

The Zamiaceae in Panama with comments on phytogeography and species relationships

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Stevenson, Dennis Wm. (New York Botanical Garden, Bronx, New York 10458, U.S.A.). The Zamiaceae in Panama. *Brittonia* 45: 1-16. 1993.—A key to, and descriptions of, the eleven species of *Zamia* in Panama are presented. Four of these are new species: *Z. cunaria*, *Z. dressleri*, *Z. ipetiensis*, and *Z. neurophyllidia*. Floristically, *Zamia* is represented in Panama by three elements: three Central American species, *Z. acuminata*, *Z. fairchildiana*, and *Z. skinneri*, which reach their southern limits in central Panama; three northern South American species, *Z. chigua*, *Z. manicata*, and *Z. obliqua*, which reach their northern limits in Panama; and five endemic Panamanian species, *Z. cunaria*, *Z. dressleri*, *Z. ipetiensis*, *Z. neurophyllidia*, and *Z. pseudoparasitica*. These distributions are interpreted by a consideration of sister group relationships based upon derived morphological character states.

Key words: Panama, Zamiaceae, *Zamia*.

As currently circumscribed (Stevenson, 1990, 1992) the Zamiaceae comprise eight genera. Five of these are endemic to the neotropics with only one, *Zamia* L., occurring in Panama. In the Flora of Panama, Woodson (1943) considered *Zamia* to be monotypic in Panama, but with reservation. Woodson was cognizant of the numerous species of *Zamia* that had been described from Central America but was hampered in his treatment of the genus by lack of specimens, incomplete descriptions derived from horticultural sources with no types, and the wholly inadequate monograph of Schuster (1932). An attempt was made by myself to update the list of *Zamia* species occurring in Panama (D'Arcy, 1987) but this could not be completed until further study as reported here.

Recent collections of *Zamia* in Central America and the typification of valid names in *Zamia* (Stevenson & Sabato, 1986) have clarified many of the problems promulgated by Schuster (1932) and perpetuated in recent works by Gomez (1982a, 1982b). These problems will be discussed here under the treatment of individual taxa. Some of the work presented here is based on an unpub-

lished manuscript by Robert Dressler which he generously gave to me some years ago.

The morphological diversity of *Zamia* is greater in Panama than any other region of the neotropics. For example, growth habit ranges from epiphytic species (*Z. pseudoparasitica* Yates) to species with trunks to five meters (*Z. obliqua* A. Br.) to species with short trunks of a meter (*Z. chigua* Seemann) to species with subterranean (hypogeous), tuberous stems (*Z. acuminata* Oersted ex Dyer). Those species with subterranean stems produce 1-5 leaves in a growth flush in contrast to the trunk forming species that produce 10-20 leaves in a growth flush. The extremes are represented by *Z. dressleri* D. Stevenson which almost invariably produces only a single leaf and large plants of *Z. obliqua* that produce more than 15 leaves. No cycad has a truly woody stem and branching is basically dichotomous and sparse (Stevenson, 1988, 1990).

Those plants that have an aerial stem, even if only 30 cm tall, are described as arborescent in contrast to the wholly underground stems that are described as hypogeous or subterranean (Stevenson, 1991). All cycads are considered to be pachycau-

lous (Stevenson, 1990) because of the usually scanty nature of the secondary xylem compared to the well developed parenchymatous pith and cortex.

There is also considerable diversity in leaf and leaflet morphology. The general aspects of leaf and leaflet diversity in *Zamia* has been discussed elsewhere (Stevenson, 1991) so that the following is limited to that found in the Panamanian species of *Zamia*. Some species (e.g., *Z. dressleri*) have only 4–8 pairs of very wide leaflets in contrast to the up to 70 pairs of narrow leaflets found in *Z. chigua*. *Zamia acuminata* often has diminutive prickles on the petiole in contrast to the heavy, often branched, prickles found on petioles of *Z. chigua*. Most Panamanian species of *Zamia* have flat, smooth leaflets, but three species (*Z. dressleri*, *Z. neurophyllidia* D. Stevenson, and *Z. skinneri* Warsz. ex A. Dietrich) have distinctive leaflets that are deeply grooved adaxially between the veins so as to appear plicate. In general *Zamia* leaflets are sessile on the rachis but one Panamanian species, *Z. manicata* Linden ex Regel, has distinct petiolules. In *Z. manicata*, there is also an abaxial, semicircular, collar or gland-like structure, of unknown function, at the junction of the lamina and the petiolule (Stevenson, 1990).

Reproductive morphology, on the other hand, is more constant, but here too the variability is greater than for other neotropical areas with strobili varying in color from light yellow to deep red-brown. Three species of *Zamia* found in Panama, *Z. cunaria* Dressler & D. Stevenson, *Z. ipetiensis* D. Stevenson, and *Z. obliqua*, have very distinctive microsporophylls in that microsporangia are found on both the abaxial and adaxial surfaces (Fig. 1) in contrast to all other cycads which have microsporangia only on the abaxial surface. The yellow seeds of the endemic *Z. pseudoparasitica* are unique in the genus.

Because the cycads are strictly dioecious and reproductive structures are infrequently encountered in the field, herbarium, or cultivation, the emphasis in the following key to species is on vegetative characters. Certainly, to use yellow seeds as the only key character for *Z. pseudoparasitica* would not be useful for a microsporangiate plant. In

addition, the vegetative characters in Panamanian *Zamias* are so distinct, as outlined above, that their use in this case is warranted.

As in previous works on cycads (e.g., Stevenson et al., 1986), specific localities of the species of *Zamia* are not given in this paper because of their endangered status and commercial value which could lead to their eradication either intentionally or unintentionally by collectors. Some of the species discussed and described in this work are locally endemic and known from only one or a few small populations and are thus particularly susceptible to over-exploitation.

All lectotypes and neotypes given in the present work are from Stevenson and Sabato (1986). Chromosome numbers are from the works of Norstog (1980, 1981) and Morretti (1990). Information on individual species are given in alphabetical order.

Key to the species of *Zamia* in Panama

- 1 Leaflets deeply grooved between veins and appearing plicate
 - 2 Leaflets large to 50 cm long and 25 cm wide
 - 3 Leaves 5 to many, stems to 2 m ... *Z. skinneri*
 - 3 Leaves 1–3, stems subterranean ... *Z. dressleri*
 - 2 Leaflets small, less than 20 cm long and 10 cm wide *Z. neurophyllidia*
- 1 Leaflets smooth and not appearing plicate
 - 4 Leaflets with distinct petiolule and gland-like collar at the base of the blade *Z. manicata*
 - 4 Leaflets sessile and without a gland-like collar
 - 5 Leaflets entire
 - 6 Leaflets gray-green; petioles without prickles; plants epiphytic *Z. pseudoparasitica*
 - 6 Leaflets green to dark green; petioles with prickles; plants terrestrial
 - 7 Leaflets imbricate, 30–80 pairs, papyraceous; petioles with many stout prickles *Z. chigua*
 - 7 Leaflets separate, 6–15 pairs, subcoriaceous; petioles with a few diminutive prickles *Z. acuminata*
 - 5 Leaflets toothed at least in upper one-third
 - 8 Leaves (3)5–many, plants arborescent
 - 9 Leaflets obovate-elliptic *Z. obliqua*
 - 9 Leaflets oblong *Z. fairchildiana*
 - 8 Leaves usually solitary (3), stem subterranean
 - 10 Leaflets oblong to oblanceolate, strongly toothed in up-

- per third; ovulate strobili 20–30 cm long *Z. cunaria*
 10 Leaflets oblanceolate, minutely toothed near apex; ovulate strobili to 10 cm long
 *Z. ipetiensis*

1. ZAMIA ACUMINATA Oersted ex Dyer (Fig. 1D)

Zamia acuminata Oersted ex Dyer in Hemsley, Biol. cent.-amer., Bot. 3(16): 194. 1884. TYPE: NICARAGUA. "ad flumen S. Juan," Oersted s.n. (HOLOTYPE: C!).

Stem subterranean, subglobose to cylindrical, to 5 cm diam. *Leaves* 1–3, to 1 m long; petiole to 60 cm, densely prickled; rachis with 6–15 pairs of leaflets, some prickles in lower third. *Leaflets* elliptic-lanceolate, subcoriaceous, cuneate basally, very long acuminate apically, margins entire, the larger median ones 20–30 cm long, 1–3 cm wide. *Polleniferous strobili* cream to tan, cylindrical, 5–8 cm long, 1–1.5 cm diam. *Ovulate strobili* cylindrical to ovoid, cream to tan, 10–20 cm long, 5–8 cm diam. *Seeds* ovoid, red. ($2n=24$.)

There have been horticultural reports of plants of *Z. acuminata* having trunks one meter in height. This appears to be a condition of pot grown plants in which it is not possible for stem and root contraction to pull the shoot underground. This is supported by field observations by myself and others where all plants of this species have subterranean stems. The very distinctive long acuminate leaflet tips (Fig. 4D) are unique in *Zamia*.

Zamia acuminata is found from near sea level in Nicaragua to 1200 m in Panama. In fact, in Panama and Costa Rica, this species is restricted to elevations between 400–1200 m.

Representative specimens examined: PANAMA. *Cocle*: Barlett 16682 (MO); Dressler 5322 (MO, PMA, US); Stevenson & Valdespinos 1147 (F, FTG, K, MO, NY, PMA, U). *Veraguas*: K. Norstog et al. s.n. (FTG).

2. ZAMIA CHIGUA Seemann (Fig. 1F)

Zamia chigua Seemann, Bot. Voy. Herald 6: 201. 1854. LECTOTYPE: Bot. Voy. Herald 5. 43. 1854. *Aulacophyllum ortgiesii* Regel, Gartenflora 25: 141–143. 1876. TYPE: COLOMBIA. Wallis 76 (HOLOTYPE: LE!).

Stem arborescent, to 2 m tall and 15 cm diam., wrinkled in appearance. *Leaves* 3–15, 0.5–3 m long; petiole to 1 m long, very densely prickled; rachis with 30–80 (less in juvenile plants) pairs of imbricate leaflets, densely prickled in lower half. *Leaflets* long lanceolate and subfalcate, chartaceous to membranous, margins entire, the larger median ones 10–30 cm long, 1–1.5 cm wide. *Polleniferous strobili* cream to light yellow, cylindrical, 10–20 cm long, 2–3 cm diam. *Ovulate strobili* tan to light brown, narrowly ovoid to cylindrical, 20–30 cm long, 8–12 cm diam. *Seeds* ovoid, red. ($2n=16$.)

Zamia chigua is the most fern-like of the Central American species of *Zamia* because of its long graceful leaves with numerous imbricate slender leaflets (Fig. 1F). It is also the species with the most numerous prickles which are quite stout and often branched. The trunk is quite heavy because of its large amount of water retentive parenchyma and often has a wrinkled appearance particularly in large plants.

In the past there has been some confusion concerning the identity of *Z. chigua* (Norstog, 1986; Sabato, 1990). The reason for this was the lack of typification of various *Zamia* species and the use of the common name of "chigua" by indigenous people in the Choco of Colombia. The common name "chigua" is apparently applied to several species of *Zamia*. As a result of this confusion, *Z. roezlii* Linden was thought to be *Z. chigua* and the latter was referred to as *Z. "helecho"* in horticulture. Thus, the chromosome numbers attributed to *Z. chigua* by Norstog (1980, 1981) were in fact from plants of *Z. roezlii* (Norstog, 1986).

Zamia chigua is found in the Chiriqui region of Panama and is disjunct in the Choco of Colombia. In Colombia, *Z. chigua* is found in lowland rainforest whereas known localities from Panama are from 600 to 1200 m. This species is probably present on the slopes of Cerro Pirre and the western slopes of Cordillera de Jurado in Darien, Panama but has yet to be collected there.

Representative specimens examined: PANAMA. *Chiriqui*: T. Antonio 5053 (MO); Croat & Grayum 59774 (MO); Dressler 5420 (MO); Knapp et al. 4186 (MO); Stevenson et al. 1148, 1151, 1152 (all F, FTG, K, MO, NY, PMA, U).

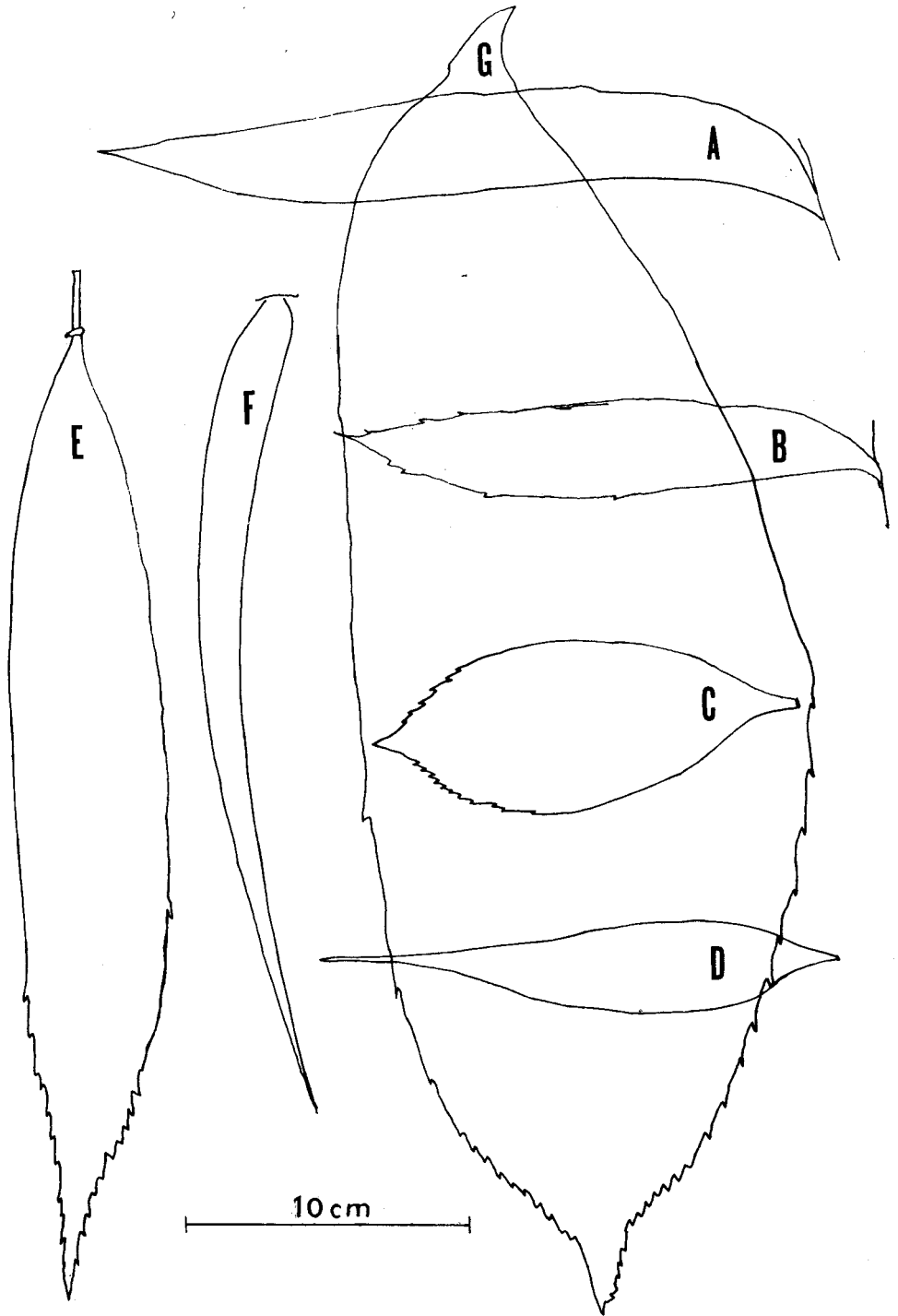


FIG. 1. Outline drawings of leaflet shapes of *Zamia* spp. found in Panama. A. *Z. pseudoparasitica*. B. *Z. fairchildiana*. C. *Z. obliqua*. D. *Z. acuminata*. E. *Z. manicata*. F. *Z. chigua*. G. *Z. skinneri*.

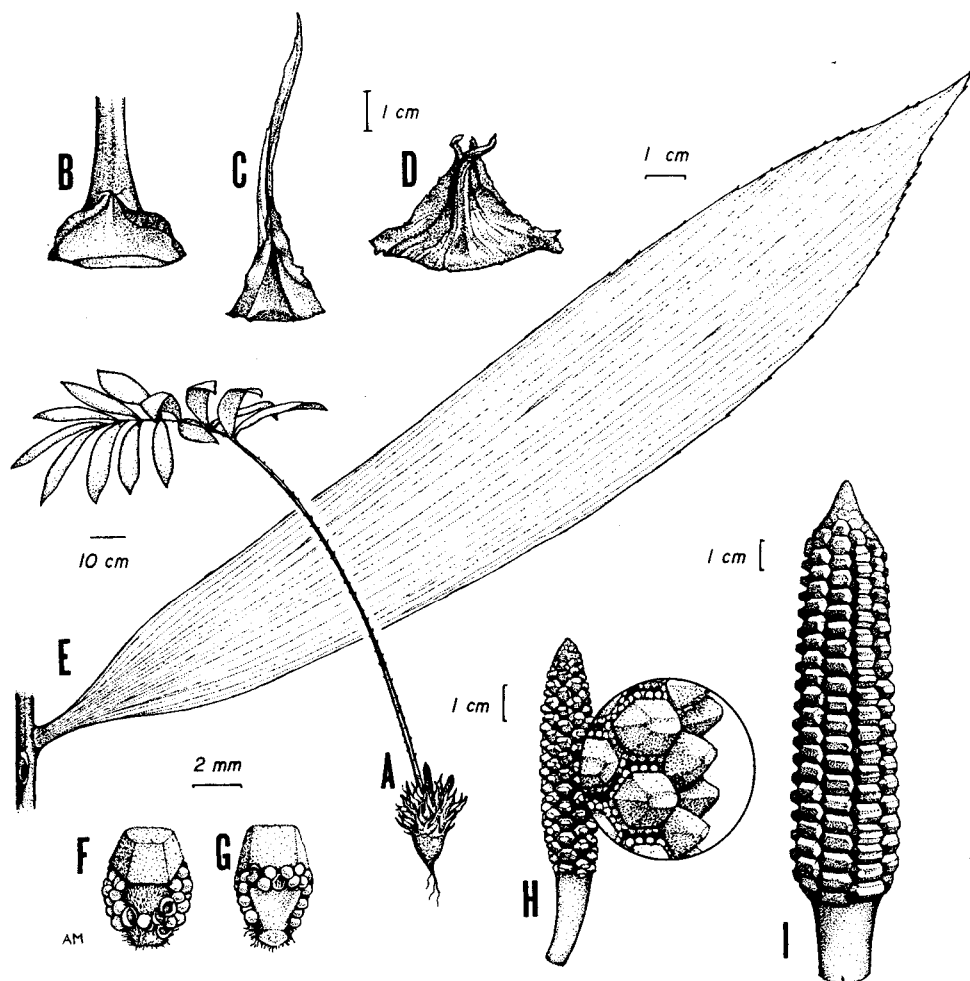


FIG. 2. *Zamia cunaria* (Stevenson et al. 1153). A. Habit. B. Leaf base. C. Acicular cataphyll. D. Ovate cataphyll. E. Median leaflet. F. Microsporophyll, abaxial view. G. Microsporophyll, adaxial view. H. Polleniferous strobilus. I. Ovulate strobilus.

3. *Zamia cunaria* Dressler & D. Stevenson, sp. nov. (Fig. 2)

TYPE: PANAMA. Cuna Yala (Comarca de San Blas): 18 Jan 1989, *D. Stevenson et al. 1153* (HOLOTYPE: NY; ISOTYPES: F, FTG, K, MO, NY, PMA, U).

Caudex subterraneus; folia plerumque solitaria, paucifoliolata, erecta; foliola mediana oblonga vel oblanceolata, acuminata, serrata; microsporophylla microsporangii adaxialibus et abaxialibus provisa; strobili feminei vinacei vel ferruginei; semina rosea.

Stem subterranean, subglobose, to 10 cm diam. *Cataphylls* of two forms either ovate

and 3–4 cm long and 4–5 cm wide, or acicular and 7–10 cm long and 2–3 cm wide. *Leaves* 1(3), 0.5–1.5 m long; petiole 15–50 cm long, sparsely to densely prickled; rachis with 3–12 pairs of leaflets. *Leaflets* oblong or oblanceolate, cuneate basally, acuminate apically, margins serrate in upper third, the larger median ones 20–40 cm long, 5–8 cm wide. *Polleniferous strobili* cream to tan, cylindrical to ovoid-cylindrical, 4–6 cm long, 1–1.5 cm diam.; peduncle 2–4 cm long. *Microsporophylls* with sterile tip composed of six steeply inclined facets surrounding a centrally depressed terminal facet, sporan-

gia present on both the adaxial and abaxial surfaces of the fertile region. *Ovulate strobili* wine-red to dark red-brown, cylindrical to ovoid-cylindrical, 15–20 cm long, 5–7 cm diam. *Seeds* pink to light red, 1.5–2 cm long, 0.5–0.8 cm diam.

Although *Zamia cunaria* is most similar to *Z. ipetiensis* which is described below, the two species are really quite distinct in both vegetative and reproductive characters (compare Figs. 2 and 4). A comparison of the two species is given under the latter.

Zamia cunaria is usually found in clay soils on slopes and ridge tops from 400 to 800 m in secondary vegetation. It is known only from the area of the Cuna Indians (whence the specific epithet) who use the seeds to make necklaces. In Cuna, the plant is known as “obset” and the ovulate strobilus as “obset e sana.”

Representative specimens examined: PANAMA. Cuna Yala (Comarca de San Blas): *D’Arcy* 9477 (MO); *Dressler* 4757 (US); *de Nevers* 4132, 4244, 4332, 4562, 4600, 4915 (all MO, PMA); *F. Stier* 108 (PMA), 144 (MO), 165 (PMA).

4. *Zamia dressleri* D. Stevenson, sp. nov. (Fig. 3)

TYPE: PANAMA. Colon: 7 Jan 1989, *D. Stevenson & I. Valdespino* 1145 (HOLOTYPE: NY; ISOTYPES: FTG, MO, NY, PMA, U).

Zamia wallisii affinis, sed foliolis sessilibus differt.

Stem subterranean, 3–5 cm diam. *Cataphylls* ovate, 1–2 cm long, 2–3 cm wide. *Leaves* usually solitary (2–3), 0.5–1.5 m long; petiole 0.3–1 m long, sparsely to densely prickled; rachis with 2–5 pairs of leaflets, occasionally with a few prickles in the lower third. *Leaflets* elliptic, grooved between the veins on the adaxial surface, cuneate basally, acuminate apically, margins serrate in upper third, the larger median ones 30–50 cm long, 12–15 cm wide. *Polleniferous strobili* cream to tan, cylindrical to elongate-cylindrical, 5–8 cm long, 1–2 cm diam. *Ovulate strobili* wine-red to dark red-brown, short pedunculate, ovoid-cylindrical, 10–15 cm long, 3–4 cm diam. *Seeds* red, ovoid, 1–1.5 cm diam.

This species is named in honor of Robert Dressler who was the first to recognize that

it is distinct, and also for his excellent work on the genus in Panama without which the present treatment could not have been completed.

Zamia dressleri is endemic to Panama where it is only known from two small disjunct populations. It is most similar to *Z. wallisii* A. Br. in that both species have solitary leaves with from two to five pairs of very large leaflets that are strongly grooved above. On the other hand, *Z. wallisii* has very distinctive adaxially grooved petioles (Sabato, 1990; Stevenson, 1990), in contrast to the sessile leaflets of *Z. dressleri*. Very little is known about the strobili of *Z. wallisii*. The pollen strobili of *Z. wallisii* are cream to tan as in *Z. dressleri* but the shape of the former is ovoid in contrast to the more elongate and cylindrical shape of the latter. The ovulate strobili of *Z. wallisii* are unknown.

Representative specimens examined: PANAMA. Colon: *J. Cowell* 165 (MO); *R. Dressler* 5135 (MO, PMA); *S. Kiem & K. Norstog s.n.* (FTG). Cuna Yala (Comarca de San Blas): *H. Herrera* 204 (PMA); *G. de Nevers* 4731, 4786, 5054 (MO, PMA).

5. ZAMIA FAIRCHILDIANA L. D. Gomez (Fig. 1B)

Zamia fairchildiana L. D. Gomez, *Phytologia* 50: 401, pl. 1E–F. 1982. TYPE: COSTA RICA. *L. D. Gomez* 7948 (HOLOTYPE: CR!).

Stem arborescent, 0.5–1 m tall, 6–15 cm diam. *Leaves* 3–10, 0.7–2 (2.5) m long; petiole densely prickled, 0.3–0.5 (0.8) m long; rachis with prickles in lower third, 10–30 pairs of leaflets. *Leaflets* oblong, subfalcate basally, acute apically, sparsely serrulate apically, the larger median ones 20–40 cm long, 2–4 cm wide. *Pollen strobili* cream to yellow, cylindrical, 10–40 cm long, 2–5 cm diam. *Ovulate strobili* yellow-green to light brown, cylindrical 20–30 cm long, 6–10 cm diam. *Seeds* red, ovoid, 1–1.5 cm long.

Zamia fairchildiana may be the most common cycad species in Panama. Its northern limit is in southeastern Costa Rica with populations occurring sporadically to Cuna Yala in eastern Panama. This species is found at elevations from 50 to 1500 m, but is most common with the largest pop-

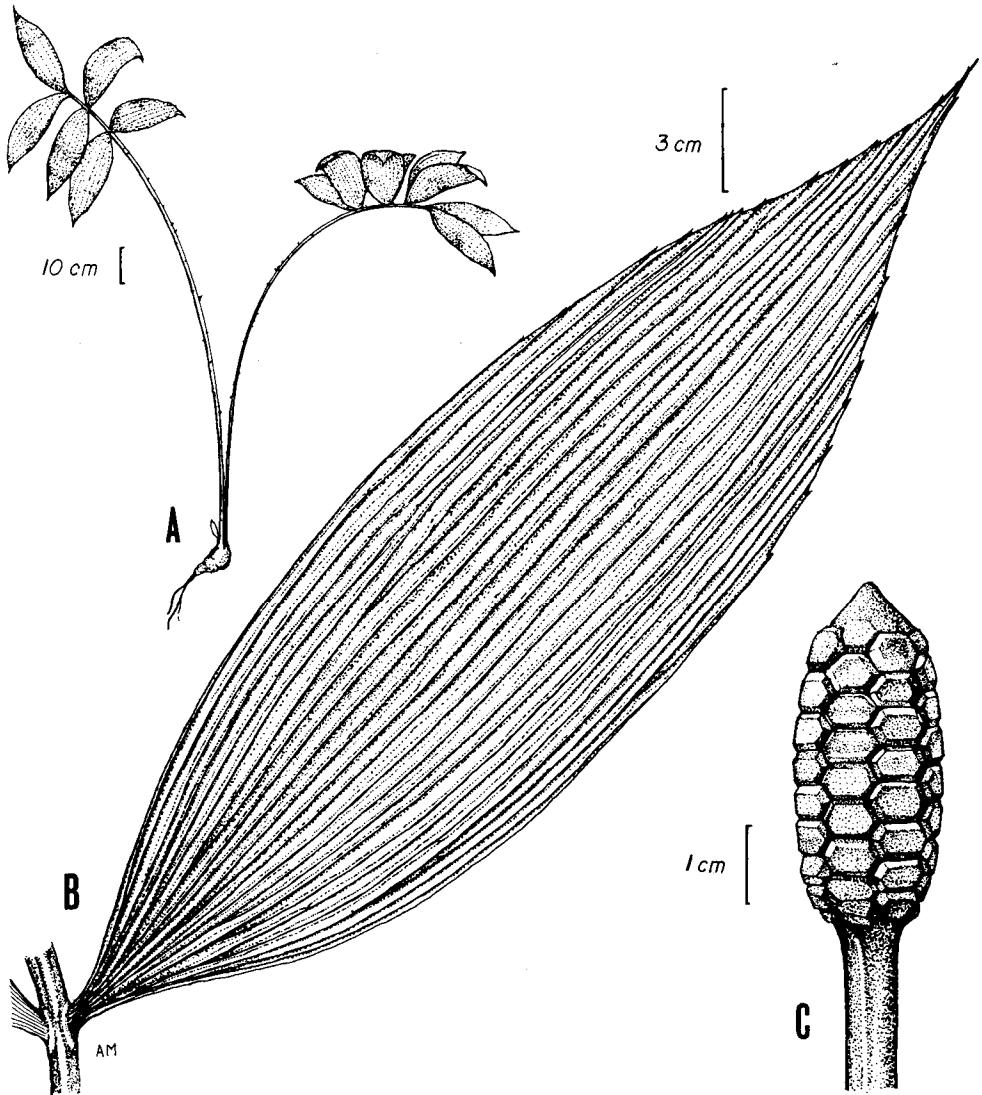


FIG. 3. *Zamia dressleri* (Stevenson & Valdespino 1145). A. Habit. B. Median leaflet. C. Ovulate strobilus.

ulations occurring from 400 to 900 m in primary and secondary rainforest.

Representative specimens examined: PANAMA. Chiriqui: Croat 35048 (MO); E. Leigh s.n. (PMA); Knapp 1588 (MO). Colon: Correa & Dressler 421; Dodge & Allen 17300 (MO); Dodge et al. 16933 (G, MICH, MO, NY, P, UC); Dressler 4897 (MO, MA). Cuna Yala (Comarca de San Blas): de Nevers 3966, 4897, 4994, 5497 (MO, PMA); Stevenson et al. 1155 (FTG, K, NY, PMA, U). Panama: Bartlett 16851 (MO); Berg & Dressler 2721 (MO); Dressler 4644 (F, MO, PMA, US); Folsom 4652 (MO); Mori 3655 (MO); Mori & Kallunki 5782 (MO); de Nevers 4943 (MO, PMA); Ste-

venson et al. 1146 (FTG, K, MO, NY, PMA, U); Systma 2858 (MO); R. & A. Tryon 5470 (MO); G. Wilder s.n. (MO).

6. *Zamia ipetiensis* D. Stevenson, sp. nov. (Fig. 4)

TYPE: PANAMA. Panama: 22 Jan 1989, D. Stevenson & I. Valdespino 1159 (HOLOTYPE: NY; ISOTYPES: FTG, MO, NY, PMA, U).

Caudex subterraneus; folia plerumque solitaria, errec-

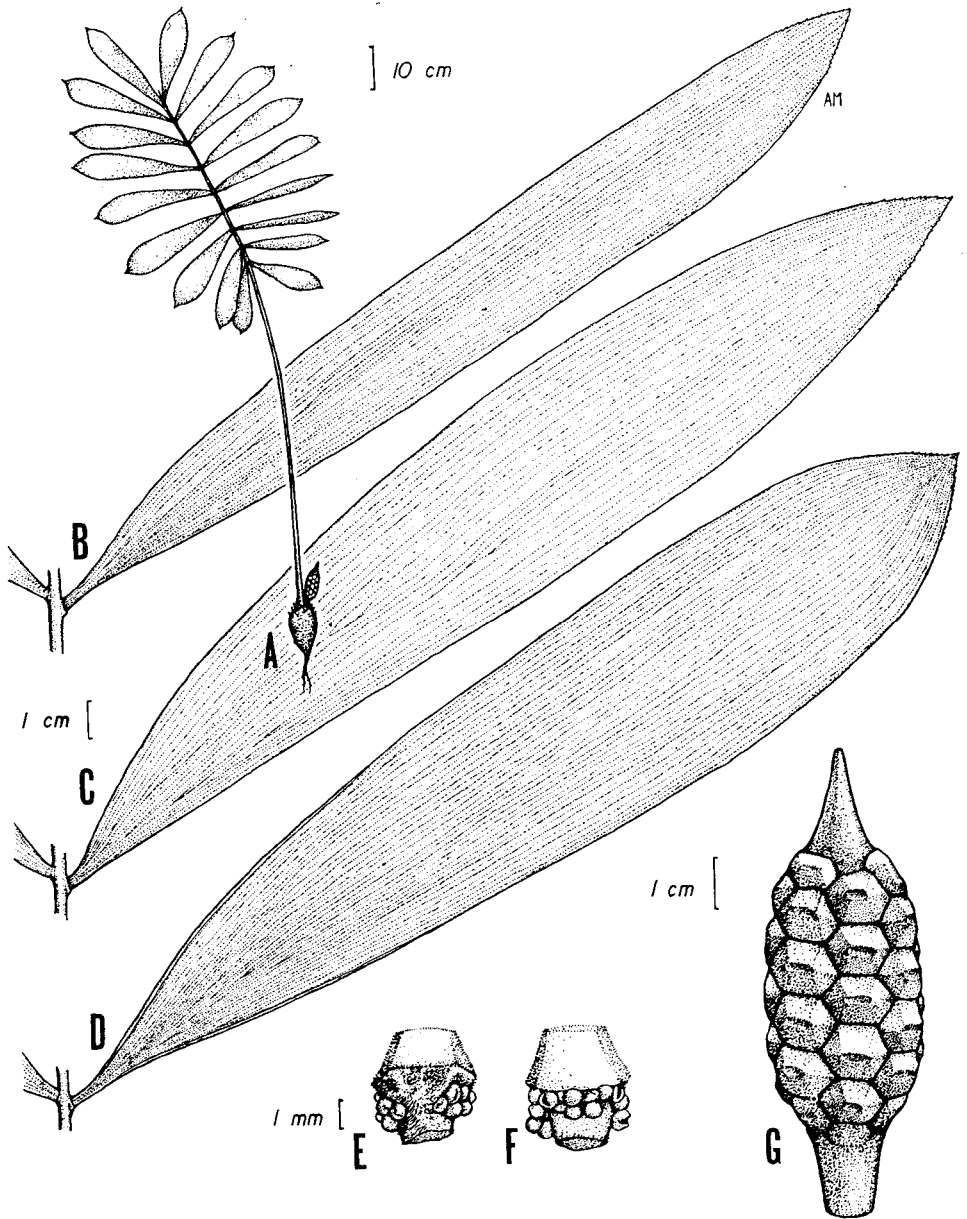


FIG. 4. *Zamia ipetiensis* (Stevenson & Valdespino 1159). A. Habit. B-D. Median leaflets. E. Microsporophyll, abaxial view. F. Microsporophyll, adaxial view. G. Ovulate strobilus.

ta, paucifoliolata; foliola mediana oblanceolata, acuminata, acumine serrulato; microsporophylla microsporangis adaxialibus et abaxialibus; strobili feminei fusciferruginei; semina rubra.

Stem subterranean, subglobose, to 10 cm diam. *Cataphylls* ovate, 3-4 cm long, 4-5 cm wide. *Leaves* 1 (3), 0.5-1.5 m long; pet-

iole 15-50 cm long, sparsely to densely prickled; rachis with 3-12 pairs of leaflets. *Leaflets* narrowly to broadly oblanceolate, cuneate basally, acuminate apically, margins finely serrulate in the tip, the larger median ones 20-40 cm long, 5-8 cm wide. *Polleniferous strobili* cream to tan, cylin-

dricul to ovoid-cylindrical, 4–6 cm long, 1–1.5 cm diam.; peduncle 2–4 cm long. *Microsporophylls* with sterile tip composed of six steeply inclined facets surrounding a centrally depressed terminal facet, sporangia present on both the adaxial and abaxial surfaces of the fertile region. *Ovulate strobili* wine-red to dark red-brown, cylindrical to ovoid-cylindrical, 15–20 cm long, 5–7 cm diam. *Seeds* pink to light-red, 1.5–2 cm long, 0.5–0.8 cm diam.

In many aspects *Zamia ipetiensis* is most similar to *Z. cunaria*. These include general growth habitat, solitary leaf production, leaf size and shape, and leaflet size and texture. Indeed, many of these features occur either singularly or in various combinations in other species of *Zamia*.

Zamia ipetiensis is endemic to a small area in Panama where it occurs from 100 to 500 m in primary and secondary rainforest.

Representative specimen examined: PANAMA. Panama: Knapp et al. 4558 (MO).

7. ZAMIA MANICATA Linden ex Regel (Fig. 1E)

Zamia manicata Linden ex Regel, Acta Horti trop. 4(4): 310. 1876. NEOTYPE: Tafel 926, fig. e in Gartenflora 27: 1878.

Z. madida R. E. Schultes, Bot. Mus. Leaf. Harv. Univ. 18(4): 114–115, pl. 18. 1958. TYPE: COLOMBIA. R. E. Schultes & I. Cabrera 18694 (HOLOTYPE: GH–2 sheets!).

Stem subterranean, globose to subcylindrical, 2–5 cm diam. *Leaves* 3–10, 0.5–2 m long; petiole 0.2–1 m long, slightly to densely prickled; rachis often with prickles in lower third, with 10–30 pairs of leaflets. *Leaflets* with distinct petiolule and abaxial gland-like collar at the juncture of the lamina, oblong to long-elliptic, margins serrate in upper third, cuneate basally, acute to acuminate apically, the larger median ones 15–35 cm long, 3–7 cm wide. *Polleniferous strobili* cream to tan, cylindrical, 4–6 cm long, 1–1.5 cm diam.; peduncle 15–30 cm long. *Ovulate strobili* wine-red to dark red-brown, cylindrical to ovoid-cylindrical, 10–15 cm long, 4–7 cm diam. *Seeds* red, 1–1.5 cm long, 0.5–0.8 cm diam. (2n=18.)

The petiolule and gland-like collar (Fig.

4E) occur among cycads only in *Z. manicata* (Stevenson, 1990). However, they are not present in seedling leaves, only diminutively present in juvenile leaves, and become distinct only in adult leaves. Also, in transplanted adult plants these structures may not be produced in the first set of leaves after transplanting.

Somehow Schuster (1932) confused *Z. manicata* with *Z. obliqua* and placed the former in synonymy with the latter. Schuster's description is a mixture of the two species. However, Braun (1875) described *Z. obliqua* with sessile elliptic to ovate-elliptic ("obelliptic") leaflets and trunks to 2.5 m and never mentioned petiolules or gland-like collars because these characters do not occur in *Z. obliqua*. In fact Schuster's concept of *Z. obliqua* was a plant with the trunks and strobili of *Z. obliqua* and the leaves of *Z. manicata*. Moreover, he described the petioles as unarmed when in fact anyone who has collected either of these species can attest to the numerous prickles. In contrast, Gomez's concept of *Z. obliqua* is in fact that of *Z. manicata*. Because of the confusion instigated by Schuster (1932), Schultes (1958) redescribed *Z. manicata* as *Z. madida* and the description of *Z. obliqua* by Gomez (1982b) is that of *Z. manicata* with both *Z. manicata* and *Z. madida* listed in synonymy. Besides the presence of petiolules and gland-like collars in *Z. manicata* and their absence in *Z. obliqua*, salient differences between these two species are subterranean stem, oblong to long elliptic (to 35 cm) leaflets, long pedunculate (15–30 cm) polleniferous strobili, microsporophylls with microsporangia only on the abaxial surface, and wine-red to dark red-brown ovulate strobili in *Z. manicata*. In contrast, *Z. obliqua* has aerial trunks to 5 m, elliptic to obovate leaflets to 10 cm long (Fig. 1C), short pedunculate (2–5 cm) polleniferous strobili, microsporophylls with microsporangia on both the adaxial and abaxial surfaces, and tan to light brown ovulate strobili.

Zamia manicata occurs in rainforest and secondary forest from 100 m to 1000 m in the Darien of Panama and contiguous Colombia.

Representative specimens examined: PANAMA. **Darien:** Allen 248 (MO); Burch et al. 1112 (US); Duke 5432 (MO); Duke & Kirkbride 14000 (MO); Hahn 155 (MO); Stern et al. 183 (G, MO). **Panama:** Allen 4523 (MO).

8. *Zamia neurophyllidia* D. Stevenson, sp. nov. (Fig. 5)

TYPE: PANAMA. Bocas del Toro: *M. Correa et al.* 3078 (HOLOTYPE: PMA!; ISOTYPE: NY!).

Zamia skinneri affinis sed truncus 5 (nec 10) dm alto diversa; foliola elliptica, 12–20 cm longa, 5–8 cm lata; strobili 15–25 cm longi; semina 1 cm usque longa.

Stem arborescent, to 60 cm tall, 6–12 cm diam. *Leaves* 3–10, 0.5–1 m long; petiole with numerous prickles, to 30 cm long; rachis with few prickles in lower third, with 5–8 (10) pairs of leaflets. *Leaflets* elliptic, grooved between the veins on the adaxial surface, cuneate basally, acuminate apically, margins serrulate in upper third, the larger median ones 12–20 cm long, 6–10 cm wide. *Polleniferous strobili* cream to tan, cylindrical to elongate-cylindrical, 5–8 cm long, 1–2 cm diam. *Ovulate strobili* brown, short pedunculate, ovoid-cylindrical, 10–15 cm long, 3–4 cm diam. Seeds red, ovoid, 1–1.5 cm diam.

The epithet is derived from the strongly nerved appearance of the leaflets.

Zamia neurophyllidia appears to be a smaller verison of *Z. skinneri*. It has smaller trunks, leaves, leaflets, pollen and ovulate strobili, and seeds. Plants at the type locality and nearby have maintained this diminutive size as adult reproductive plants for nearly thirty years. Thus, *Z. neurophyllidia* appears to be a distinct local endemic species related to *Z. skinneri*.

Zamia neurophyllidia, endemic to Panama, occurs from 100 to 200 m in rainforest that is occasionally flooded.

Representative specimens examined: PANAMA. **Bocas del Toro:** Dressler & Kennedy (NY); Gentry 2740 (MO, PMA); Hart 179 (US); Nee & Hansen 14079 (MO); H. Stork s.n. (US).

9. *ZAMIA OBLIQUA* A. Braun (Fig. 1C)

Zamia obliqua A. Braun, Monatsber. Konigl. Preuss. Akad. Wiss. Berlin, Apr 1875: 376. 1875. TYPE:

COLOMBIA, Seemann 1569 (NEOTYPE: BM–2 sheets!).

Z. obliqua Regel ex Ducos, Ill. hort. 24: 140. Planche 289, 1877. LECTOTYPE: Planche 289. nomen illegit.

Stem arborescent, 0.5–5 m tall, 5–12 cm diam. *Leaves* 5–20, 1–2.5 m long; petiole with numerous small prickles, 30–70 cm long; rachis with prickles in lower third, 10–20 pairs of leaflets. *Leaflets* elliptic to obovate, obliquely cuneate basally, acuminate apically, margins serrulate in upper third, the median ones 5–10 cm long, 3–6 cm wide. *Polleniferous strobili* cream to tan, cylindrical to ovoid-cylindrical, 4–6 cm long, 1–1.5 cm diam.; peduncle 2–4 cm long. *Microporphylls* with sterile tip composed of six steeply inclined facets surrounding a centrally depressed terminal facet, sporangia present on both the adaxial and abaxial surfaces of the fertile region. *Ovulate strobili* cream to tan, cylindrical to ovoid-cylindrical, 15–25 cm long, 5–8 cm diam. *Seeds* red, 1–1.5 cm long, 0.5–0.8 cm diam. ($2n=18$.)

Zamia obliqua is one of most beautiful of the New World cycads with its straight, slender, smooth, gray trunks of 5 m bearing some 20 leaves. As discussed above under *Z. manicata*, *Z. obliqua* has been confused with that species but there is no close resemblance between them other than the fact that they both belong to the same genus.

Zamia obliqua occurs in primary and secondary rainforests from near sea level to 500 m in southern Panama to the southern Choco in Colombia.

Representative specimens examined: PANAMA. **Chiriqui:** Busey 424 (MO). **Colon:** Croat 9924 (MO, SCZ). **Darien:** Allen 4554 (MO); T. Antonio 4391, 4564 (MO); Dressler 5310 (MO, PMA, US); Duke 4878 (MO); Goldman 1983 (US); Hammel 7321 (MO); Knapp & Mallet 3052 (MO); Stern et al. 94 (G, MO, NY, P, UC, US); Stern et al. 832 (G, MO, UC); Stevenson & Valdespinos 1157, 1158 (FTG, K, MO, NY, PMA, U); Sytsma 3353 (MO).

10. *ZAMIA PSEUDOPARASITICA* Yates in Seemann (Fig. 1A)

Zamia pseudoparasitica Yates in Seemann, Bot. Voy. Herald 6: 202. 1854. TYPE: PANAMA. Warszewicz s.n. (HOLOTYPE: BM!).

Z. pseudoparasitica var. *latifolia* Schuster, Pflanzenr. 99: 142. 1932. LECTOTYPE: description.

Plants epiphytic. *Stem* arborescent, to 1

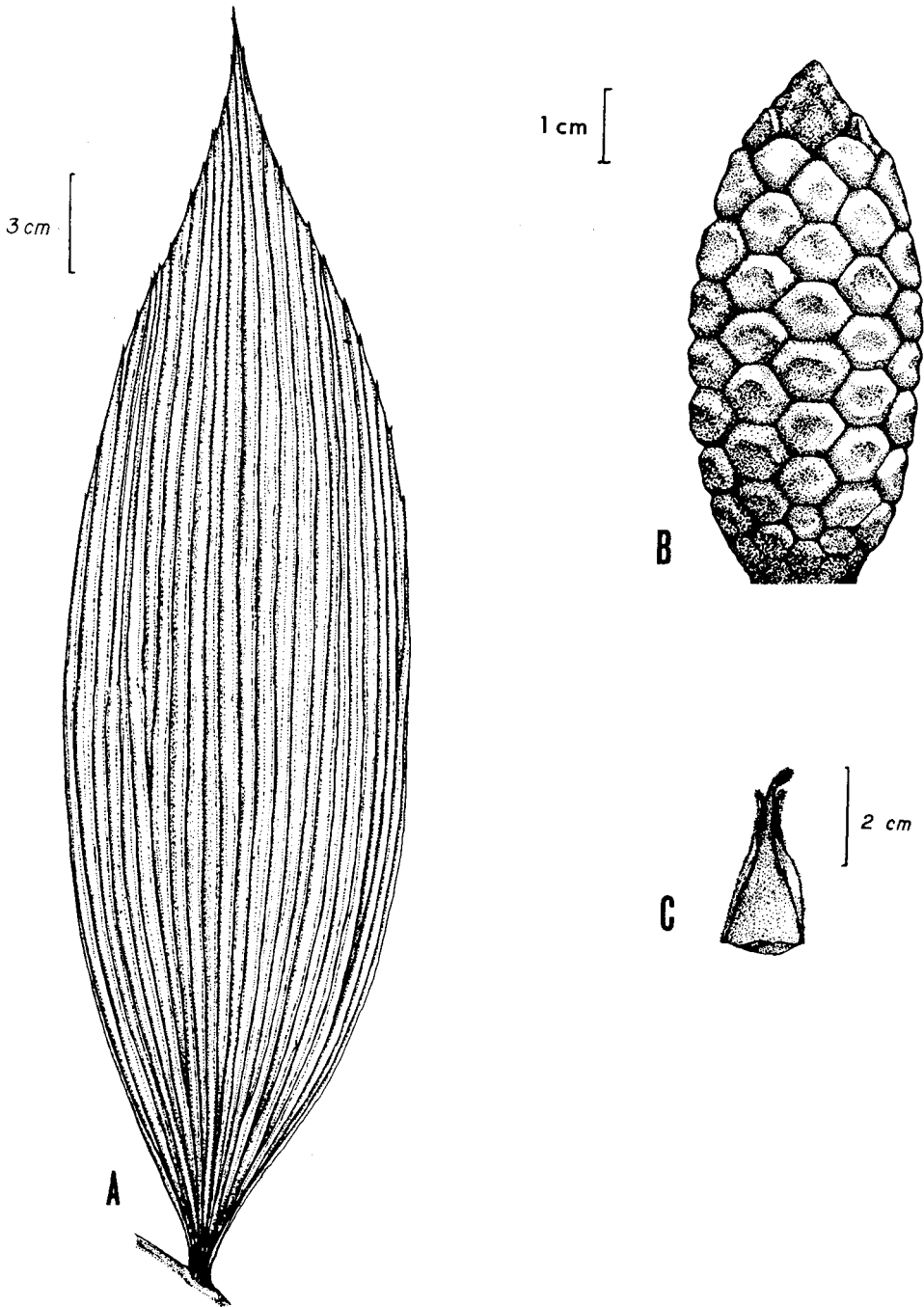


FIG. 5. *Zamia neurophyllidia* (Correa et al. 3078). A. Median leaflet. B. Ovulate strobilus. C. Cataphyll.

m long and 15 cm diam. *Leaves* 3–10, 1–3 m long; petiole inermis, 0.3–1 m long; rachis inermis, with 20–50 pairs of leaflets. *Leaflets* gray-green, oblanceolate, suffalcate basally, acute apically, margins entire, the median ones 30–50 cm long, 2–4 cm wide. *Polleniferous strobili* cream to tan, cylindrical, 25–50 cm long, 2–4 cm diam. *Ovulate strobili* yellow-green to tan, cylindrical to ovoid-cylindrical, 25–50 cm long, 8–12 cm diam. Seeds yellow, sarcotesta becoming mucilaginous, 1.5–2.5 cm long, 1–1.5 diam. ($2n=16$.)

Zamia pseudoparasitica is the only truly epiphytic cycad and is not found as a terrestrially growing plant. It hangs from branches by the tap and lateral roots and generally is found from 7 to 20 meters above the ground on large trunks and in lower crotches of large canopy trees. The portion of these trunks with plants of *Z. pseudoparasitica* are generally devoid of other epiphytes such as bromeliads, orchids, ericads, etc. The stem of *Z. pseudoparasitica* grows upwards but as the plant becomes larger and heavier it becomes pendulous and the stem develops a pronounced U-shape. As with most cycads, coralloid roots are produced but unlike other cycads the coralloid roots occur in dense hemispherical clusters that attain diameters of 5–10 cm. The leaves, strobili and seeds are among the largest in the genus. The seeds are unique in *Zamia* because of their distinct yellow sarcotesta. This unique sarcotesta is thick and becomes mucilaginous upon ripening and produces a distinctive sour odor. Neither plants or seedlings have been found growing on the forest floor under trees with ovulate plants even though old ungerminated seeds have been found. Thus, it appears as if *Z. pseudoparasitica* is dispersed by animals, most likely frugivorous bats.

Zamia pseudoparasitica, endemic to Panama, occurs from 50 to 1000 m in trees on steep slopes in rainforest. It appears to be limited to primary forest, perhaps because it cannot become established in secondary forest.

Representative specimens examined: PANAMA. *Bocas del Toro*: *H. & A. Churchill* 6270 (MO); *Stevenson et al.* 1149 (FTG, K, MO, NY, PMA, U). *Cocle*:

Croat 44601 (MO); *D'Arcy* 11361 (MO); *Folsom* 2388, 7103 (both MO); *Hammel* 4136 (MO); *Knapp* 3778 (MO); *Maas* 2735 (MO, U); *Norstog s.n.* (FTG). *Colon*: *Holdridge* 6255, 6257 (PMA). *Veraguas*: *Dressler* 4848 (MO, PMA), 5199 (MO, PMA, US); *S. Kiem & K. Norstog s.n.* (FTG); *Watson* 650 (FTG).

11. *ZAMIA SKINNERI* Warszewicz ex A. Dietrich (Fig. 1G)

Zamia skinneri Warszewicz ex A. Dietrich, *Allg. Gartenzeit.* 19: 145–146. 1851. *cum icone*. *Aulacophyllum skinneri* (Warszewicz ex A. Dietrich) Regel, *Gartenflora* 25: 143. 1876. LECTOTYPE: *Icone* in *Allg. Gartenzeit.* 19: 1851.

Stem arborescent, to 2.5 m tall. *Leaves* 3–6, 1–2 m long; petiole 0.5–1 m long, sparsely to densely prickled; rachis with 6–10 pairs of leaflets, occasionally with a few prickles in the lower third. *Leaflets* elliptic, grooved between the veins on the adaxial surface, cuneate basally, acuminate apically, margins serrate in upper third, the median ones 30–50 cm long, 12–15 cm wide. *Polleniferous strobili* cream to tan, cylindrical to elongate-cylindrical, 8–12 cm long, 1–2 cm diam. *Ovulate strobili* brown, short pedunculate, cylindrical to ovoid-cylindrical, 20–40 (50) cm long, 8–12 cm diam. Seeds red, ovoid, 1.5–2.5 cm diam. ($2n=18$.)

Zamia skinneri is the largest Central American *Zamia* and is unmistakable with its massive trunk, leaves, and strobili. This species would appear to be part of a complex composed of *Z. dressler* and *Z. neurophyllidia* in Panama, *Z. amplifolia* Masters and *Z. roezlii* Linden in the Choco of Colombia and adjacent Ecuador, and *Z. wallisii* in Northern Antioquia, Colombia. This grouping is based upon the common occurrence of the plicate appearance of the leaflets of these species. This character, simultaneous rather than sequential leaf production, prompted Regel (1876) to erect the segregate genus *Aulacophyllum*. However, no other synapomorphies have been found to support *Aulacophyllum* as a genus (Sabato, 1990). Moreover, the distinction between simultaneous and sequential leaf production in *Zamia* seems problematic at best.

Zamia skinneri occurs in primary rainforest from Nicaragua to central Atlantic Panama at elevations from 50 to 750 m.

Representative specimens examined: PANAMA. **Bocas del Toro:** Dressler 4800 (MO, PMA, US); Hart 179 (US). **Cocle:** Valdespino et al. 1316 (PMA, NY). **Veraguas:** Croat 27409 (MO); S. Kiem & K. Norstog s.n. (FTG); Maas & Dressler 1650 (MO, U); von Wedel 1007 (MO).

Problematic Species of *Zamia* in Panama

There is one specimen of a partial leaf of *Z. roezlii* at K that was supposedly collected near Chagres, Panama by Warszewicz. This specimen has no year or collection number and is the only known collection from Panama. Warszewicz was known to have travelled and collected in Central America and Colombia in the mid-1840s. His collection and description provided the basis for the publication of *Z. skinneri*. However, *Z. roezlii* is known only from southern coastal Colombia and contiguous Ecuador. I have concluded that it probably does not occur in Panama and that Warszewicz's collections became confused as to locality. *Zamia roezlii* is similar to *Z. skinneri* but has narrower (2–5 cm) subfalcate, oblanceolate leaflets with acute tips and an entire margin as opposed to the elliptic, wider (12–15 cm) leaflets with acuminate tips and margins serrate in the upper third.

At the time that Dietrich (1851) described *Z. skinneri* from Warszewicz's notes and sketches, he also described *Z. lindleyi* Warszewicz ex A. Dietrich from the same source. As noted by Stevenson and Sabato (1986), none of the specimens have survived so *Z. lindleyi* was typified by the accompanying illustration. This was necessary because there are no collections of *Zamia* that match this illustration. As described and illustrated, *Z. lindleyi* resembles most closely *Z. chigua* but differs in having only one-third to one-half as many leaflets, which are neither imbricate nor subfalcate. In other respects, *Z. lindleyi* resembles *Z. roezlii* but lacks the characteristic grooves on the adaxial leaflet surface of the latter. Thus, *Z. lindleyi* must remain a *species dubium*.

Finally, it should be noted that *Z. pseudomonticola* L. D. Gomez may occur in extreme western Panama. This species is known only from western Costa Rica near

the border with Panama. It superficially resembles *Z. acuminata* from which it differs in having a short (to 70 cm) trunk, petioles without prickles, and broader (4–7 cm wide) but similar shaped leaflets.

Phytogeography and Species Relationships

Sabato (1990) provided a brief review of the distribution of *Zamia* in the West Indies and South America but omitted Central America because of the then lack of knowledge of the genus and its distribution in Panama. The present study with its delimitation of the species and their distribution patterns in Central and South America makes possible some testable hypotheses on the phytogeography of *Zamia* in this region and species relationships for the taxa included in this treatment.

The present treatment recognizes eleven species of *Zamia* in Panama. Of these eleven species, five are endemic to Panama, three extend into Costa Rica and Nicaragua to the north, and the other three are found to the south in northern to central Colombia.

CENTRAL AMERICAN SPECIES

The Central American elements, *Z. acuminata*, *Z. fairchildiana*, and *Z. skinneri*, reach the southern limits of their distribution in central Panama. In fact, *Z. fairchildiana* occurs only in the area of southern Costa Rica to central Panama. None of the three Central American elements has obvious counterparts north of the Rio San Juan in Nicaragua. *Zamia acuminata* and *Z. fairchildiana* appear to form an unresolved clade, based upon leaflet and reproductive morphology, with *Z. pseudomonticola*, a restricted endemic of southern Costa Rica, and this clade has no obvious counterparts south of central Panama. Current data indicate that this is an isolated group within the genus. *Zamia skinneri*, on the other hand, does have counterparts in South America. In terms of growth form, and leaf and reproductive morphology, *Z. skinneri* is most closely related to the Panama endemic *Z. neurophyllidia* as discussed below. These two species could be a Central Amer-

ican clade with southern limits in central Panama or part of a South American clade of *Zamia* that reaches its northern limit in Central America. The latter seems to be the case when one considers *Z. amplifolia* and *Z. roezlii* both from the Pacific slopes of the central Choco of Colombia to contiguous Ecuador. These two species share derived features of strobilus, leaf, leaflet and trunk morphology with *Z. skinneri*. I propose that these four species form a clade in *Zamia*. If so, then the distribution of the clade is disjunct with two members centered in southern Colombia and two members in eastern Panama. I interpret the Panamanian taxa as representing a northern limit for a South American clade that had past continuity in distribution with only the northern and southern limits of the former range surviving at present. In other words, extinction has occurred in the central part of a formerly wide range.

SOUTH AMERICAN SPECIES

Another three species, *Z. chigua*, *Z. manicata*, and *Z. obliqua*, are taxa that reach their northern limits in Panama. *Z. chigua* occurs disjunctly in eastern Panama on the western side of the Cordillera de Talamanca, and again in the central Choco of Colombia on the Pacific slopes of the Andes. This species is more common and has a wider distribution range in the Choco than it does in Panama. It appears that this is a South American species with its northernmost limits being represented by relict populations in eastern Panama. I suspect that *Z. chigua* will eventually be found to occur in the Darien of Panama and, thus, exhibit a more continuous distribution.

Zamia manicata is found from northwestern Antioquia, Colombia to central Darien, Panama. This species is apparently endemic to this area and has no obvious near relative in either Colombia or Panama but rather appears related to an undescribed species of *Zamia* from Amazonian Peru (Sabato, 1990). If so then *Z. manicata* is also a member of a South American clade whose northern limit is in Panama.

Zamia obliqua is the third example of a South American *Zamia* that has its north-

ern limit of distribution in Panama. This species is commonly found from southcentral Choco, Colombia to central Darien, Panama with disjunct populations occurring to western Chiriqui in Panama. There is one collection of *Z. obliqua* from central Peru (Sabato, 1990). This represents a disjunct southern limit for the species that may be represented by a single population, as recent attempts to locate this species in Peru have failed.

SPECIES ENDEMIC TO PANAMA

The species of *Zamia* endemic to Panama, *Z. cunaria*, *Z. dressleri*, *Z. ipetiensis*, *Z. neurophyllidia*, and *Z. pseudoparasitica*, represent differing patterns of distribution and relationship from the previous discussion. The most bizarre and enigmatic species of all cycads is *Z. pseudoparasitica*, the only known epiphytic cycad. It is endemic to the eastern Atlantic coastal area of Panama and has no known close relatives. The species is unique not only in its habitat requirements but also in root, leaf, and reproductive morphology (see discussion under the species). These derived attributes, probably the result of the epiphytic nature of the species, make it difficult to ascertain any sister group relationship between *Z. pseudoparasitica* and any other species in the genus. Although dispersal agents, particularly long distance ones, are neither required nor known for neotropical cycads (Stevenson, 1991), *Z. pseudoparasitica* has seeds obviously designed for dispersal and given its habitat requires a dispersal agent. However, such an agent is unknown. While vicariance can be used to explain distribution patterns in neotropical cycads (Stevenson et al., 1986) this is not the case with *Z. pseudoparasitica*, which leaves open to conjecture any ancestral relationship based upon morphology given the number of autapomorphies in this species. The most plausible relationship would appear to be with *Z. fairchildiana* based upon leaflet anatomy and distribution.

Zamia neurophyllidia is almost certainly a sister species to *Z. skinneri* based upon morphology and distribution. *Zamia neurophyllidia* occupies a specialized lowland

wet habitat within a restricted portion of the southern part of the distribution of *Z. skinneri*. Thus, *Z. neurophyllidia* is here interpreted as a local endemic derived from habitat specialization within the more general habitat of its sister species.

General leaflet morphology would lead one to conclude that *Z. dressleri* is also related to *Z. skinneri*. However, strobilus morphology and growth habit are so different in *Z. dressleri* as compared to *Z. skinneri* that it is more tenable to consider *Z. wallisii* from northern Colombia as the sister species to *Z. dressleri*. *Zamia dressleri* only differs from *Z. wallisii* in that the former has distinctive adaxially grooved petiolules whereas the latter has sessile leaves. I would suggest that these two species are local relicts of a more widely distributed ancestral species similar to *Z. dressleri*. It is interesting to note that these two species occupy that portion of the range where *Z. skinneri* and its relatives, also with adaxially grooved leaflets, are presumed to have disappeared as discussed above.

The other two species endemic to Panama, *Z. cunaria* and *Z. ipetiensis*, are obvious sister species that are found in two different, physically separated mountain ranges and most likely developed from a common ancestral species by vicariance. Morphologically, these two species appear to be most similar to *Z. muricata* Willd. which is found in Venezuela north of the Rio Orinoco and contiguous Colombia. The nearest relative to *Z. muricata* is *Z. lecointei* Ducke which is found in the Rio Negro watershed of Venezuela and Colombia. I would also include *Z. ulei* Dammer which is western Amazonian in this group. These five species appear to form a South American group within *Zamia* and southern Panama represents its northern limit.

In conclusion, Panama is unique in the neotropics with respect to the cycad genus *Zamia* because it is the northern limit of South American species and/or sister taxa of those species, it is the southern limit of more widespread Central American species of *Zamia*, and it is an area of localized endemic species. In terms of area, Panama has the greatest morphological diversity as well

as the greatest number of species of *Zamia* in the neotropics. Most species of *Zamia* in Central and South America are local endemics. Given the age of *Zamia* in the neotropics dating at least to the Paleocene (Sabato, 1990), this narrow endemic pattern of species of *Zamia* fits well with the concept of neotropical refugia (Prance, 1982). This is supported by the distribution of these species (see maps in Sabato, 1990) where each refugium west of coastal South America has its own endemic species of *Zamia* and in general these species are limited in distribution to these refugia.

Acknowledgments

I am indeed grateful to those whose help and discussions made this work possible. I thank Robert Dressler for sharing his many years of fieldwork and his unpublished manuscript on the cycads of Panama and for his critical review of the present work. This work simply would not have been possible without his magnanimous cooperation. I am indeed indebted to my colleagues at the University of Panama, Mireya Correa and Alberto Taylor, for the use of herbarium and laboratory facilities and useful discussions. Ivan Valdespino, Edgardo Valdespino, Heraclio Herrera, and Greg de Nevers were extremely helpful in the fieldwork. I thank Maria Lucia Kawasaki for help with Latin, Knut Norstog who instigated this research on my part, Lisa Campbell for editorial expertise, and James Eckenwalder and Thomas Zanoni for constructive reviews.

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