A NEW CLIFF-DWELLING SPECIES OF *ZAMIA* (ZAMIACEAE) FROM BELIZE

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ABSTRACT

Zamia meermanii (Zamiaceae), a new cliff-dwelling species from Central Belize is described. It is distinguished by having 1 to 3 pendent leaves carrying coriaceous leaflets that are entire or crenulately notched on distal third, distinctly nerved on the adaxial surface, and bearing persistent tomentum on the abaxial surface. It is compared to *Zamia furfuracea* L.f. which it most closely resembles, as well as to Mesoamerican cliff-dwelling species *Zamia cremnophila* Vovides, Schutzman & Dehgan and *Zamia sandovalii* Nelson.

RESUMEN

Se describe **Zamia meermanii** (Zamiaceae), una nueva especie de Belize Central que crece en precipicios. Se puede distinguir porque tiene de 1 a 3 hojas colgantes que llevan folíolos coriáceos enteros o con muescas crenuladas en el tercio distal, con nerviación apreciable en la superficie adaxial, y tomento persistente en la superficie abaxial. Esta especie se compara con *Zamia furfuracea* L.f., la especie más semejante, y también se compara con las otras especies Mesoamericanas que también crecen en precipicios, que son *Zamia cremnophila* Vovides, Schutzman & Dehgan y *Zamia sandovalii* Nelson.

INTRODUCTION

Zamia is a New World genus ranging from the southeastern USA to Bolivia. It currently comprises 57 species (Hill et al. 2007) and is considered to be the most ecologically and morphologically diverse cycad genus (Norstog & Nicholls 1997). It includes species growing in areas with extremely high rainfall, such as *Z. roezlii* Linden from the Colombian Chocó region, and adjacent coastal Ecuador to species growing in full sun in extremely dry conditions, such as *Z. encephalartoides* Stevenson from the Santander region of Colombia. The genus also includes the only known obligately epiphytic cycad, *Z. pseudoparasitica* Yates, as well as two cliff-dwelling species: *Z. cremnophila* Vovides, Schutzman & Dehgan, and *Z. sandovalii* Nelson.

Jan Meerman, a Dutch ecologist who resides in Belize, discovered a third cliff-dwelling species of *Zamia* in February of 1999 together with Martin Meadows of the Belize Botanic Gardens during a Rapid Ecological Assessment of a private protected area. Since discovering the plant, Meerman has been collecting ecological and distribution data for this species, some of which is used in this description. He was instrumental in bringing a team from Montgomery Botanical Center to Belize to study this taxon and other Belizean Zamiaceae in August and September of 2008.

DESCRIPTION

Zamia meermanii Calonje, sp. nov. (**Figs. 1–2**). TYPE: BELIZE. BELIZE DISTRICT: 60 m, 28 Aug 2008, *M. Calonje, J. Meerman & P. Griffith BZ08-152* (HOLOTYPE: BRH; ISOTYPES: FTG, MO, NY, XAL).

Species insignis habitui scopulicolus; caudex brevis, 1–3 foliis pendulis praeditus; foliola coriacea, marginibus integris vel crenulatis triente apicali, nervis distinctis adaxialibus, et paginis abaxialibus ad maturitates pubescentibus pro parte maxima secus margines.

Stems globose to cylindrical, to 27 cm long and 18 cm wide, solitary or occasionally branching on older plants. Cataphylls chartaceous, stipulate, triangular with lanceolate apex. Leaves 1–3 per stem, pendent, 42–146.5 cm long. Petiole 26–60 cm long with abruptly swollen base 2–3 cm wide, variously unarmed or carrying numerous prickles (50+) up to 3 mm tall. Rachis 50 to 109 cm long, unarmed or bearing a few prickles (< 20). Leaflets 7–23 pairs per leaf on adult plants, spaced 3–8 cm apart from each other with the point of attachment to the rachis 8.5–13.3 mm wide, obovate to oblanceolate or narrowly oblong, coriaceous, 12.5–32 cm long, 3.4–7.5 cm wide, with 31–56 veins prominently raised on adaxial surface, visible but not

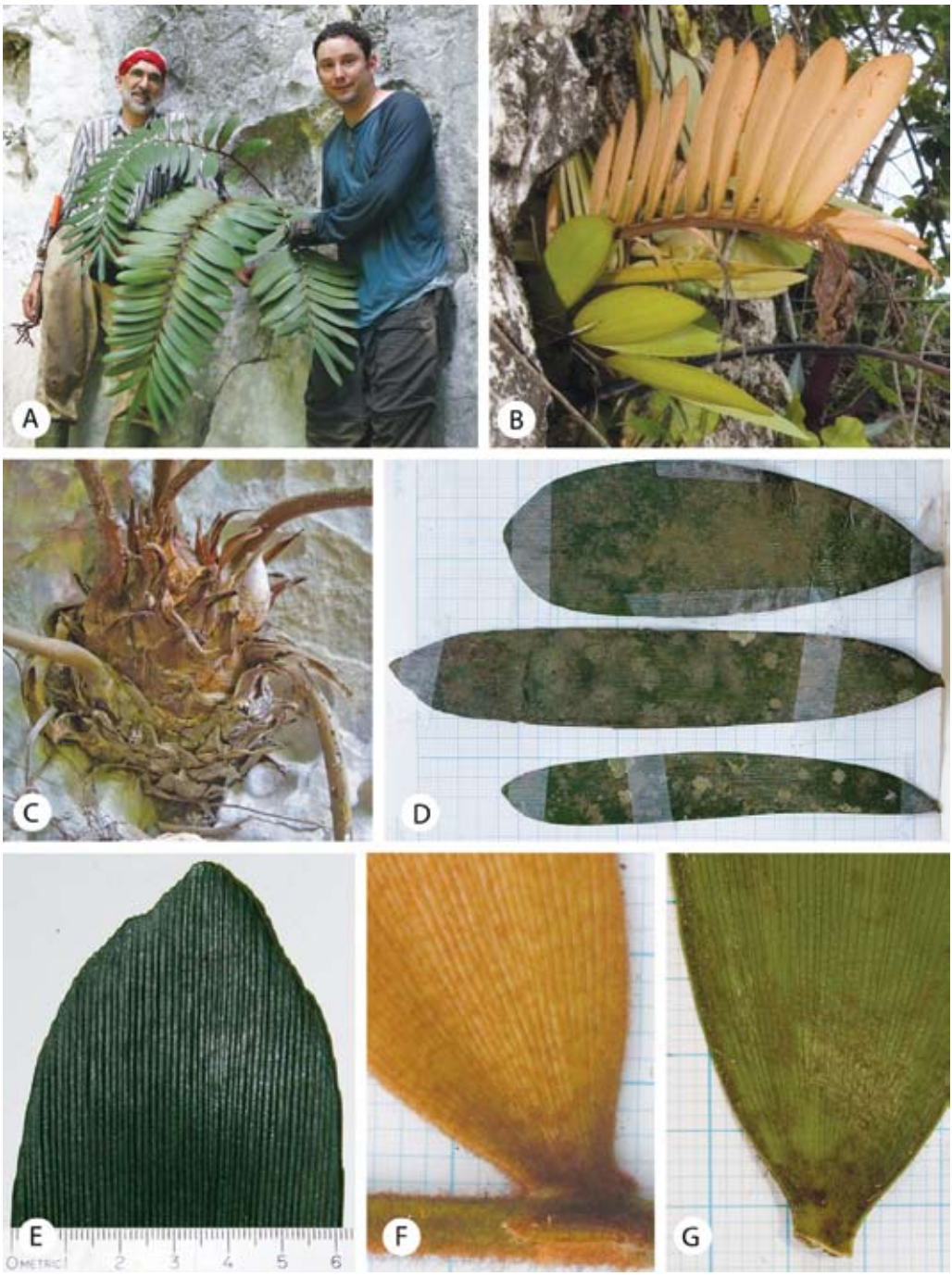

Fig. 1. (A) Habit of plant, Jan Meerman on left, Michael Calonje on right. (B) Emergent leaf showing leaf damage by *Eumaeus toxea* herbivory. (C) Detail of trunk and petioles. (D) Variation in leaflet shape. (E) Closeup of apex on adaxial surface of leaflet showing raised veins and crenulate teeth. (F) Closeup of rachis and leaflet base of immature leaf showing distinctive orange tomentum. (G) Closeup of abaxial surface near leaflet base showing persistent tomentum on adult leaf. A and C represent Calonje et al. BZ08-152; B and F represent Calonje et al. BZ08-156; D, E and G represent Calonje et al. BZ08-125.

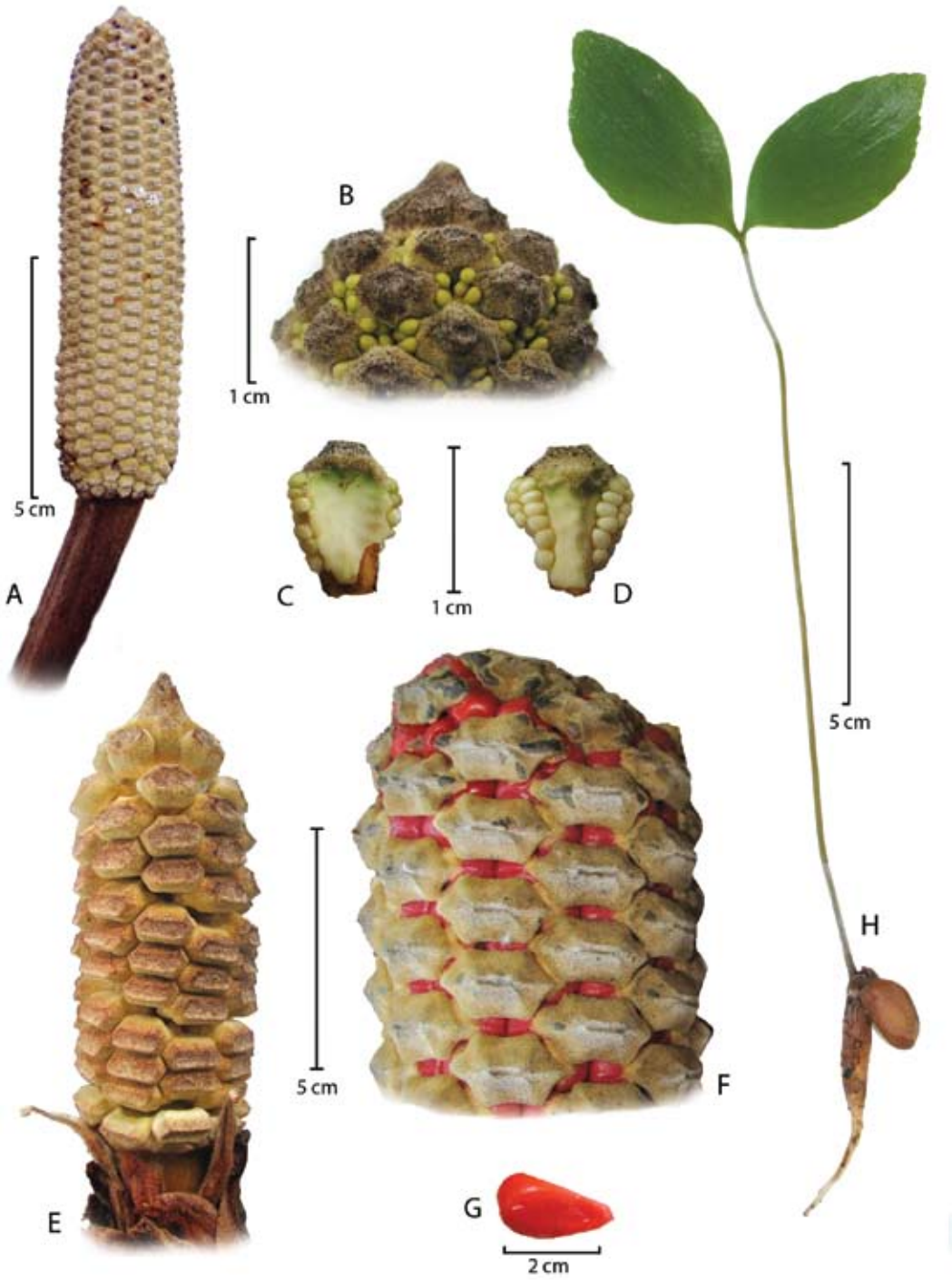

Fig. 2. (A) Immature microsporangiate strobilus. (B) Apex of microsporangiate strobilus just prior to pollen release. (C) Adaxial view of microsporophyll. (D) Adaxial view of microsporophyll. (E) Megasporangiate strobilus at receptive stage. (F) Megasporangiate strobilus at seed dehiscience. (G) Mature seed with sarcotesta. (H) Seedling with eophyll. Photographs A–E from cultivated specimens at Greenhills Botanical Collections; F and G from megasporangiate strobilus collected in habitat by Martin Meadows; H represents Calonje et al. BZ08-152.

protuberant on abaxial surface; margins entire or crenulately notched in the distal third; surface on emergent leaves reddish-brown, but densely white-tomentose, turning cream-colored with saffron-orange tomentum, and gradually maturing to green and glabrous adaxially, with some persistent brown tomentum abaxially along leaflet margins and near the point of attachment to the rachis. Eophylls typically carrying a single pair of ovate leaflets. Microsporangiate strobilus conical-cylindrical, erect, at pollen release 13–16 cm long, 2.2–2.5 cm diam., occurring individually or in groups of 2–5 or more, cream to brown colored; peduncle 9–10 cm long, 0.9–1 cm diam., covered by ferrugineous pubescence. Microsporophylls arranged in 12–18 columns, 17–30 rows; obtrullate, distal face hexagonal to oblong-hexagonal, 5.5–6 mm wide, 2.5–3 mm tall, and 1–2 mm thick ; microsporangia spheroidal, 1–1.6 mm diam., present on abaxial surface, absent on adaxial surface, 22–28 per microsporophyll arranged in two separate groups along margins. Megasporangiate strobilus cylindrical, solitary, erect at maturity, 12–20 cm long, 6–7 cm diam., tan to light-brown tomentose from emergence to maturity; peduncle 8–12 cm long, 1.5–3 cm wide, tan to brown tomentose. Megasporophylls arranged in 6–10 columns, 7–15 or more rows; distal face oblong-hexagonal, 1.5–2.2 cm wide, 1.0–1.5 cm tall, 1–1.2 cm thick, extruded to a narrow, depressed terminal facet. Seeds with sarcotesta ovoid-pyramidal, red at maturity, 2.0–2.5 cm long, 1–1.2 cm wide; sclerotesta ovoid to ovate, 1.5–1.8 cm long, 0.9–1.1 cm wide.

Other vouchers examined: **BELIZE. Belize District:** 40–70m, 25–26 Aug 2008, *M. Calonje & J. Meerman* BZ08-120 (FTG), BZ08-122 (FTG), BZ08-124 (FTG), BZ08-125 (BRH, FTG, MO, NY, XAL), BZ08-126 (FTG), *BZ08-140* (FTG), *BZ08-146* (FTG); 60 m, 28 Aug 2008, *M. Calonje, J. Meerman & P. Griffith* BZ08-154 (FTG); 70m, 27 Aug 2008, *M. Calonje, J. Meerman & P. Griffith* BZ08-156 (BRH).

Etymology.—The specific epithet honors Jan Meerman, who discovered the species.

Distribution and habitat.—Endemic to Cayo and Belize Districts in Belize, it occurs in seasonally dry tropical evergreen broad-leaved lowland forests on steep karstic hills as defined by Meerman and Sabido (2001), reaching elevations of up to 200 m. The arboreal vegetation is characterized by species such as *Comocladia guatemalensis* Donn. Sm., *Metopium brownei* (Jacq.) Urb., *Plumeria rubra* f. *acutifolia* (Poir.) Woodson, *Bursera simaruba* (L.) Sarg., *Forchhammeria trifoliata* Radlk. var. *trifoliata* , *Coussapoa oligocephala* Donn.Sm., *Caesalpinia gaumeri* Greenm., *Erythrina standleyana* Krukoff, *Pseudobombax ellipticoideum* A. Robyns, and *Thouinia paucidentata* Radlk. Disturbed open spots are characterized by the endemic *Louteridium donnell-smithii* S. Watson. These forests are semi-deciduous, with more than half of the trees being leafless for at least one month during the dry season, and with several species being leafless for four months per year. This semi-deciduous character implies that the amount of light reaching the forest floor (and under-canopy cliffs) is dramatically different between the dry and rainy seasons.

Scattered throughout these hills are vertical limestone cliffs where this species is found. It appears to be an obligate cliff-dwelling species, as it is typically found growing in cracks and crevices on sheer vertical walls and absent from the surrounding forest floor. The cliff faces are largely bare but depending on the level of weathering of the rock and the amount of shading they receive, the accompanying cliff vegetation consists largely of herbaceous plants, hemi-epiphytes and vines such as *Adiantum tenerum* Sw., *Agave angustifolia* Haw., *Anthurium schlechtendalii* Kunth subsp. *schlechtendalii*, *Anthurium verapazense* Engl., *Philodendron radiatum* Schott var. *radiatum*, *Clusia* sp., *Begonia sericoneura* Liebm., *Pitcairnia recurvata* (Scheidw.) K. Koch, *Tradescantia spathacea* Sw., *Passiflora cobanensis* Killip, and *Passiflora xiikzodz* J.M. MacDougal subsp. *xiikzodz*.

Climate.—The average annual precipitation within this species' range is estimated at 2000–2500 mm, with a distinct dry season occurring from February through May. The wettest month is July with an average monthly range of 300–440 mm, and the driest month is April with a range of 50–70 mm. The temperature ranges from 18°C to 31°C, with an annual mean temperature of 25°C. The coldest month is January and the warmest month is May. (Data derived from GIS analysis using Worldclim 1.4 climate layers as described by Hijmans et al. (2005)).

Conservation status.—The extent of occurrence for this species is estimated to be 750 sq. km as delimited by the geographic range occupied by suitable karst hills in Belize and Cayo districts. The area of occupancy, which includes only these karst formations, is 300 sq. km. Based on an average estimated population density

of 30 adult plants per km^2, the estimated total population size for this species is 9,000 plants (Meerman, unpub. data). The karst hills where this species occurs are often isolated and separated by unsuitable habitats such as lowland forest, lowland savannas, and agricultural areas. In addition, this species occurs in discrete populations of only a few individuals, and does not appear to occur on all suitable habitats within its geographic range. As a result of the isolation between karst mountains and the clumped distribution of this species, populations are considerably fragmented. Visits to 12 different localities where this species occurs appear to indicate that reproduction is occurring and seedling regeneration is healthy.

The primary threat to this species appears to be fire, utilized in adjoining areas for slash and burn agriculture. These fires have been observed spreading up surrounding karst hills and decimating native vegetation. Another important threat to this species is mining for construction aggregates and dolomite, with several active and planned quarries in the region. Recent fieldwork in Belize suggests that illegal wild collection of cycad plants and seeds has occurred in the past and may present an additional threat to this species. Hopefully, the difficult terrain and inaccessibility of this cliff dwelling plant, combined with the fact that approximately 50% of its area of occupancy lies within protected areas will help minimize the risk of illegal harvesting. Specific locality information has been purposefully withheld in order to further minimize this risk.

Due to its limited extent of occurrence and area of occupancy, the fragmented nature of its populations, and the threats caused by fire, mining, and illegal harvesting, this species should be listed as Endangered (EN) based on IUCN Red List criteria ab(i–iv) and 2ab(i–iv) (IUCN, 2001).

Reproductive phenology.—Elongating microsporangiate strobili have been observed in August and September in habitat, and pollen releasing strobili have been observed in October and November under cultivation at Green Hills Botanical Collections near San Ignacio. A single mature megasporangiate strobilus, with about a third of the seeds already dehisced, was collected in September of 2006, and another, totally dehisced with most seeds cleaned of sarcotesta, was collected in January 19 of 2006 by Martin Meadows of Belize Botanic Gardens. During the course of fieldwork with this species in August of 2008 our team found several distinct groupings of seedlings with newly-emerged eophylls, indicating that megasporangiate strobili probably disintegrated two to three months earlier. Further work is required to better understand the reproductive phenology of this species.

Ecology.—A large number of young seedlings observed during the course of fieldwork indicate that reproduction is healthy and the pollinating agent is active, although it has not yet been observed. Seedlings germinating on the forest floor suffer 100% mortality within a year or two, suggesting the forest floor habitat is unsuitable for this species (J. Meerman, pers. comm.). In August of 2008 our team observed a female plant with its peduncle attached and several seedlings growing directly underneath on the forest floor. Several of these seedlings from this same strobilus had also germinated in a fissure on the cliff directly above the mother plant, indicating that some unknown dispersal agent had moved individual seeds or a piece of the strobilus to this location. Larvae of *Eumaeus toxea* Godart butterflies were observed feeding on emergent leaves.

DISCUSSION

Zamia meermanii is most similar in appearance to *Zamia furfuracea* L.f. from southeastern Veracruz, Mexico. Both species have obovate to oblanceloate or narrowly oblong coriaceous leaflets with persistent tomentum on the abaxial side of leaflets, distinct veins on the adaxial side of leaflets, and a similar number of maximum leaflet pairs per leaf (ca. 25). *Zamia meermanii* differs from *Zamia furfuracea* in having usually solitary stems as opposed to freely branching stems; holding 1–3 pendent leaves per crown, rather than 5–7 erect or slightly arching leaves per crown; eophylls with a single pair of leaflets rather than eophylls with two pairs of leaflets, leaves cream-colored and covered with saffron-orange tomentum just prior to maturing as opposed to light green with predominantly white tomentum prior to maturing; coriaceous leaflets to 0.8 mm thick compared to coriaceous or extremely coriaceous leaflets to 1 mm thick; leaflet length to 28

Table 1. Diagnostic reproductive characters for *Zamia furfuracea* and cliff-dwelling *Zamia* species.

	Zamia meermanii	***Zamia cremnophila***	***Zamia sandovalii***	***Zamia furfuracea***
Microsporangia per microsporophyll	22–28	14–18	14–18	40–42
Microsporangia diameter (mm)	1–1.6	0.65–0.78	0.6	0.8–1.2
Microsporangiate strobilus peduncle length (cm)	9–10	2.5–3	6.7	8–10
Megasporangiate strobilus length (cm)	12–20	8.5–14	9–17	10–24
Megasporophyll rows	7–15	4–8	4–7	4–15
Megasporophyll width (cm)	1.5–2.2	1.6–2.6	2.5–3.5	1.5–1.8
Megasporantiate strobilus peduncle length (cm)	8–12	4–5	3.6–6	10–20
Sclerotesta length (mm)	1.5–1.8	1.5–1.7	1.8–2.2	1.1–1.5

Data derived from measurements by author, Whitelock 2002, Nelson 2006, and Schutzman et. al. 1988.

cm compared to 18 cm; protuberantly raised veins on adaxial surface to 1.5 mm wide rather than slightly raised, narrower veins to 0.8 mm wide; and 22–28 microsporangia on abaxial side of microsporophylls as opposed to 40 or more on *Z. furfuracea*.

Zamia meermanii shares this unusual cliff-dwelling habit with two other Mesoamerican *Zamia* species: *Zamia cremnophila* from Mexico and *Zamia sandovalii* from Honduras. All three species typically carry 1–3 pendent leaves. *Zamia meermanii* is easily differentiated from the two other species by leaflet features alone (see key below).

1. Leaflets with distincly raised veins on adaxial surface and persistent tomentum on abaxial surface _____ **Z. meermanii**

1. Leaflets plane, without distinctly raised veins on adaxial surface and without persistent tomentum on abaxial surface.
   2. Adaxial surface of petiole with distinct longitudinal groove _____ **Z. cremnophila**
   2. Adaxial surface of petiole rounded, without longitudinal groove _____ **Z. sandovalii**

It has distinctly raised veins on the adaxial surface, persistent tomentum on the abaxial surface, and margins that are entire or crenulately notched in the upper third, whereas *Z. sandovalii* and *Z. cremnophila* both have plane leaflets with no distinct raised veins on the adaxial surface, are glabrous on the adaxial surface, and have margins that are distinctly toothed on the distal half. *Zamia sandovalii* median leaflets are strongly falcate as opposed to those of *Z. meermanii* and *Z. cremnophila*, which are typically straight. *Zamia meermanii* and *Z. cremnophila* eophylls typically possess two leaflets, whereas *Z. sandovalii* eophylls typically possess four leaflets.

In addition to the vegetative characters that easily distinguish these three species, reproductive characters are also useful (Table 1). *Zamia meermanii* microstrobili have longer peduncles and possess more and larger microsporangia per microsporophyll than *Z. cremnophila* and *Z. sandovalii*. Megastrobili of *Z. meermanii* can be longer and with more sporophyll rows and have longer peduncles than either *Z. cremnophila* or *Z. sandovalii*. Seeds of *Z. sandovalii* are the largest of the group, and those of *Z. meermanii* and *Z. cremnophila* are of a similar smaller size. Until a well-resolved phylogeny of *Zamia* is available, we have no way to determine if the cliff-dwelling habit evolved more than once in the genus.

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