A new arborescent species of *Zamia* from the Central Cordillera of Tolima, Colombia (Cycadales, Zamiaceae), with comments on the *Z. poeppigiana* species complex

MICHAEL CALONJE¹, HECTOR EDUARDO ESQUIVEL², DENNIS STEVENSON³, CLAUDIA CALONJE¹, AND DEICY PAVA²

¹ Montgomery Botanical Center, 11901 Old Cutler Road, Miami, FL 33156, U.S.A.; e-mail: michaelc@montgomerybotanical.org

² Herbario TOLI, Grupo de Investigación en Biodiversidad y Dinámica de Ecosistemas Tropicales, Universidad del Tolima, Ibagué, Colombia; e-mail: hesquive@ut.edu.co

³ The New York Botanical Garden, Bronx, NY 10458-5126, U.S.A.; e-mail: dws@nybg.org

Abstract. Zamia tolimensis, a large arborescent species from the Central Cordillera of Tolima, Colombia, is described and illustrated. It is compared to *Z. lindenii* and *Z. poeppigiana*, the two most similar species. From these it is distinguished by leaflets with fewer teeth, sparse prickles on its petioles, beige-yellow ovulate strobili with shorter peduncles, and more microsporangia aggregated into a single group on the abaxial surface of the microsporophyll. Brief descriptions of *Z. lindenii* and *Z. poeppigiana* are also provided, as well as a key to separate the three species.

Key Words: Zamia, Zamiaceae, cycad, Tolima, Zamia lindenii, Zamia poeppigiana.

Only two collections of Zamia from the department of Tolima, Colombia, were known to the authors prior to this publication. The first was collected in 1923 by Russian botanist Georg Woronow, and the second in 1944 by American botanist Elbert Little. Both collections are thought to have occurred within the present-day municipality of Planadas along the Central Cordillera mountain range in southern Tolima. These specimens, representing large arborescent plants with falcate leaflets, superficially resemble specimens of Z. poeppigiana Mart. & Eichler and were cited as belonging to this species in Stevenson's (2001) treatment of Colombian Cycadales. A third collection, von Eggers 14034 (K), was listed in the same treatment as a collection from Tolima under Z. poeppigiana, and was listed as collected in Colombia's Upper Magdalena Valley in Stevenson's (2004a) English version of the treatment. Lindstrom and Idarraga (2009) listed the same specimen as a paratype for Z. incognita Lindstrom & Idarraga, again providing the Upper Magdalena Valley of Colombia as the locality. The collection in question was

examined at five different herbaria (C, F, GH, K, S) and it was determined that it was not collected in Colombia, but rather in the vicinity of Balao, Guayas Province, Ecuador. It has been assigned to *Zamia lindenii* Regel ex André in this paper.

In a recent study of the floristic diversity conducted by members of the "Biodiversidad y Dinámica de Ecosistemas Tropicales" research team of the Universidad del Tolima, two populations of this long-lost taxon were located within the municipality of Rioblanco and identified as a possible new species by the second author on the present paper.

These populations were visited and studied from June 22–24, 2010, during fieldwork led by the Universidad del Tolima and the TOLI herbarium (Ibagué, Tolima, Colombia) in collaboration with Montgomery Botanical Center (Miami, FL) and the Dolmetsch Arboretum (Cali, Colombia). New information uncovered from these populations during the course of this fieldwork has led us to conclude that these plants represent a previously undescribed species, formally described below. Zamia tolimensis Calonje, H. E. Esquivel & D. W. Stev., sp. nov. Type: Colombia. Tolima: Mun. de Rioblanco,1500–1650 m, 23 Jun 2010, H. E. Esquivel, M. Calonje, D. Pava & C. Calonje 3601 (holotype: TOLI; isotypes: CAUP, CHOCO, COAH, COL, CUVC, FAUC, HUA, HUQ, JAUM, PSO, SURCO, TOLI, TULV, UIS). (Figs. 1, 2)

Zamia poeppigiana Mart & Eichler et Z. lindenii Regel ex André aemulans, sed foliolis sparse denticulatis vel integris, megastrobilo flavido-fulvo vel fulvo et erecto, petiolo sparse aculeato, microsporangiis tantum in superficie abaxiali dispositis, in fasciculum singularem aggregatis differt.

Stem epigeous, globose to cylindrical, to 4 m tall and 10-30 cm in diam., erect or sometimes prostrate, typically solitary but occasionally branching. Cataphylls chartaceous, narrowly triangular, light beige-yellow to beige tomentellous, to 15 cm long and 4 cm wide at base. Leaves pinnately compound, up to 34 per stem, erect or arching, to 3.25 m long. Petiole up to 80 cm long, sparsely armed with 0-15(-30) prickles to 3.4 mm long, petiole base swollen and glabrous, up to 6 cm long, and 3.5-6 cm thick. Rachis to 2.45 m long, unarmed or sparsely armed with prickles in the proximal third. Leaflets subopposite to subalternate, up to 46 pairs per leaf, each linear-lanceolate with elongate acuminate tip and a distinct longitudinal furrow, straight to strongly falcate, margins entire or dentate with up to 16 teeth on distal half, light green and glabrous when emerging, glossy bright green at maturity; basal leaflets $39-45 \times 3-3.4$ cm; median leaflets $30-45 \times 2.2-$ 4 cm, spaced 3–5.2 cm apart on rachis; apical leaflets 13–40×2–4 cm. Pollen strobili 4–9 per stem, up to 31×4.5 cm, beige-yellow when emerging, maturing to beige tomentellous, peduncles to 28.5×2.5 cm, beige-yellow tomentellous in new strobili, becoming glabrous green at maturity; microsporophylls arranged in 21-28 orthostichies of 32–36 sporophylls each, obtrullate, $12-13 \times$ 8–9 mm at pollen shedding, distal sterile portion cuneiform truncate encompassing 1/ 4-1/3 of total length of sporophyll, beigeyellow to beige tomentellous, face hexagonal, 6-6.2×6-6.2 mm, distal facet shallowly indented, microsporangia 41-63 per

microsporophyll, 1.5x1 mm, limited to the abaxial surface and aggregated into a single group, proximal half of stalks free of microsporangia. Ovulate strobili solitary, erect, cylindrical, beige-yellow to beige tomentellous, at maturity 35-37×11-13 cm, sterile apex obtuse and 2-6 cm long, strobilus axis glabrous; peduncles 7-9 cm long, 3.5-6 cm wide, beige-yellow to beige, tomentellous, obscured by cataphylls; megasporophylls arranged in 7-10 orthostichies of 9-12 sporophylls each, megasporophyll stalks 3.5-4.5 cm long, glabrous; distal portion peltate with hexagonal to oblong-hexagonal distal face $2-3 \times 4-7.2$ cm and 1-1.5 cm thick, terminal facet broad, slightly protruding, and indented. Ovules attached to flattened tomentellous appendages protruding beyond distal portion. Ovules white, 12-16×10-13 mm. Seeds with sarcotesta ovoid-pyramidal, red at maturity, 3-3.8×2.2-2.6 cm; sclerotesta ovoid to ovoid-pyramidal, 2.8-3.6× 2.1-2.4 cm.

Distribution and habitat.—Zamia tolimensis occurs on steep slopes in clay soils covered by a layer of humus in the understory of montane rain forests and lower montane wet forests, 1400–2000 m. It has only been collected in the department of Tolima, but may also occur in adjacent Huila. In both populations studied, the dominant element of the vegetation was *Phytelephas schottii* H. Wendl, a species of ivory nut palm. The populations studied occurred from 1400-1650 m, but local inhabitants report that the altitudinal range of Z. tolimensis extends above that of the *Phytelephas*. American botanist Elbert Little, who collected this species in 1944 at approximately 2000 m. noted in his specimen label that this Zamia was associated with "Clusia, melastomes, and tree ferns" but did not mention the occurrence of Phytelephas.

The annual precipitation in the extent of occurrence for this species ranges from 2400-2600 mm per year, with a bimodal distribution pattern. The rainiest months are March through May and November; and the driest month is July. The temperature is cool, ranging between 13° and 21° C. (Data derived from GIS analysis using Worldclim 1.4 climate layers as described by Hijmans et al., 2005).

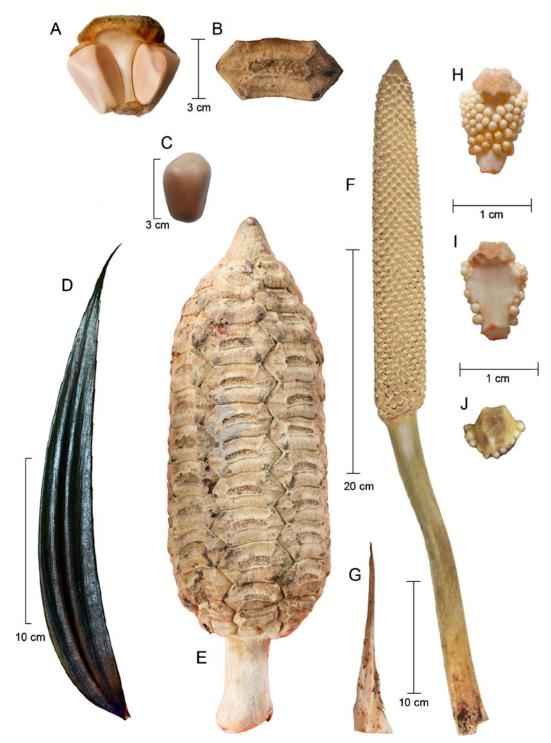


FIG. 1. Reproductive and vegetative characters of *Zamia tolimensis*. A. Near-mature megasporophyll, adaxial view. B. Megasporophyll face, frontal view. C. Mature sclerotesta . D. Median leaflet. E. Near-mature ovulate strobilus. F. Pollen strobilus at pollen-release stage. G. Cataphyll. H. Microsporophyll, abaxial view. I. Microsporophyll, adaxial view. J. Microsporophyll face. All photographs taken of plants from type locality.



FIG. 2. Reproductive and vegetative characters of *Zamia tolimensis*. A. One of the coauthors (HEE) observing plant with near-mature ovulate strobilus. B. Leaf of plant with the first author (MC). C. Two of the coauthors (HEE and DP) collecting data from a 3 m tall plant. D. Juvenile pollen strobili. Photographs taken at type locality.

Etymology.—The specific epithet was chosen to honor Tolima, the department in Colombia where this species has been collected.

Vernacular name.—*Palma de yuca*, referring to its palm-like appearance and the resemblance of the young stem to a tuber of cassava (*Manihot esculenta* Crantz).

Phenology.—Newly emerging, pollenreleasing, and old-pollen strobili were observed in June 2010. Ovulate strobili were observed at various stages, from nearing receptivity to adult sized with pink seeds, the latter possibly two to three months away from nearing maturity.

Ecology.—In both populations, larvae of a species of *Eumaeus* Hübner were observed feeding on emerging leaves. In the type locality, an elongated male strobilus just prior to pollen release was found harboring hundreds of clavicorn beetles of *Pharaxonotha* Reitt., known pollinators of other *Zamia* species (Tang, 1987; Vovides, 1991; Stevenson et al., 1998).

Conservation Status.— The two populations visited were located in small forest fragments of less than one hectare. In the first population, only 11 adult-sized plants were observed with little strobilus production or seedling regeneration. In the type population, 53 adult plants were observed with abundant strobilus production and seedling regeneration. In both cases, local inhabitants assured us that the species was common in other nearby forested areas, but these other forest fragments were not considered safe to travel to at the time due to political turmoil associated with Colombia's armed conflict. The primary threat to this species in these localities appears to be habitat destruction for coffee production and cattle ranching, a process that continues unabated.

The other locations where this species was previously collected in 1923 and 1944 are in the municipality of Planadas, approximately 20 linear km south of the visited populations. These locations were not be visited because of the precarious safety situation in the area. It is unknown if *Zamia tolimensis* is still extant in these locations, but deforestation has been intense throughout the entire distribution range for this species. Based upon all known collections, the extent of occurrence for this species is estimated to be approximately 1000 km². However, considering that over 70 years have passed since these historic collections occurred in a region that has been intensely deforested, we take a precautionary approach to evaluating the conservation status of this species, including only the two presently known populations of this species in the evaluation.

The extent of occurrence for this species is estimated at 25 km² and the area of occupancy is estimated at 0.2 km². Based on the limited extent of occurrence and area of occupancy, the small number of plants observed, the fact that only two small extant populations are known at this time, and the continuing deforestation in the region, we recommend an IUCN Red List Category of CR (Critically Endangered) for this species based on criteria B1ab(i-v)+2ab(i-v)+ D (IUCN, 2001). Specific locality information has been withheld from this paper to minimize the risk of illegal harvesting of this critically endangered species.

Additional specimens examined. COLOMBIA. Tolima: Mun. de Rioblanco, 1400–1600 m, 22 Jun 2010, *Esquivel et al. 3600* (ANDES, FMB, HPUJ, HUAZ, HUC, LLANOS, TOLI, UPTC, VALLE); *Woronow 6992* (LE); *Little 8758* (COL, US).

Zamia tolimensis has morphological affinities with Z. lindenii and Z. poeppigiana Mart. & Eichler, two other large arborescent South American species. All three species appear to belong to a group of closely related species referred to here as the Z. poeppigiana species complex. Of the three species, Z. lindenii and Z. poeppigiana appear to be the most similar, and as a result have been considered by some authors as synonymous (Sabato, 1990; Stevenson, 2001; Nicolalde-Morejón, 2007) or as separate species (Whitelock, 2002; Lindstrom, 2009).

Although the type localities of Zamia lindenii and Z. poeppigiana are located in different countries and separated by the Andes, their descriptions and type specimens are very similar. This was first pointed out by Sabato (1990), who considered both species to be conspecific, and by Stevenson (2001) who placed Z. lindenii under synonymy with Z. poeppigiana. Whitelock (2002) treated both as separate species, mentioning that Z. lindenii had pendent ovulate strobili, linear leaflets, and densely brown-tomentellous emerging leaves compared to the erect strobili, more falcate leaflets, and glossy, glabrous green emerging leaves in *Z. poeppigiana*.

Stevenson (2004a) noted the trans-Andean distribution of the types for both species, and mentioned that seeds of Zamia lindenii were reported to be oval and unflattened, whereas those of Z. poeppigiana were reported to be oblong and flattened. However, he pointed out that the difference needed to be confirmed with herbarium material. In a subsequent paper, Stevenson (2004b) reported that oblong and flattened seeds were also observed in specimens and fresh seeds of Z. lindenii. Nicolalde-Morejón (2007) noted the trans-Andean distribution of both species and the fact that relationship between these two species needed to be resolved by obtaining additional morphological and phylogenetic evidence. Most recently, Lindstrom (2009) formally segregated the two species based on their trans-Andean distribution, alleged differences in seed shape, strobili habit (pendent vs. erect), and leaflet length.

Besides the separation of both species by the Andes, the most useful characters mentioned by previous authors appear to be the pendent ovulate strobili, unique to *Zamia lindenii*, the differences in the amount of tomentum on the leaflets and petioles of new leaves, and general differences in leaflet shape, the latter which are quite variable and not always useful as a diagnostic character. Leaflet width appears to be more useful in distinguishing the two species than leaflet length, and seed shape is variable for both species, with both having seeds that can be oval and unflattened or oblong and flattened, even within the same strobilus.

Character differences have not been particularly tractable in the past because of a paucity of collections. In the past 20 years numerous new collections have been made that have allowed for the discrimination of these two species. While *Z. lindenii* has been extensively collected in Ecuador and is relatively common in botanical gardens, *Z. poeppigiana* from Peru remains more enigmatic, as it has not been collected as much and is very rare in botanical gardens. Nevertheless, we feel that reasonable amount of new information has now been accumulated to resolve the question.

Zamia tolimensis, Z. lindenii, and Z. poeppigiana are large, arborescent plants of similar dimensions with leaflets exhibiting a distinct longitudinal crease and margins with distinctly spreading teeth (Fig. 1). However, the median leaflets of Z. tolimensis are sometimes entire, or dentate with 1–16 teeth distally, whereas the leaflets of Z. poeppigiana and Z. lindenii typically have 18 or more teeth beginning in the proximal half of the leaflet. Zamia tolimensis leaflets most closely resemble those of Z. poeppigiana. Both are normally narrowly lanceolate (2.5–4 cm wide) and often strongly falcate, whereas leaflets of Z. lindenii are broadly lanceolate (3.7-4.8 cm wide) and straight (Fig. 3). However, leaflet shape is variable in all three species, and both linear and falcate leaflets can be found in each species, even within a single leaf.

Zamia tolimensis petioles are sparsely armed, with up to 30 prickles (typically less than 15), these rarely extending beyond the proximal third of the rachis, whereas the petioles of Z. poeppigiana and Z. lindenii are moderately armed with 35 or more stout prickles, these often extending into the distal half of the rachis.

The ovulate strobili of *Zamia tolimensis* are beige-yellow to beige, the megasporophyll distal portions slightly protruding, with a broad depressed terminal facet along the same plane as the sporophyll face. In contrast, the ovulate strobili of *Z. poeppigiana* and *Z. lindenii* are reddish-brown to dark brown with the sterile peltate distal portions of the megasporophylls strongly protruding to a narrow depressed terminal facet. The ovules of *Zamia tolimensis* are attached to distinctive

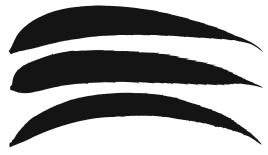


FIG. 3. Leaflet silhouettes of three species of Zamia. Top: Z. tolimensis, from type locality. Middle: Z. lindenii, from Montgomery Botanical Center accession # 20001000*F. Bottom: Z. poeppigiana, from Plowman & Ramírez 7575 (MO).

flattened tomentellous appendages extending laterally from the distal peltate portion of the sporophyll. In contrast, the ovules of the other two species are attached directly to the rear side of the pelate portion of the sporophyll. Zamia tolimensis has ovulate strobili that remain erect at maturity, whereas those of Z. poeppigiana are typically leaning, and those of Z. lindenii are pendent. The seeds of Z. tolimensis are ovoid to ovoid-pyramidal in shape, whereas the seeds of both Z. lindenii and Z. poeppigiana are oblong-ovoid-pyramidal or oblong-ovoid, and often strongly flattened longitudinally. The sclerotesta of the three species are similar in length, but the sclerotesta of Z. tolimensis, exceeding 2.2 cm in width, is wider than that of the other two species, which have sclerotestas that do not exceed 1.8 cm in width.

The pollen strobilus of Zamia tolimensis is beige-tomentellous at maturity, whereas that of Z. lindenii is dark brown-tomentellous at maturity. Live pollen strobili of Z. poeppigiana have not been examined by us, but herbarium specimens of pollen strobili appear lighter brown to tan compared to those of Z. lindenii, which are dark brown on both live plants and herbarium specimens. The microsporangia of all three species are limited to the abaxial surface of the microsporophyll. The microsporangia are aggregated into a single group of 40 or more per microsporophyll in Z. tolimensis, whereas in the other two species they are separated into two distinct groups with fewer than 38 microsporangia.

Zamia tolimensis is the only described species of Zamia known to occur on the Central Cordillera of Colombia, and its distribution is disjunct from those of Z. lindenii and Z. poeppigiana (Fig. 4). It occurs from 1400-2000 m on the eastern slope of the Central Cordillera of the Andes in Colombia, an altitudinal range that is unusual for Zamia in the country. Most Colombian species of Zamia occur in warm climates below 1000 m, and only Z. montana (1750-2080 m) and Z. wallisii (1000-1500 m) are known to occur at comparable elevations. Zamia poeppigiana occurs on the eastern slope and Amazonian lowlands of Peru and Brazil from 155-1300 m, and Z. lindenii occurs in the western slope of the Andes and the Pacific lowlands of Ecuador and extreme

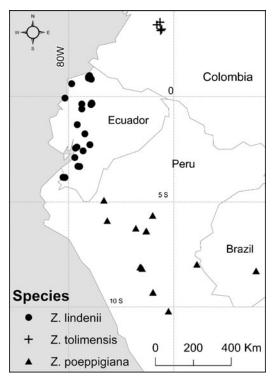


FIG. 4. Distribution of *Zamia lindenii*, *Z. poeppigiana*, and *Z. tolimensis*.

northern Peru from near sea level to 1050 m. Zamia poeppigiana and Z. lindenii are geographically separated by the Andes and also occur at different latitudes, with the southernmost Z. lindenii collection occurring at 3° 50' S, and the northernmost Z. poeppigiana collection occurring at 4° 54' S. Although there are collections of Z. lindenii from the Pacific lowlands of Ecuador about 50 km from the Colombian border, to our knowledge there are no specimens of either species from Colombia. Schuster (1932) listed a specimen of Zamia (Lehmann 600) near Barbacoas, Nariño, as Z. poeppigiana; however, this specimen could not be located and was probably destroyed at B during World War II. All extant collections of Zamia we have examined come from the vicinity of Barbacoas (i.e., Bernal & Galeano 892, COL, NY; Bernal & Hammel 1324, COL, MO) are Z. roezlii Regel.

A key to Z. tolimensis, Z. poeppigiana, and Z. lindenii is provided below. For the latter two species, revised descriptions are provided to further clarify geographic distribution and characters.

Key to the species of the Zamia poeppigiana complex

- 1. Median leaflets with marginal teeth beginning below distal half, typically 18 or more per leaflet; petioles moderately or strongly armed with 35 or more prickles, these extending beyond proximal third of rachis; microsporangia less than 38 per microsporophyll aggregated into two separate groups; ovulate strobili dark brown to grey, with tomentellous cone axes and with long peduncles (>12 cm), extending beyond cataphylls; sclerotesta narrower than 1.8 cm wide.
 - Median leaflets typically broadly lanceolate, usually>3.8 cm wide; petioles on young leaves densely tomentellous; ovulate strobili pendent at maturity, mature megasporophyll stalks densely tomentellous Ecuador and northern coastal Peru.
 Median leaflets typically parrowly lanceolate, usually
 S cm wide; petioles on young leaves clabrow; ovulate strobility periods on young leaves on young leaves
- Zamia lindenii Regel ex André, Ill. Hort. 22: 23, pl. 195. 1875. *Aulacophyllum lindenii* (Regel ex André) Regel, Gartenflora 25: 141. 1876. Type: plate 195 (lectotype, designated by Stevenson and Sabato, 1986; epitype, designated by Lindstrom, 2009: Ecuador: ex. Hort. Linden, 1880, *B. Roezl s.n.*, K).

Stem epigeous, globose to cylindrical, to 4 m tall and 10-30 cm wide, erect or prostrate, typically solitary but occasionally branching. Cataphylls chartaceous, narrowly triangular, tomentellous, to 14 cm long and 3 cm wide at base. Leaves pinnately compound, up to 30 per stem, erect to arching, to 3 m long; petiole to 80 cm long, rachis to 220 cm long; petiole and rachis densely tomentellous on young leaves, gradually becoming glabrous with some trichomes persisting on abaxial side of rachis, moderately to strongly armed with prickles to 4 mm long throughout petiole and extending to the distal half of rachis or beyond. Leaflets subopposite to subalternate, to 44 pairs per leaf, broadly lanceolate with a distinct longitudinal furrow, typically straight but occasionally moderately falcate, margins dentate with 22-60 teeth to 3 mm long on distal 3/4-1/2 of leaflet, light green and densely tomentellous when emerging, glossy bright green at maturity; median leaflets 22-42×(2.1-)3.6-4.8 cm. *Pollen strobili* one to many per stem, to 38×4 cm wide, dark brown tomentellous throughout all stages of maturity, peduncle to $23 \times 1.5 - 2.2$ cm, brown tomentellous at all stages of maturity; microsporophylls arranged in 18-26 orthostichies of 32-36 sporophylls

each, obtrullate, $11-12 \times 6-7$ mm at pollen shedding; peltate sterile portions strongly protuberant, 4-5 mm long, encompassing 1/3to 1/2 of total length of sporophyll, dark brown tomentellous; face hexagonal, 6–7 mm tall, 6-7 mm wide, distal facet shallowly indented, microsporangia 24-32 per microsporophyll, limited to the abaxial surface and separated into two separate groups aggregated along the margin of the sporophyll blade. Ovulate strobili one to several per stem, pendent at maturity, dark-brown tomentellous, when young, light brown to grey at maturity, $35-50 \times 10-15$ cm, peduncle to $25 \times 2 - 2.5$ cm, extending beyond cataphylls, dark-brown tomentellous when young, gradually progressing to green and glabrous at maturity; strobilus axis and megasporophyll stalks densely tomentellous; megasporophylls arranged in 8-14 orthostichies of 6-25 sporophylls each, 4-5×2-3 cm with stalks 3-3.5 cm long, faces of sterile peltate distal portions hexagonal to oblonghexagonal, $2-3 \times 2.5-3$ cm, 1-1.5 cm thick, protruding to small, depressed terminal facet 0.5×1 cm. Seeds with sarcotesta ovoid pyramidal to oblong pyramidal, often somewhat flattened longitudinally, red at maturity, 2.8- $3.5 \times 1.4 - 2.1$ cm wide, and sclerotesta $2.5 - 3.2 \times 1.4 - 2.1$ cm wide, and sclerotesta $2.5 - 3.2 \times 1.4 - 2.1$ 1.2-1.9 cm wide. 2n=16 (Norstog, 1980).

Vernacular names.—"Monte de piña", "palma de goma", "palma tabaquillo", "pichi-richi".

Additional specimens examined. ECUADOR. Azuay: 850 m, Steyermark 52703 (F, NY, P); 800 m, Hirsch E370 (F). Bolívar: Lockwood 825 (GH). Chimborazo: Rose & Rose 22613 (US). El Oro: 500 m, Balslev et al. 62526 (AAU). Esmeraldas: Beck et al. 2214 (NY); Clark et al. 9642 (NY); 280 m, Gentry et al. 72867 (MO); 100 m, Holm-Nielsen et al. 25747 (AAU); 130 m, Holm-Nielsen et al. 25816 (AAU); 200 m, Holm-Nielsen et al. 25852 (AAU); 200 m, Janovec et al. 1275 (NY); Ortíz et al. 44 (NY); Pennington 1770 (K), Pennington et al. 15019 (K). Guayas: 6-350 m, Cerón et al. 17793 (MO); 350-380 m, Cerón 20073 (MO); von Eggers 14034 (C, F, GH, K, S); Haenke 2302 (NY); Lehmann 5292 (K). Los Ríos: 220 m, Dodson & McMahon 4289 (AAU, SEL); 70 m, Dodson & Gentry 12698 (MO, SEL); Horn s. n. (US); Ståhl & Andersson 6309 (NY); Thomas & Rios 6724 (NY). Manabí: 50 m, Neill et al. 11272 (MO). Pichincha: 1050 m, André 3687 (F, GH, K, NY, P, US); 1125 m, Balslev et al. 62517 (AAU); 100 m, Kvist 40203 (AAU, MO, NY); 1000-1400 m, Dodson & Gentry 9715 (MO, SEL); 1300 m, Dodson & Gentry 13694 (SEL); 1050 m, Holm-Nielsen et al. 24865 (AAU). Without precise locality: von Eggers 14895 (F); Horn s.n. (US); Rimbach 85 (F); Rimbach 252 (US); Rimbach 568 (S).

PERU. Tumbes: 720 m, *Diaz et al.* 5117 (MO); 600–800 m, *Simpson & Schunke* 428 (COL, F, NY, US).

- Zamia poeppigiana Mart. & Eichler, Fl. Bras. 4(1): 414–416, t. 109, (1863). Type: Peru. Maynas Alto, Tocache River, 1830, *E.F. Poeppig s.n.* (lectotype, designated by Stevenson and Sabato, 1986: F, ex W; isotype: GH!, ex W).
- Zamia baraquiniana Hort. Gard. Chron. 349. 1868; et Regel, Gartenfl. 27: 7. 1878. Type: ex Horto Petropolitano, *E.A. von Regel s.n.* (neotype, designated by Stevenson and Sabato, 1986: LE; isoneotype: K).
- Zamia wielandii Schuster, Pflanzenr. 99: 149. 1932. nom. illegit, superfluous name for Z. baraquiniana Regel.

Stem epigeous, globose to cylindrical, to 3 m tall and 10-30 cm wide, erect or prostrate, typically solitary but occasionally branching. Cataphylls chartaceous, narrowly triangular, grey-tan tomentellous, to 13×3 cm at base. Leaves pinnately compound, up to 35 per stem, erect to arching, to 3 m long, petiole to 90 cm long, rachis to 210 cm long; petiole and rachis glabrous, moderately to strongly armed with prickles to 4 mm long throughout the petiole and extending to the distal half of rachis or beyond. Leaflets subopposite to subalternate, to 49 pairs per leaf, narrowly lanceolate with a distinct longitudinal furrow, typically falcate but occasionally straight, margins dentate with 20-42 teeth on distal 3/ 4-1/2 of leaflet, light green and glabrous when emerging, dark green at maturity; median leaflets 32-45×2.5-3.8 cm. Pollen strobili one to many per stem apex, to 27×2.5 –4 cm, peduncle to $15 \times 1.5 - 2$ cm; microsporophylls arranged in 18-22 orthostichies of 40-50 sporophylls each, obtrullate, 8.2-8.6×6.4-7.3 mm at pollen shedding; distal peltate sterile portions strongly protuberant, 2.6-3.2 mm long, encompassing 1/3 to 2/5 of total length of sporophyll; face hexagonal $4-5 \times 4-5$ mm, distal facet shallowly indented; microsporangia 24-36 per microsporophyll, limited to the abaxial surface and separated into two separate groups aggregated along the sporophyll blade margin. Ovulate strobili one to several per crown, leaning at maturity, reddish-brown tomentellous when young, dark brown at maturity, 35-50×10-12 cm, peduncle to 15 cm long, 2-3 cm diameter, extending beyond cataphylls, light to dark brown tomentellous, strobilus axis densely tomentellous; megasporophylls arranged in 8–14 orthostichies of 8–30 sporophylls each, 4-5×2.2-3 cm with glabrous stalks 3.4-4 cm long, faces of sterile peltate distal portions hexagonal to oblong-hexagonal, 2- $3 \times 2.2 - 3$ cm, 1-1.5 cm thick, protruding to a small, depressed terminal facet, to 1×0.5 cm. Seeds with sarcotesta ovoid pyramidal to oblong pyramidal, often somewhat flattened longitudinally, red at maturity, $3-4 \times 1.1-$ 1.6 cm, sclerotesta $2.5-3.2 \times 1-1.5$ cm.

Vernacular name.—Macha piña (Peru), catuabao (Brazil).

Additional specimens examined. BRAZIL. Acre: Tarauacá, *Daly et al. 8342* (NY); *Figueiredo et al. 874* (NY).

PERU. Amazonas: Prov. Bagua, 550 m, Vásquez et al. 20108 (MO); 695 m, Plowman 5536 (GH). HUÁ-NUCO: 750–800 m, Plowman & Ramírez 7575 (AAU, F, GH, MO, NY); 700–780 m, Plowman et al. 11232 (F, FTG, GH, K, MO, NY). LORETO: 155–210 m, Williams 5373 (F, US). PASCO: 380 m, Foster 7933 (MO). SAN MARTÍN: 500 m, Gentry et al. 25710 (MO); Plowman 7601 (F); 700 m, Rimachi 5185 (K, MO, NY); 750–1000 m, Rimachi 5356 (MO); 475 m, Plowman & Schunke 11543 (F, K, MO). UCAYALI: 800–850 m, Graham 2694 (F, FTG).

Acknowledgments

The herbarium of Universidad del Tolima (TOLI) kindly provided the herbarium infrastructure for preparation and preservation of herbarium specimens. Edgar Gómez and Her-

iberto Díaz, local guides in the Municipio de Rioblanco, provided assistance with the fieldwork. Libby Besse, James Graham (The Field Museum, Chicago, Illinois), Chris Hardy (Millersville University), and Loran Whitelock provided photographs and/or information on Zamia poeppigiana from Peru and Ecuador and Douglas Daly (New York Botanical Garden) for plants in Brazil. Favio González (Universidad Nacional de Colombia) and Patrick Griffith (Montgomery Botanical Center) provided helpful comments on the manuscript. Montgomery Botanical Center provided funding for fieldwork in support of this study. Live plants of Zamia lindenii were studied at Montgomery Botanical Center, Fairchild Tropical Botanical Garden, Marie Selby Botanical Garden, and The New York Botanical Garden. Support to Dennis W. Stevenson was provided by NSF grants BSR 8607049, EF 0629817, and IOS 0421604.

Literature Cited

- Hijmans, R. J., S. E. Cameron, J. L. Parr, P. G. Jones & A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25: 1965–1978.
- **IUCN.** 2001. IUCN Red List categories and criteria: Version 3.1. IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, U.K.
- Lindstrom, A. J. 2009. Typification of some species names in *Zamia* L. (Zamiaceae), with an assessment of the status of *Chigua* D. Stev. Taxon 58: 265–270.

- Lindstrom, A. J. & A. Idarrága. 2009. Zamia incognita (Zamiaceae): the exciting discovery of a new gymnosperm from Colombia. Phytotaxa 2: 29–34.
- Nicolalde-Morejón, F. 2007. Taxonomía, distribución y estado de conservación de Zamia en Ecuador. Memoirs of the New York Botanical Garden 97: 45–63.
- Norstog, K. 1980. Chromosome numbers in Zamia (Cycadales). Caryologia 33: 419–428.
- Sabato, S. 1990. West Indian and South American cycads. Memoirs of the New York Botanical Garden 57: 173–185.
- Schuster, J. 1932. Cycadaceae. In: A. Engler (ed.), Das Pflanzenreich 99(4): 1–168. W. Engelmann, Leipzig.
- Stevenson, D. W. 2001. Cycadales. Flora de Colombia 21: 1–92.
- ——. 2004a. Cycads of Colombia. Botanical Review 70: 194–234.
- 2004b. Zamiaceae of Bolivia, Ecuador, and Peru. Pp. 173–194. *In:* T. Walters & R. Osborne (eds.), Cycad classification: Concepts and recommendations. CABI Publishing, Wallingford, England.
- —, K. Norstog & P. Fawcett. 1998. Pollination biology of cycads. Pp. 277–294. *In:* S. Owens & P. Rudall (eds.), Reproductive Biology: In systematics, conservation, and economic botany. Royal Botanic Gardens, Kew.
- —, & S. Sabato. 1986. Typification of names in *Zamia* and *Aulacophyllum* (Zamiaceae). Taxon 35: 134–144.
- Tang, W. 1987. Insect pollination in the cycad Zamia pumila (Zamiaceae). American Journal of Botany 74: 90–99.
- Vovides, A. P. 1991. Insect symbionts of some Mexican cycads in their natural habitat. Biotropica 23: 102–104.
- Whitelock, L. M. 2002. The Cycads. Timber Press, Portland, OR.