zamia hymenophyllidia, Z. multidentata 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, 132 m, 19 Oct 2010, *I. Huamantupa et al. 14338* (AMAZ!); 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. Lindström et al. 955* (AMAZ 37415!). USA. Illinois: Cultivated *ex* Leticia, Amazonas, Colombia, *T.C. Plowman 11800* (NY Barcode 278468!).

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

PERU: Loreto: Alto Amazonas, 180 m, 29 Aug 2011, *R. Fernández 3610* (USM No. 250334!); Requena, 90–110 m, 12 Oct 2014, M. Ríos *et al.* 4362 (AMAZ!)

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, 315 m, 24 Feb 2002, *A.J. Lindström AL-919* (AMAZ No. 37417!);
275 m, 25 Feb 2002, *A.J. Lindström AL-930* (USM No. 215150!); 335 m, 25 Feb 2002, *A.J. Lindström AL-934* (AMAZ No. 27677!); 24 Feb 2002, *A.J. Lindström AL-936* (FTG!, W Nos. 2012-0010011 / barcode W0215388!, 2012-0010012 / barcode W0215389!); 260 m, 11 May 1989, *C. Listabarth 11-11589* (USM, W!); *C. Listabarth 12-11589* (USM, W!); 260 m, 1 Feb 1993, *C. Listabarth 14-1293* (USM, W!).