Phytotaxa 98 (2): 27–42 (2013)
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.98.2.1

Clarification of *Zamia acuminata* and a new *Zamia* species from Coclé Province, Panama

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Abstract

Zamia acuminata has remained an obscure, poorly understood species for over a century due to possibly misinterpreted or erroneous locality data on the unicate sterile type specimen, a very brief protologue description, the misidentification of the plants from El Valle de Antón in Panama as *Z. acuminata*, and the erroneous determinations of plants of *Z. acuminata* from Costa Rica as *Z. fairchildiana*. Recently collected material from San José Province in Costa Rica is here determined to be identical to the single sterile leaf material of the holotype of *Zamia acuminata*. We consider Z. *acuminata* to be a Costa Rican endemic species restricted to the western Talamanca mountain range in San José Province, and that the *Zamia* from El Valle de Antón in Panama, which has previously been referred to as *Zamia acuminata*, to be a new species, here described as *Zamia nana.*

Key words: Cycadales, Mesoamerica, Zamiaceae

Introduction

Zamia acuminata Oerst. ex Thiselton-Dyer (1884: 194) was described by British botanist William Thiselton-Dyer based on a unicate sterile specimen collected by Danish botanist Anders Sandøe Ørsted (21 June 1816–3 September 1872). This specimen, consisting of a single leaf, is currently deposited at the Natural History Museum of Denmark (*A.S. Ørsted s.n.*, C). It was not assigned a collection number by Ørsted and includes no description of the plant or of its habitat. However, the original label contains the hand written inscription “ad flumen S. Juan Nicaragua”, suggesting that the specimen was collected near the Rio San Juan that forms the natural border between Costa Rica and Nicaragua. The specimen has no collection date, but was likely collected sometime between 1846 and 1848, when Ørsted traveled in Nicaragua and Costa Rica (see Ørsted, 1863). Thiselton-Dyer prepared his description of *Zamia acuminata* based solely on this specimen, the description is limited to a characterization of the leaf and leaflets and does not include the description of other taxonomically useful characters such as reproductive structures. The Latin description in the protologue is reproduced below from Thiselton-Dyer followed by a translation in English:

> *Folia jugo-pinnata; petiolo sparsimaculeato, triquetro, glaberrimo; foliolis utroque latere ad 8, falcato-lanceolatis, apicem versus caudato-acuminatis, basi maxime angustatis, utrique integerrimis, membranaceis, 30 nerviis, 10–11 pollicibus longis, 1 1/2–1 3/4 pollicibus latis.*
>
> Leaves opposite-pinnate, petiole sparsely prickly, triangular, glabrous, leaflets 8 per side, falcate-

Accepted by Maarten Christenhusz: 14 Mar. 2013; published online in PDF: 8 May 2013

lanceolate, apex caudate-acuminate, narrowing at the base, each entire, membranous, with 30 nerves, 10–11 inches [25.40–27.94 cm] long, 1 1/2–1 3/4 inches [3.81-4.45 cm] wide.

Zamia acuminata has always been considered a valid name and has never been placed in synonymy of another species. However, despite the fact that it has been over 160 years since the holotype was collected, no additional specimens resembling the type have been collected anywhere in Nicaragua (Stevenson 2001) or in the vicinity of the San Juan River in adjacent Costa Rica.

In 1976, Robert Dressler collected specimens of a small *Zamia* he identified as *Z. acuminata* in El Valle de Antón, an extinct volcano crater in the Coclé Province of Panama. Dressler noted in an unpublished manuscript on Panamanian *Zamia*, that "the Panamanian material closely matches photographs of Ørsted's specimens". Stevenson (1993) followed Dressler's concept in his treatment of Panamanian *Zamia* and this concept was subsequently followed by several additional authors (e.g., Norstog & Nicholls 1997, Jones 2002). This Panamanian taxon is well represented in herbaria and living botanical collections as *Z .acuminata*, despite having much smaller leaves and leaflets than the holotype and occurring approximately 480 km away from the purported type locality. Based primarily on the distance separating Ørsted's collection from Panamanian collections, several cycad researchers, including Whitelock (2002) and Schutzman (2004) have suspected that the Panamanian plants may represent an undescribed species.

A few intriguing insights into the *Z. acuminata* conundrum came to the second author accidentally while conducting some research on *Zamia* on the Pacific Slope of Costa Rica in 2004. Two locations in the Cantón de Puriscal in San José Province were visited following the locality data for some specimens determined as *Z. fairchildiana* Gómez (1982: 401), a large arborescent species occurring in eastern Costa Rica and adjacent Panama. The plants found at these localities were not as large nor did they have the tall trunks up to 2 m tall that are typical of *Z. fairchildiana*. Instead, the plants were small and mostly acaulescent or with short trunks to 40 cm tall. These plants were not only much smaller than *Z. fairchildiana*, but they were lacking microsporangia on the abaxial side of the microsporophylls, an unusual character shared by both *Z. fairchildiana* and its closely-related sister species, *Z. pseudomonticola* Gómez (1982: 402). Furthermore, the leaflets had long, drawn out tips matching the shape and dimension of those of the *Z. acuminata* holotype, but were considerably larger than the leaflets of the *Zamia* from El Valle de Antón in Panama (Fig. 1). Based on the examination of additional herbarium specimens from Costa Rica from several herbaria (CR, MO, USJ), we determined that this taxon occurs at several localities in San José Province, and that the leaves appear to match the dimensions of the *Z. acuminata* holotype more closely than do those of the Panamanian taxon.

To assess whether the leaflet dimensions of the *Zamia acuminata* holotype are more similar to the *Zamia* from Valle de Antón, Panama (referred to here as *Zamia sp.* [Valle de Antón]) than to the *Zamia* from San José Province, Costa Rica (referred to here as *Zamia sp.* [San José Province]), median leaflets were measured from herbarium specimens, in situ plants, and habitat-collected plants cultivated at Montgomery Botanical Center (Table 1). Leaflet length and width were plotted, showing the *Z. acuminata* holotype nested within *Zamia sp.* (San José Province) and well outside the dimensions of *Zamia sp.* (Valle de Antón), suggesting that the Costa Rican plants belong to true *Z. acuminata* (Fig. 2). Discriminant analysis (implemented with JMP 9.0, SAS Institute, Cary, NC) based on leaflet length and width always classified the *Z. acuminata* holotype with *Zamia sp.* (San José Province). Three individuals of *Zamia sp.* (Valle de Antón) were classified with *Zamia sp.* (San José Province), most likely because these specimens were collected from juvenile plants with small leaves. However, no individuals of *Zamia sp.* (Valle de Antón) were classified as *Zamia sp.* (San José Province). Under the assumption that the holotype of *Zamia acuminata* corresponds to *Zamia sp.* (San José Province), discriminant analysis produces a 91% accurate classification. Based on the statistical similarities in leaflet dimensions as well as the exact match in leaflet shape, *Zamia sp.* (San José Province) will be considered the true *Z. acuminata* for the remainder of this discussion, whereas the *Zamia* species from Valle de Antón is considered an undescribed species, which we formally describe in this paper.

FIGURE 1. Same-scale comparison of (A) holotype of *Zamia acuminata* (A.S. Ørsted s.n., C) superimposed with (B) a fresh leaflet of *Zamia* collected in San José Province, Costa Rica (population represented by voucher A.J. Lindström 376, CR), and (C) a leaflet from a herbarium specimen collected in Valle de Antón, Coclé Province, Panama (from *Stevenson & Valdespinos 1147*, FTG).

TABLE 1. *Zamia* leaflet measurements used in the analysis and collectors of the specimens.

Taxon	Collector	length (cm)	width (cm)
Zamia sp. (Valle de Antón)	*Bartlett 16682* (MO)	13.6	2.04
Zamia sp. (Valle de Antón)	*Dressler 5322* (F)	18.362	2.8
Zamia sp. (Valle de Antón)	*Dressler 5322* (MO)	15.702	2.645
Zamia sp. (Valle de Antón)	*Dressler 5322* (US)	18.319	2.435
Zamia sp. (Valle de Antón)	*Galdames et al. 4394* (SCZ)	14.272	2.672
Zamia sp. (Valle de Antón)	*Stevenson & Valdespinos 1147* (PMA)[4/5]	16.413	2.14
Zamia sp. (Valle de Antón)	*Stevenson & Valdespinos 1147* (FTG)	19.65	2.575
Zamia sp. (Valle de Antón)	*Schmalzel et al. 1041*	16.327	3.19
Zamia sp. (Valle de Antón)	*Stevenson & Valdespinos 1147* (K)	17.07	2
Zamia sp. (Valle de Antón)	*Stevenson & Valdespinos 1147* (PMA)[2/5]	23.16	2.76
Zamia sp. (Valle de Antón)	Montgomery Botanical Center # 200026*B	13	2.7
Zamia sp. (Valle de Antón)	Montgomery Botanical Center # MBC 99508*B	12.7	2.9
Zamia acuminata (holotype)	*Oersted s.n.* (C)	28.35	4.03
Zamia sp. (San José Province)	*Calonje MAC04-001* (FTG)	21.54	3.34
Zamia sp. (San José Province)	*Morales 763* (CR)	18.518	2.448
Zamia sp. (San José Province)	*Gentry et al. 79295* (CR)	25.6	4.1
Zamia sp. (San José Province)	Calonje MAC08-375 (field data)	27	3.7
Zamia sp. (San José Province)	Calonje MAC08-376 (field data)	23.5	3.8
Zamia sp. (San José Province)	Calonje MAC08-377 (field data)	24.5	4.3
Zamia sp. (San José Province)	Calonje MAC long leaved plant (field data)	29	4.2
Zamia sp. (San José Province)	*Valverde 697* (CR)	23.269	5.516
Zamia sp. (San José Province)	*Calonje MAC04-001* (USJ)	20.4	3.374
Zamia sp. (San José Province)	*Cascante 1036* (CR)	17.68	4.27
Zamia sp. (San José Province)	*Gomez-Laurito 1564* (USJ)	23.9	4.53
Zamia sp. (San José Province)	*Grayum 8574* (CR)	25.48	4.4
Zamia sp. (San José Province)	*Grayum 8606* (CR)	20.29	3.14
Zamia sp. (San José Province)	*Grayum & Kress 8574* (MO)	26.47	4.07
Zamia sp. (San José Province)	*Morales 2054* (MO)	21.352	3.24
Zamia sp. (San José Province)	*Morales 3920* (MO)	20.071	3.04
Zamia sp. (San José Province)	Calonje, Rio Lanas lflt 12 (field data)	34	3.95
Zamia sp. (San José Province)	Calonje, Rio Lanas lflt 10 (field data)	27.75	4.3
Zamia sp. (San José Province)	Calonje, Rio Lanas lflt 13 (field data)	29.934	3.6
Zamia sp. (San José Province)	Calonje, Rio Lanas lflt 4 (field data)	25.495	5.1
Zamia sp. (San José Province)	Calonje, Rio Lanas lflt 2 (field data)	24.27	3.74
Zamia sp. (San José Province)	Calonje, Rio Lanas lflt 19 (field data)	25.245	4.62

Interestingly, most specimens circumscribed as *Zamia acuminata* in this paper have previously been determined in herbaria and publications as *Z. fairchildiana*, and although several authors have mentioned that *Z. acuminata* occurs or is likely to occur in Costa Rica, no detailed information on the distribution and morphological characteristics of these Costa Rican plants has previously been published.

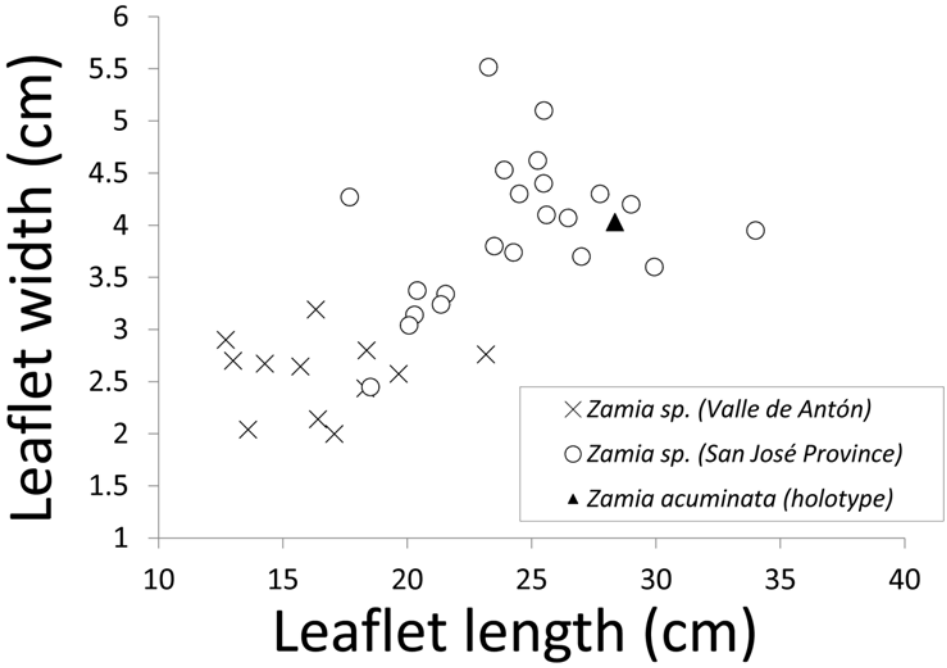

FIGURE 2. Leaflet length x width of *Zamia acuminata* vs. *Zamia sp.* Valle de Antón.

Zamia acuminata was first collected in Costa Rica in 1976 by Costa Rican botanist Jorge Gómez-Laurito. This collection was annotated as *Z. acuminata* by Bart Schutzman in 1998 (see specimen *J. Gómez-Laurito1564*, USJ), but was not included under this species in Merrello's (2003) treatment of Costa Rican Zamiaceae, or in any other publications that we are aware of. All other collections of *Z. acuminata* examined prior to our fieldwork in Costa Rica were previously determined as *Z. fairchildiana*. Luis Diego Gómez (1982) mentioned that *Z. acuminata* occurred in tropical moist lowland and premontane forests of Costa Rica, but did not provide specific distribution data nor did he cite any specimens. Likewise, both Whitelock (2002) and Jones (2002) included Costa Rica within the geographic range of this species, but neither provided specific distribution data. In a treatment of Zamiaceae for Costa Rica, Merello (2003) presumed *Z. acuminata* may occur in Costa Rica based on the fact that the San Juan River, where the holotype was reportedly collected, forms the border between Nicaragua and Costa Rica. However, Merello also noted that no collections of this species had been made in Costa Rica. From the above it becomes apparent that while it has been assumed that *Z. acuminata* could occur in Costa Rica based on the type locality mentioning the San Juan River, it has remained an obscure and enigmatic species since its initial discovery by Ørsted.

All recent collections of *Z. acuminata* have been made in San José Province on the Pacific slope of the Western end of the Talamanca mountain range and no collections apart from the holotype collection are reported between this area and the San Juan River, which is 95 km away and on the opposite (Caribbean basin) side of the Cordillera de Talamanca (Fig. 3). However, there are at least twenty-five recent collections of *Zamia* in the vicinity of the San Juan River, but they all are readily assigned to *Z. neurophyllidia* Stevenson (1993: 100;.see Appendix 1), a large arborescent species in the *Z. skinneri* Warsz. in Dietrich (1851:146)-complex (Taylor *et al.* 2008, 2012). Taxa belonging to this species complex are often called "pleated-leaflet" zamias, and have very broad, conspicuously veined leaflets that are quite distinct from species with unclearly veined leaflets. With the exception of the holotype of *Z. gomeziana* Acuña (2010: 29; *G. Herrera & A. Chacón 2865*, CR) collected on Fila Matama in 1989, all Costa Rican *Zamia* collections occurring on the Atlantic side of the continental divide formed by the Talamanca, Tilarán and Guanacaste mountain ranges belong to *Z. neurophyllidia*, whereas most collections on the Pacific side belong to species with "plane" (i.e., not conspicuously veined) leaflets such as *Z. fairchildiana*, *Z. pseudomonticola* and *Z. acuminata*. This

biogeographical pattern of pleated-leaflet zamias occurring mostly on the Caribbean side of the continental divide, and most plane-leaflet zamias occurring on the Pacific side extends into western Panama (Fig 3).

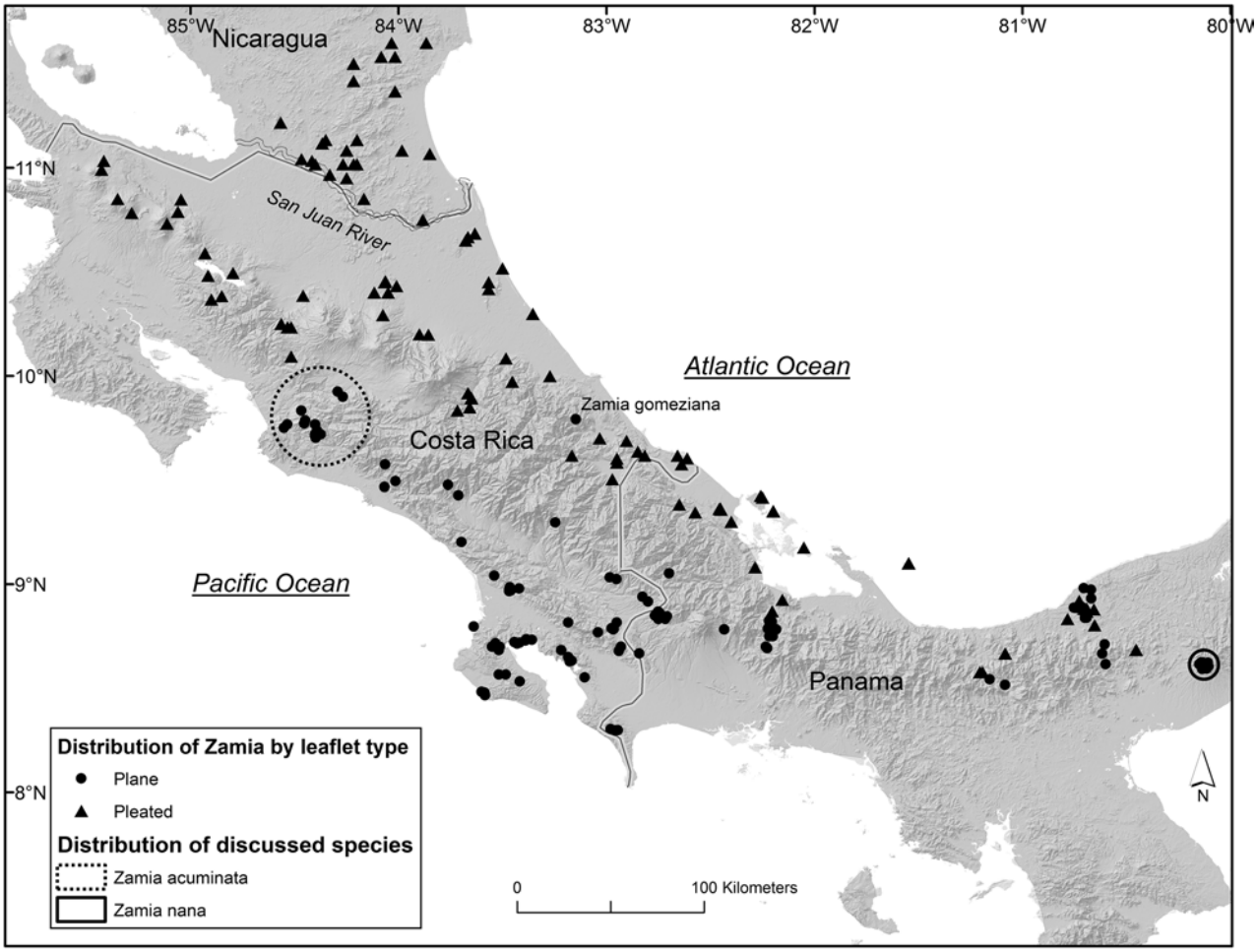

FIGURE 3. Distribution of *Zamia* in Costa Rica, southern Nicaragua and western Panama by leaflet type. Note disjunct distribution of *Z. acuminata* and *Z. nana*, as well as the San Juan River, the reported type locality for *Z. acuminata*.

Several facts suggest that the *Zamia acuminata* holotype may not have been collected near the San Juan River: (1) the San Juan River, found on the Caribbean side of the continental divide, is outside the biogeographical region where most plane-leaflet *Zamia* species occur; (2) no additional collections matching the type have been collected in this region in 128 years of botanical exploration and (3) specimens exactly matching the holotype have only been collected in San José Province on the Pacific side of Costa Rica.

The reasons for this apparent geographic disparity between the presumed type locality for *Z. acuminata* and the disjunct location of recent collections resembling the holotype cannot be known for sure, but there are a few likely scenarios. One possibility is that the original label of the *Zamia acuminata* holotype, which reads "ad flumen San Juan", has been misinterpreted. According to Cassell's Latin dictionary (Simpson 1977), the world "flumen" means "river", but the Latin word "ad" can alternatively mean "at" or "to", so the locality on the holotype label could be interpreted as "at the river San Juan", or "to the river San Juan". If the latter were true, then the collection could have been made along the way on a trip Ørsted made to the San Juan River and not necessarily collected along the river itself. Another possibility is that the specimen was erroneously labeled, a distinct possibility considering that the specimen was not numbered or dated and was collected on a long, complicated journey. In fact, in a book he wrote about his travels in Costa Rica and Nicaragua from 1846 to 1848 (Ørsted 1863), Ørsted provides the itinerary for a 85 mile long trip he took from Alajuela, Costa Rica, to the San Juan River in Nicaragua. From Alajuela, Ørsted travelled by road through the village of San

Pedro de Poas, between the Barva and Poas volcanoes to the village of San Miguel and to a town called Muelle near present day Puerto Viejo de Sarapiquí. From here he continued by boat via the Sarapiquí River to the San Juan River (Fig 4). It is possible that Ørsted may have collected the holotype of *Z. acuminata* towards the beginning of his trip to the San Juan River, as today the species is found in the Zona Protectora El Rodeo, only 13 km SW of Alajuela. The historic distribution for the species may have extended onto the Central Plateau, but this area currently hosts 50% of the population of Costa Rica and has been largely deforested (UNEP 2010). Ørsted did assign collection numbers to most of his collections so the fact that his specimen of *Zamia acuminata* is not numbered may mean that its label could have been lost or mixed with that of another gathering. Another possibility is that the specimen could have been collected early on in the journey to the San Juan River, but was grouped and labeled with his other collections from along that river. Alternatively, the collection could have been mixed up at a later date, as Ørsted also collected extensively in the mountains of present-day San José Province. Due to the possibly misinterpreted or erroneous type locality, the identification of plants from El Valle de Antón in Panama as *Z. acuminata*, and the determinations of plants of true *Z. acuminata* from Costa Rica as *Z. fairchildiana*, *Z. acuminata* has remained an obscure, poorly understood species for over 120 years. Based on our evidence, unless specimens resembling the holotype are collected once again in the vicinity of the San Juan River, we conclude that *Z. acuminata* is to be considered a Costa Rican endemic restricted to the western Talamanca mountain range in San José Province, its range possibly extending into neighboring Alajuela Province.

FIGURE 4. Path taken by Ørsted from Alajuela to the San Juan River, the reported type locality for *Zamia acuminata*. Ørsted travelled by land until the town of Muelle, where he continued by canoe on the Sarapiquí River to the San Juan River. Map recreated based on travelogue in Ørsted (1863).

To clarify the circumscriptions, a new treatment based upon new specimens that include reproductive material treatment is given below for *Z.acuminata* and the Panamanian material, which we now know to belong to an undescribed species: *Z. nana*.

Taxonomy

Zamia acuminata Oerst. ex Thistelton-Dyer (1884: 194). Type: NICARAGUA. 'ad flumen Rio San Juan', *Ørsted s.n.* (holotype C, isotype K) (Fig. 5).

Stem solitary, typically subterranean but sometimes short-arborescent to 40 × 7–8 cm in diameter, bark smooth, tan, with thin layer of cork. *Cataphylls* triangular basally, linear-lanceolate apically, papyraceous 5–6 cm long, 1–2 cm wide at base, with a pair of stipules, not persistent. *Leaves* 2–7, rarely up to 10, 100–177 cm; petioles 60–89 cm, moderately armed with prickles most numerous at base, bases swollen and glabrous; rachises 53–89 cm, sparsely armed with prickles in lower third, ending in terminal acute spine. *Leaflets* 13–19 typically subopposite, slightly keeled, median leaflets chartaceous to papyraceous, glabrous green, margins entire, distinctly folded inward, lanceolate, falcate, long-acuminate apically 17.7–34.0 × 2.45–5.50 cm, pinnae spacing 3.0–6.3 cm; new emergent leaves light green, glabrescent; petioles and rachises brown tomentose in new leaves, becoming glabrous at maturity. *Eophylls* with 2 pairs of pinnae, petiole 13–14 cm, rachis 1.8–2.0 cm, pinnae 15–17 × 2.9– 3.4 cm. *Pollen strobili* 1–3 per stem apex, grey-tan tomentose with greenish undertones, cylindrical, 7.0–8.5 cm long, 1.5–1.6 cm in diameter, sterile apex distinctly protruding, 5 mm; peduncle brown-tomentose, 1.7–2.2 × 0.4–0.6; microsporophylls spirally arranged in 10–15 orthostichies of 13–20 sporophylls each, 0.4–0.5 cm wide, 0.5–0.6 cm long, terminal facet flat, not well defined, bearing 16–22 sporangia aggregated into a single group on abaxial surface only. *Ovulate strobilus* typically solitary but up to two per stem apex, tan to grey-tomentose with green undertones, globose to ovoid, 12.0–13.5 cm long, 6.0–7.5 cm wide, sterile apex acute, 1.0–3.5 cm tall; peduncle densely brown tomentose, to 2–4 cm long, 1.0–1.2 cm in diameter; strobilus axis glabrous; megasporophylls spirally arranged in 6–8 orthostiches with 3–5sporophylls each, grey to brown-tomentose, facet hexagonal, plane (not depressed), 36–37 mm wide, 26–27 mm tall, and 15 mm thick, center of facet 28 mm wide, pedicel glabrous, 2.0–2.5 cm long, 14 mm tall. Seed ovoid-pyramidal, 2.5 cm long and 1.7 cm wide, sclerotesta 2.0–2.5 cm long and1.1.0–1.3 cm wide, sarcotesta red at maturity.

Distribution:—*Zamia acuminata* occurs on the western end of the Talamanca mountain range in San José Province, but its range may extend into neighboring Alajuela and Puntarenas Provinces, as several collections occur near the Provincial borders.

Habitat:—100–1300 m elevation in tropical moist forest, tropical wet forest, premontane wet forest and premontane rain forest (sensu Holdridge 1967). Annual precipitation is 2500–3000 mm, with peak rainfall in September.

Reproductive phenology:—Immature microsporangiate strobili as well as near-mature and mature ovulate strobili were observed in late October and early November of 2004 and December of 2010. In May of 2008, only old microsporangiate strobili and immature ovulate strobili were observed.

Etymology:—In reference to the long acuminate leaflet tips.

Conservation status:—The previous taxonomic confusion with this species has affected the IUCN Red List conservation status for this species, as prior assessments were primarily based on the Panamanian taxon that we now realize is an undescribed species (see below). Including only the recent collections in San José province of Costa Rica, the extent of occurrence for the species is calculated at 370 km2. Based on the forested area within the extent of occurrence, the area of occupancy is calculated to be approximately 160 km2. The species is known from at least 10 populations more than half of which occur within protected areas and none that seem severely affected by deforestation or other threats. As with many other cycads, the potential threat of illegal plant collecting for the horticultural trade might be the greatest concern. Based on the above, we recommend an IUCN Red List Category (IUCN 2001) of VU (Vulnerable) for this species based on criteria B1ab(i-v) + B2ab(i-v).

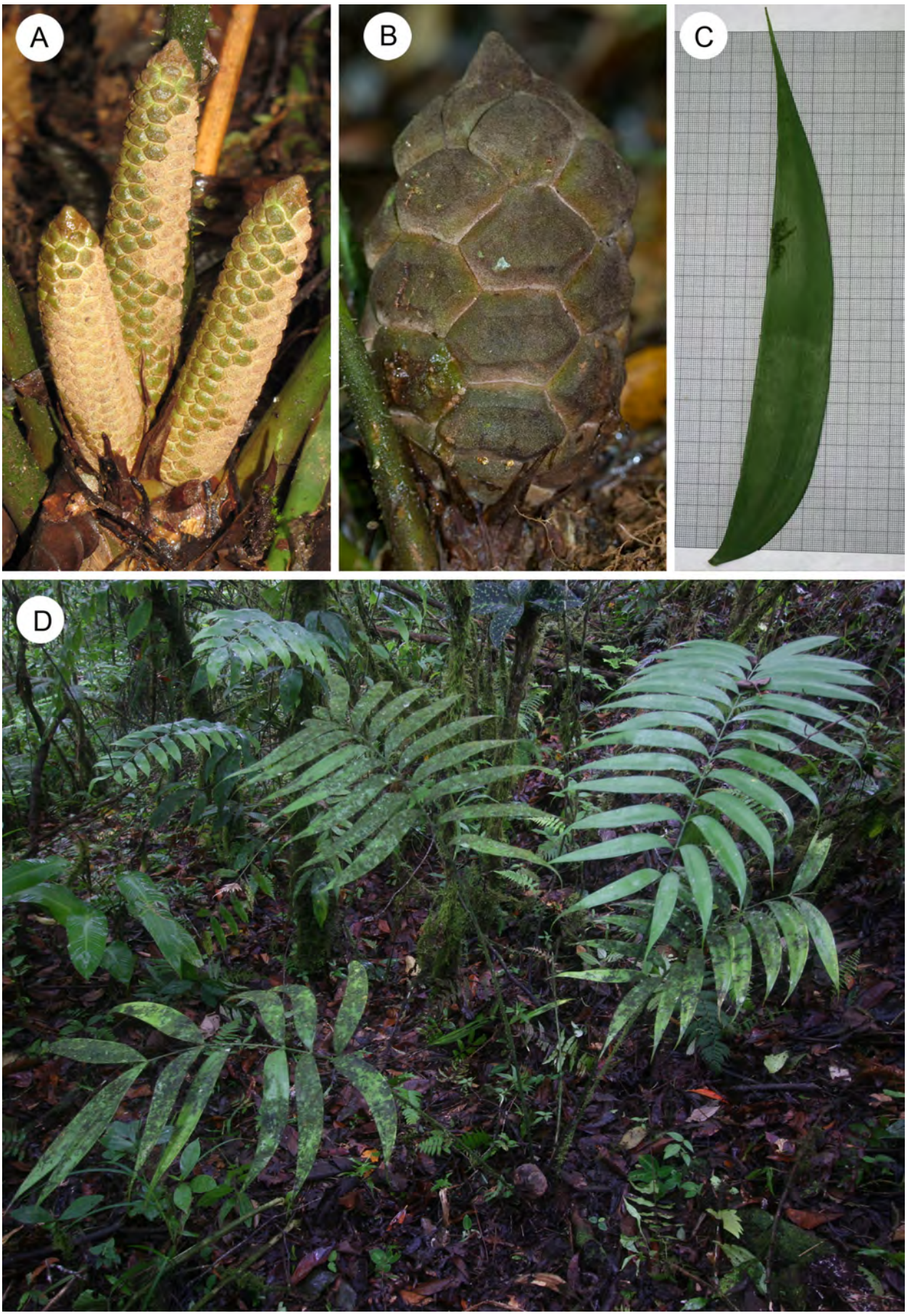

FIGURE 5. *Zamia acuminata* in habitat in Cantón de Puriscal, San José Province, Costa Rica. A. Juvenile pollen strobili. B. Immature seed strobilus. C. Typical median leaflet. D. Plant in habitat with immature seed cone.

Additional specimens examined:—COSTA RICA. San José Province: Cantón de Mora**,** Zona Protectora El Rodeo, 900–1000 m, *A. Cascante 1036* (CR); Quebrada Micos, ca. 8.5 km by road West of Ciudad Colon, 600 m, *M. Grayum & P. Sleeper 6099* (CR, MO); Ciudad Colón, Zona Protectora El Rodeo, 850–900 m, *O. Valverde 697* (CR); Cantón de Turrubares: Valle del Tárcoles, S.E. de San Luis, entre Quebrada Zorrillal y Cerro San Luis, 600–950 m, *B. Hammel & J. González 20028* (MO); Carara National Park, near Rio Carara, 120 m, *A. Gentry et al. 79295* (CR); Reserva Biológica Carara, Western part of Montañas Jamaica, ca. 3.5 km NE of Bijagual de Turrubares, 500–600 m, *M. Grayum, & J. Kress 8574* (CR, MO); Cantón de Puriscal: Turrubares, carretera de Tufares a Alto Gloria, 700 m, *M. Calonje et al. MAC04-001* (CR, FTG, USJ); Slopes of Cerro Pelón along Rte. 239 ca. 1 km South of San Martin, 800 m, *M. Grayum et al. 8606* (CR, MO); Salitrales de Puriscal, camino a Parrita, *J. Gómez-Laurito GL_1564* (USJ);Z.P. La Cangreja, Cuenca del Tulín, Mastatal, Altos Fila Cangreja, 900–1000 m, *Q. Jímenez & A. Solano 2307* (MO); Albergue de Montaña La Potenciana, Camino al Rio Lanas, 964 m, *A.J. Lindström 376* (CR); Z. P. La Cangreja, Santa Rosa de Puriscal, 350 m, *J.F. Morales 763* (CR); Z.P. La Cangreja, Cuenca del Rio Negro, San Martín de Puriscal, bosque primario al este de la Fila Vara Blanca, 800 m, *J.F.* Morales *2054* (MO); San Martín de Puriscal, bosque primario remanente en la Fila Vara Blanca, 800–950 m, *J.F. Morales 3920*(MO).

Discussion:—Most Costa Rican collections of *Z. acuminata* from Costa Rica have been previously determined as *Z. fairchildiana*. The reason for this may be that all three species of *Zamia* occurring on the Pacific slope of Costa Rica (*Z. acuminata*, *Z. fairchildiana*, and *Z. pseudomonticola*) have leaflets with entire margins that are somewhat variable in shape and comparable in dimensions, making it difficult to differentiate between them based on sterile herbarium specimens alone. However, *Z. fairchildiana and Z. pseudomonticola* are much larger plants, with stems attaining heights of over two meters tall, whereas *Z. acuminata* typically has subterranean stems or short stems to 40 cm tall. *Zamia acuminata* is easily differentiated from the two other species by the presence of microsporangia only on the abaxial surface of the sporophyll, whereas both *Z. fairchildiana* and *Z. pseudomonticola* have microsporangia on both the abaxial and adaxial surfaces. The mature ovulate strobili of the three species are also easily differentiated. *Zamia acuminata* has brown-grey tomentose strobili with green undertones, acute sterile apices and peduncles obscured by cataphylls, *Z. fairchildiana* has light tan tomentose strobili with acute sterile apices and peduncles visible beyond cataphylls, and *Z. pseudomonticola* has glabrous, dark green strobili with short obtuse sterile tips and peduncles obscured by cataphylls. *Zamia obliqua* Braun (1875: 376) was also reported to be in Costa Rica by Merello (2003) based on a collection from a single stemless plant in the Golfo Dulce region of Costa Rica (*R. Aguilar et al. 2970,* CR, MO). While this specimen has unusually broad and dentate leaflets that somewhat resemble *Z. obliqua*, the collection locality is more than 300 km west of the nearest locality for this species in Panama. We believe this specimen more likely represents a juvenile *Zamia fairchildiana*, as this species is extremely abundant throughout the coastal Golfo Dulce region where this specimen was collected. While leaflet dentation is not common in *Zamia fairchildiana*, it does occur on some plants, and is most common in juvenile individuals. The leaflet texture on the purported *Z. obliqua* collections also appears to be unusually soft for *Z. obliqua* or *Z. fairchildiana*, suggesting perhaps that the leaves that were collected had not yet hardened into their final shape.

In addition to the confusion caused by the erroneous determinations of *Z. acuminata* specimens, the name has been erroneously assigned for the past 36 years to an undescribed taxon from El Valle de Antón, Coclé Province in Panama. Below we provide a formal description for this Panamanian species, including a comparison with *Zamia acuminata*.

Zamia nana A.Lindstr., Calonje, D.W.Stev. & A.S.Taylor, *sp. nov*. Type: PANAMA, Coclé Province: Mun. Antón, El Valle: 1020 m, *D. Stevenson & I. Valdespinos 1147*, 9 January 1989 (holotype PMA [5 sheets], isotypes F, FTG, K, MO, NY, U). (Figs. 6, 7).

Diagnosis:—Similar to *Zamia acuminata* but differs from it in having an overall smaller size, a subterranean stem, dark brown strobili, and outwardly extruded megasporophylls and microsporophylls with ornate and distinctly indented

terminal facets in contrast to *Zamia acuminata* which attains a larger overall size, has semi-epigeous stems to 50 cm long, tan-grey strobili, and microsporophylls and megasporophylls which are more or less flattened with inornate, smooth terminal facets.

Stems subterranean, occasionally dichotomously branched, subglobose to cylindrical, 10–20 cm× 7–8 cm diameter, smooth tan surface. *Cataphylls* broadly triangular, drawn out apex, papyraceous, slight tomentum that sheds as maturing, pair of rudimentary stipules, not persistent. *Leaves* 1–5, rarely up to 11, 40–100 cm; petiole 19.5–60 cm, sparsely prickled, brown shedding tomentum; rachis with few prickles in lower third, triangular in cross-section, brown shedding tomentum; 26.5–57 cm long. *Leaflets* 9–34, opposite to alternate, slightly keeled, very variable in length, width and shape even on the same leaf, median pinnae, sub-coriaceous, medium to light green, margins entire with sharp distinct edge, elliptic-lanceolate, cuneate basally, long acuminate apically, 10.5–25.0 × 1.6–4.1cm, spaced 1.8–4.5 cm, base 3 mm wide; new emergent leaves light green, slightly tomentose. *Eophylls* with 2 pairs of leaflets, petiole unarmed and immature petiole brown tomentose, turning glabrous green at maturity. *Pollen strobili*, 1–3 per stem apex, sequential, covered in dense cream to brown tomentum, conical, at dehiscience 4.0–7.0 cm × 1.5–2.3 cm, sterile apex 3–4 mm long, blunt; peduncle brown tomentose, 2.5–3.5 × 0.5–0.7 cm, microsporophylls spirally arranged in 10–11 orthostichies of 10–22 sporophylls each, 8–10 mm × 5–7 mm, sporophyll face 5–7 × 3 mm tall, sterile tips conically pointed, with terminal facet distinctly extruded outward, fertile region bearing 25–35 microsporangia aggregated into single group and spreading to the edges, present only on abaxial surface. *Ovulate strobili* 1–2 per stem apex, tan to dark-brown tomentose, cylindrical to ovoid, at maturity 6–10× 3–6cm, sterile apex acute, 10–13 × 8–9 mm at base, peduncles dark green covered in cream to brown tomentum, flattened or angled, 4.0–5.0× 1.5 cm, megasporophylls spirally arranged in 5–6 orthostichies with 5–10 sporophylls each, distinct abaxial side flaps partly covering ovules, facets slightly protruding, velvet brown tomentose, 14–17 × 17–20 mm, sporophylls 15 mm deep, 17–20 mm wide, pedicel 6–8 mm long, light pink, glabrous, strobilus axis light pink, glabrous. Seed, ovoid, sclerotesta 14–15 × 9–10 mm, sarcotesta red at maturity. Chromosome number: 2n = 24 (Norstog 1997, as '*Z. acuminata*').

Distribution:—Central Panama, Coclé Province, within the remnant crater of the extinct volcano El Valle de Antón and on Cerro Turega, approximately 3 km West of the crater rim.

Habitat:—The caldera of El Valle volcano collapsed approximately 56,000 years ago, forming a crater about 30 km2 in area. The crater then gradually filled with water, forming a huge lake with 90 m of sedimentary deposits (Hidalgo 2007). Approximately 12,000 years ago a breach in the southwest caldera wall caused the lake to drain and formed the valley, where the town of El Valle de Antón is currently located (NASA 2012). The zamias are common on the lower inner ridges of the crater, from 625 up to 1020 m, on flatland in open forest or on steep rocky slopes in clay and volcanic silt soil overlaid by medium brown humus soil with 12 cm of leaf litter, high moisture content and a pH of 5.5. The habitat consists of 80 % leaf litter, 10 % branches and stones, 10 % associated plants. Generally, *Z. nana* is found dominant in understory of low (8–10 m canopy) evergreen tropical forest of mostly an *Erythrina, Inga,* (Fabaceae) and *Phytelephas* (Arecaceae). Measured illuminance was14–400 Lux, typically 30–100 with 85% humidity. It co-occurs with a few other understory plants, such as *Begonia* sp. (Begoniaceae), *Pitcairnia heterophylla* (Lindl.) Beer (Bromeliaceae), *Philodendron* and *Anthurium* species (Araceae) and *Pteris* sp. (Pteridaceae) along with some widely scattered shrubs. Associated flora in height range of 10–80 cm and consists mainly of *Clusia* sp. (Clusiaceae), *Costus* sp. (Costaceae), *Monstera* sp. (Araceae), *Heliconia latispatha* Benth., and scattered individuals of individuals of *Chamaedorea tepejilote* Liebm. (Arecaceae) were seen at one population.

Reproductive phenology:—The pollinator of *Zamia nana* appears to be a single unidentified erotylid beetle of the genus *Pharaxonotha*. The sex ratio has been checked during four coning periods (1999-2002) and it is basically 1.00 (Taylor *et al*. 2012). Receptive ovulate strobili typically open at the top and often in vertical splits along the cone. Receptive ovulate strobili as well as pollen shedding microsporangiate strobili have been observed in habitat in late January and February, and an absence of microsporangiate strobili was observed in mid-April. Mature seeds have been observed from October through late January. Cultivated plants

FIGURE 6. *Zamia nana* in habitat in El Valle de Antón, Panama. A. Pollen strobilus at pollen dehiscence. B. Immature seed strobilus at receptivity stage. C. Plant in habitat.

in Thailand show similar coning pattern with ovulate strobili being receptive in January and February. Seeds take 9–11 months to ripen, typically in November and December and 15–20 days to germinate.

Ecology:—Eggs, larvae and adults of butterflies belonging to the genus *Eumaeus* have been observed on new leaves as well as on microsporangiate and ovulate strobili in two populations of *Zamia nana*.

Etymology:—The epithet is in reference to the small stature of this species.

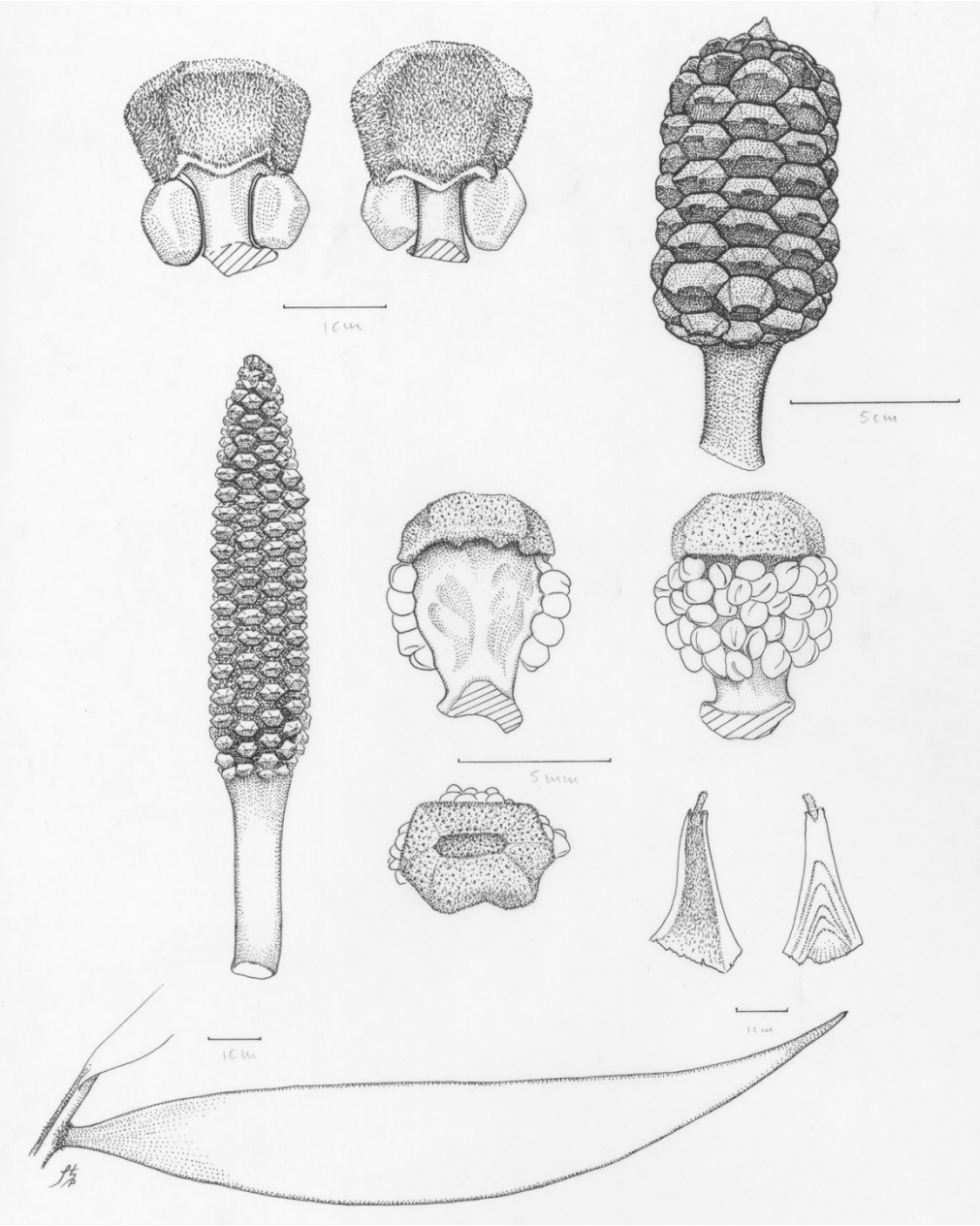

FIGURE7. *Zamia nana*. Pollen strobili (Lindstrom, 05-080), Ovulate strobili and cataphylls (Lindstrom, 05-079), leaflet (Stevenson & Valdespinos 1147). Illustration by Stig Dalstrom, from Holotype PMA. (Scale Bar = 1 mm)

Conservation status:—This taxon was previously erroneously listed as *Zamia acuminata* on the IUCN Red List, where it received a conservation status listing of Vulnerable based on criteria B2ab(v); C1. However, the previous listing may not be accurate since it combined both *Zamia nana* and *Zamia acuminata* in its assessment. The entire extent of occurrence for the species, which is restricted to the interior of the crater of the extinct El Valle de Antón volcano and Cerro Turega approximately 3 km West of the crater rim, is estimated to be 40 km2. Fewer than six populations are known and the total number of adult plants is calculated to be between 500–1000 plants. The largest threats are habitat destruction for residential

development and other uses, as well as extraction of plants for sale at local markets. It is estimated that at least 50% of the original habitat has been deforested. We propose an IUCN redlist classification of EN, based on small extent of occurrence, small population size, and continuing decline.

Additional specimens examined:—PANAMA. Coclé: Mun. Antón, El Valle: *H. Barlett 16682* (MO); *R. Dressler 5322* (F, MO, PMA, US); Cerro Gaital. 625 m, *C. Galdames et al. 4394* (SCZ); Piedra Pintada, 775 m, *A.J. Lindström 05-079, 05-080* (PMA); El Valle: *R. J. Schmalzel et al. 1041* (MO, NY, PMA); Shaded low forest on south rim of the extinct crater of El Valle de Anton Volcano, *S. Kiem & K. Norstog 70* (FTG); Cocle: 1 km before El Valle in road over culvert, in woods above road, 750 m, *D. Hodel et al. 1251* (MO) [photographs only].

Discussion:—*Zamia nana* has leaflets similar in shape to those of *Z. acuminata*, but is readily distinguishable vegetatively due to its smaller overall size (Table 2) and hypogeous stems compared to the larger size and semi-epigeous stems of *Zamia acuminata*. The two species are also easily identifiable by their reproductive structures. *Zamia nana* has dark brown megasporangiate and microsporangiate strobili, megasporophyll and microsporophyll faces that are outwardly extruded and ornate with narrow, strongly indented terminal facets, whereas *Zamia acuminata* has gray-tan megasporangiate and microsporangiate strobili, with megasporophyll and microsporophyll faces that are more or less flattened, with inornate, smooth terminal facets.

TABLE 2. Vegetative dimensions of *Zamia acuminata* and *Zamia nana.*

	Petiole length (cm)	Rachis length (cm)	Leaflet length (cm)	Leaflet width (cm)
Zamia acuminata	60–89	53–89	17.7–34.0	2.45–5.50
Zamia nana	15–60	27–36	13.5–23.2	2.0–3.3

Acknowledgements

The first author wishes to thank Mr. Kampon Tansacha, Director of Nong Nooch Tropical Botanical Garden, Thailand for full financial support for field work. Mrs. Galdames at the Smithsonian Research Center Herbarium in Panama for providing access to the herbarium and discussion about Panamanian Biogeography. Bernard Fisher for additional field data and invaluable help and discussions. Jean Michel Maes (Museo Entomologico, León, Nicaragua) provided comments about *Zamia* along the San Juan River in Nicaragua. The HULE herbarium of the Universidad Nacional Autónoma de Nicaragua provided specimen data for *Zamia* collections along the San Juan River. Ib Friis and Olof Ryding of the Herbarium of the Natural History Museum of Denmark in Copenhagen provided high resolution scans of the holotype of *Zamia acuminata* as well as information on Anders Ørsted. Willie Tang provided photographs and additional data about *Z. acuminata* in support of our research. Javier Francisco-Ortega and Patrick Griffith critically read an early draft of the manuscript. The Organization for Tropical Studies helped with the logistics of acquiring MINAE research and collection permits for fieldwork in 2004 and 2006. Montgomery Botanical Center provided funding for field research in Costa Rica in 2004, and Panama in 2009. This work was supported in part by NSF Grants BSR 8607049, EF 0629817 and IOS 0421604 to DWS.

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Appendix 1. *Zamia* specimens examined from the vicinity of the San Juan River in Nicaragua and Costa Rica, all determined as *Z. neurophyllidia*.

COSTA RICA. Limón: Cerro Coronel, East of Laguna Danto, *W.D. Stevens 23771* (CR, MO); Cerro Coronel, East of Rio Zapote, along and above new road within 1 km of Rio Colorado, tall evergreen forest and edge of Raphia swamp on gentle to moderate slope, *W.D. Stevens 24338* (CR, MO); Hills 3.5 km from South of Islas Buena Vista in the Rio Colorado, 16 km SW of Barra de Colorado, premontane wet forest on low hills, *G. Davidse, G. & G. Herrera 31276* (CR, MO).

NICARAGUA . Atlántico Sur: Caño Montecristo, al este del Campamento Germán Pomares, 60–90 m, *P.P. Moreno 15127* (MO); Río Punta Gorda, Atlanta, 2 km al S de Carolina del Sur, 60 m, *P.P. Moreno & J.C. Sandino* 12859 (MO); Noroeste del poblado de Nueva Atlanta, 30–35 m, *R.M. Rueda et al. 3146* (HULE, MO); Río Punta Gorda, al sur de San José, 50–100 m, *R.M. Rueda et al. 3651* (HULE, MO); Municipio de Nueva Guinea, Reserva Indio-Maíz, Colinas de Piedras Fina, 200–300 m, *R.M. Rueda et al. 9778* (HULE, MO); Municipio de Nueva Guinea, Reserva Indio-Maíz, Río Pijibaye entre el caño Bijagua y el cerro Chiripa, 50–200 m, *R.M. Rueda et al. 10054* (HULE, MO); Río Punta Gorda, Atlanta, al SE de "La Richard", 30 m, *J.C. Sandino 13102* (MO). Rio San Juan: Río Santa Cruz; bosque tropical húmedo, 40–50 m, *M. Araquistain 3240* (MO); Boca de Sábalo; bosque siempreverde, 70–100 m, *P.P. Moreno 26815* (MO); Near Caño Chontaleño, 20 km NE of El Castillo (Río Indio watershed); tropical wet forest, 200 m, *D.A. Neill 3386* (MO); Reserva Indio-Maíz, Municipio del Castillo, Estación experimental La Lupe, 100 m, *R.M. Rueda & W. Velásquez 14992* (HULE, MO); Municipio de El Castillo, Reserva Indio-Maiz, Zona de Amortiguamiento, Estación Biológica La Lupe, 100–200 m, *R.M. Rueda et al. 10375* (HULE, MO); Sobre el Río San Juan, en el caño el Sarnoso, ubicado a una hora río abajo del puesto de MARENA, Bartola, 50–100 m, *R.M. Rueda et al. 1992* (HULE, MO); Río San Juan, Río Sábalos, Caserio de Buena Vista, 2 h al Caserío de Gordiano, en la cercanía de la Propiedad de José Martínez, 50–200 m, *R.M. Rueda et al. 2115* (HULE, MO);Reserva Indio-Maíz, Municipio de el Castillo, a lo largo del caño el Pavon, a 3 km de su desembocadura en el Río Bartola, *R.M. Rueda et al. 5151* (HULE, MO); Reserva Indio-Maíz, Municipio del Castillo, a 5 km de la cabecera del Río Bartola, en dirección al Cerro El Diablo, *R.M. Rueda et al. 5242* (HULE, MO); Reserva Indio-Maíz, Municipio del Castillo, a 8 km de la cabecera del Río Bartola, en dirección al Cerro El Diablo, *R.M. Rueda et al. 5328* (HULE, MO); Reserva Indio-Maíz, Municipio de el Castillo, Cerro el Diablo, 250–400 m, *R.M. Rueda et al. 5424* (MO); Reserva Indio-Maíz, Municipio de el Castillo, 3 km al norte de la desembocadura del Caño Chontaleño, *R.M. Rueda et al. 5739* (HULE, MO); Reserva Indio-Maíz, Municipio de San Juan del Norte, cerro Cantagallo, 50–100 m, *R.M. Rueda et al. 5938* (HULE, MO); Municipio del Castillo, Estación Biológica Bartola, sobre el Río Bartola a 3 km de la desembocadura, 50–100 m, R.M. Rueda et al. 8174 (HULE, MO); Reserva Indio-Maíz, Municipio de San Juan del Norte, Río Indio, Cerro Canta Gallo, 150–200 m, *R.M. Rueda et al. 8547* (HULE, MO); Reserva Indio-Maíz, Municipio de San Juan del Norte, a lo largo del caño que baja del Cerro Gigante, 200–300 m, *R.M. Rueda et al. 9070* (HULE, MO); Municipio El Castillo, Reserva Indio-Maíz, Cerro Bolivar, 150–280, *R.M. Rueda et al. 9127* (HULE, MO); Municipio El Castillo, Reserva Indio-Maiz, Cerro El Diablo, 100–200, *R.M. Rueda et al. 9527* (HULE, MO); El Castillo, lowland disturbed forest on sandy clay soils, 35–50m, *J. Salick 7827* (MO).