The Zamiaceae in Panama with comments on phyto geography and species relationships

DENNIS W.M. STEVENSON

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 Zamiass in Panama are presented. Four of these are new species: Z. cusaria, Z. dressleri, Z. ipetens, and Z. neprophyllida. Floristically, Zamiass is represented in Panama by three elements: three Central American species, Z. acuminata, Z. faurzellidiana, 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. cusaria, Z. dressleri, Z. ipetens, Z. neprophyllida, and Z. pseudoparasitica. These distributions are interpreted by a consideration of sister group relationships based upon derived morphological character states.

Key words: Panama, Zamiaceae, Zamiass.

As currently circumscribed (Stevenson, 1990, 1992) the Zamiaceae comprise eight genera. Five of these are endemic to the neotropics with only seven, Zamiass, occurring in Panama. In the Flora of Panama, Woodson (1943) considered Zamiass to be monotypic in Panama, but with reservation. Woodson was cognizant of the numerous species of Zamiass 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 Zamiass species occurring in Panama (D’Arcy, 1987) but this could not be completed until further study as reported here.

Recent collections of Zamiass in Central America and the typification of valid names in Zamiass (Stevenson & Sahain, 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 Some of the work presented here is based on an unpublished manuscript by Robert Dressler which he generously gave to me some years ago. The morphological diversity of Zamiass 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 See- mann) to species with subterranean (hypogeous), tuberous stems (Z. acuminata Ger- sted ex Dyer). Those species with subterranean stems produce 1–3 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 13 leaves. No cycad has a truly woody stem and branching is basically dichoto- mous 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 un- derground stems that are described as hypogeous or subterranean (Stevenson, 1991). All cycads are considered to be pachycar-
lous (Stevenson, 1990) because of the usu-
ally scanty nature of the secondary xylem
comparable to the well developed parenchym-
atous 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. chi-
gua. Zamia acuminata often has diminu-
tive 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. neuro-
phyllidia D. Stevenson, and Z. skinneri
Warzea, ex A. Dietrich) have distinctive leaf-
lets that are deeply grooved axially be-
 tween the veins so as to appear plicate. In
general Zamia leaflets are sessile on the ra-
chis but one Panamanian species, Z. manic-
cata Linden ex Regel, has distinct petio-
lules. 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 petiole (Stevenson, 1990).
Reproductive morphology, on the other
hand, is more constant, but here too the
variability is greater than for other neo-
tropical areas with strobili varying in color
from light yellow to deep red-brown. Three
species of Zamia found in Panama, Z. ca-
naria Dressler & D. Stevenson, Z. itepetnis
D. Stevenson, and Z. obliqua, have very
distinctive microsporophylls in that micro-
sporangia are found on both the abaxial and
axial surfaces (Fig. 1) in contrast to all
other cycads which have microsporangia
only on the abaxial surface. The yellow seeds
of the endemic Z. pseudoparapistaca are
unique in the genus.
Because the cycads are strictly dioecious
and reproductive structures are infrequently
encountered in the field, herbarium, or cul-
tivation, the emphasis in the following key
to species is on vegetative characters. Cer-
tainly, to use yellow seeds as the only key
character for Z. pseudoparapistaca would
not be useful for a microsporangiate plant. In
addition, the vegetative characters in Pan-
amanian Zamia are so distinct, as outlined
above, that their use in this case is war-
ranted.
As in previous works on cycads (e.g., Ste-
venson et al., 1986), specific localities of the
species of Zamia are not given in this paper
because of their endangered status and com-
mercial value which could lead to their eradica-
tion either intentionally or uninten-
tionally 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 par-
ticularly susceptible to over-exploitation.
All lectotypes and neotypes given in the pre-
vious work are from Stevenson and Sa-
bato (1986). Chromosome numbers are from
the works of Norstog (1980, 1981) and Mo-
reti (1990). Information on individual spe-
cies 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
4. Leaves 1–3, stems subterranean. Z. dressleri
5. Leaflets small, less than 20 cm long and 10
   cm wide . Z. neurophyllidia
6. Leaflets smooth and not appearing plicate
7. Leaflets with distinct petiole and gland-
like collar at the base of the blade. Z. manicata
8. Leaflets sessile and without a gland-like
   collar
5. Leaflets entire
6. Leaves grey-green; petioles without
   prickles; plants epiphytic Z. pseudoparapistaca
7. Leaves green to dark green; petioles
   with prickles; plants terrestrial
8. Leaves inemicate, 30–80 pairs, papyr
   yaceous; petioles with many
   stout prickles . Z. chigua
9. Leaves separate, 6–15 pairs, sub-
   coriaceous; petioles with a few
   diminutive prickles . Z. acuminata
10. Leaves hard at least in upper ter-
    ritories
11. Leaves (35–)many, plants arborescent
12. Leaves obovate-elliptic. Z. oblongue
13. Leaves oblong . Z. floridana
14. Leaves usually solitary (3), stem
   subterranean
15. Leaves obtuse to oblongo-
   lanceolate, strongly toothed in up-
per third; ovulare strobili 30- 
30 cm long. ... Z. cuniamata
10. Leptilis elliptic lanci, minutely 
when ovulare strobili to 10 cm long... Z. wentworthii

1. ZAMIA ACUMINATA Oersted ex Dyer (Fig. 1D) Zamia acuminate Oersted ex Dyer in Hemsl, Biol. cent. am., Bot. 3 (16): 194, 1884. Type: NICA-
RAGUA, "ad Dv. S. Juan," Oersted s.n. (holotype: C). Stem subterrestrial, subglobulous to cylin-
drical, to 5 cm diam. Leaves 1-3, to 1 m long; petiole to 60 cm, densely prickled; ra-
chas with 6-15 pairs of leaflets, some prick-
les in lower third. Leptilis elliptic lanci-
core, subcircular, cuneate basally, very 
long acuminate apically, margins entire, 
the larger median ones 20-30 cm long, 1-3 cm wide. Pollenferous strobili cream to tan, cy-
lindrical, 5-8 cm long, 1-1.5 cm diam. Ovu-
late strobili cylindrical to ovoid, cream to 
tan, 10-20 cm long, 5-8 cm diam. Seeds 
avoid, red. (2n=24).
There have been horticultural reports of 
plants of Z. acuminata having trunks one 
meter in height. This appears to be a con-
dition of pot grown plants in which it is not 
possible for stem and root contraction to 
pull the shoot underground. This is sup-
ported by field observations by myself and 
others where all plants of this species have 
subterranean stems. The very distinct 
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 spe-
cies is restricted to elevations between 400-
1200 m. 
Representative specimens examined: PANAMA, Chiriqui: Balboa 16682 (MO), Dressler 5322 (MO, PMA, 
U), Stevenson & Valderrama 3347 (V, FGT), K. MO, 
NY, PMA, US, Vergez: R. Norstog et al. s.n. (FGT).

2. ZAMIA CHIGUA Seemann (Fig. 1F) Zamia chigua Seemann, Bot. Voy. 6: 291. 
Alopecushops variegati Regel, Gartenflora 25: 141-
143: 1874. Type: COLOMBIA, Wallis 76 (holotype: LEF).
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 younger plants) pairs of imbricate leaflets, 
densely prickled in lower half. Leptilis long 
lancolate and subfalcate, chartaceous to 
membranous, margins entire, the larger me-
dian ones 10-30 cm long, 1-1.5 cm wide. 
Pollenferous strobili cream to light yellow, 
cylindrical, 20-30 cm long, 2-3 cm diam. 
Ovulare strobili tan to brown, narrow 
ovid to cylindrical, 20-30 cm long, 8-12 
 diam. Seeds ovoid, red. (2n=16.)
Zamia chigua is the most-fem-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 particular-
ly in large plants.
In the past there has been some confusion 
concerning the identity of Z. chigua (Nor-
stog, 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 Columbia. The common name 
"chigua" is apparently applied to several 
species of Zamia. As a result of this con-
fusion, 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. chig-
ua 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 distinct in the Choc-
co of Colombia. In Colombia, Z. chigua is 
found in lowland and forest areas whereas 
known localities from Panama are from 600 to 1200 
m. This species is probably present on the 
slopes of Cerro Pire and the western slopes of 
Cordillera de Jurado in Darien, Panama 
but has yet to be collected there.
Representative specimens examined: PANAMA, 
Chiriqui: E. Antonio 5553 (MO), Cote & Griswold 
59774 (MO), Dressler 5420 (MO), Saenger et al. 4106 
(MO), Seibert et al. 1148, 1151, 1152 (all FGT, 
K, MO, NY, PMA, U).
3. Zamia cusaria Dressler & D. Stevenson, sp. nov. (Fig. 2)


Culetex subterranea; folia plurumque solitaria, paucifoliata, erecta; foliola mediana oblonga vel oblanceolata, acuminata, serrate; microsporophyllia microsporangis adaxialis et abaxialis provin; strobili fertini visacei vel ferrugine; semina rosea.

Stem subterranean, subglobose, to 10 cm diam. Cataphyll 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, sparingly 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, cylin-drical to ovoid-cylindrical, 4-6 cm long, 1-1.5 cm diam.; peduncle 2-4 cm long. Microsporophyll with sterile tip composed of six steeply inclined facets surrounding a centrally depressed terminal facet, sporan-
gla present on both the adaxial and abaxial surfaces of the fertile region. *Ovulate strobili* wine-red to dark 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. iepetensis* 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 strobili as "obset e sana."

Representative specimens examined: PANAMA. Cuna Yala (Comarca de San Blas): D’Arcy 9477 (MO). Dresler 4737 (US), de Nevers 4132, 4244, 4322, 4560, 4600, 4917 (sM, MO, PMA); F. Star 154 (PMA), 144 (MO, 165 (PMA).

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

**TYPE:** PANAMA. Colon: 7 Jan 1989, D. Stevenson & J. Valdezposo 1145 (Holotype: NY); (Isotypes: FTG, MO, NY, PMA, U).

*Zamia drexleri* affinis, sed foliis sessilibus differt.

Stem subterranean, 3.5–5 cm diam. *Cataphylls* ovate, 1–2 cm long, 2.5–3 cm wide. Leaves usually solitary (2–3), 0.5–1.5 m long; petiole 0.3–1 m long but sparsely to densely pricked; 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 the upper third, the larger median ones 30–50 cm long, 12–15 cm wide. *Ovuliferous strobi* cream to tan, cylindrical to elongate-cylindrical, 5–8 cm long, 1–2 cm diam. *Ovulate strobili* wine-red to dark brown, short pedunculate, ovoid-cylindrical, 10–15 cm long, 3.4 cm diam. Seeds red, ovoid, 1.5 cm diam.

This species is named in honor of Robert Drexler 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. wallissii* 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. wallissii* 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. dressleri*. The pollen strobili of *Z. wallissii* 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. wallissii* are unknown.

Representative specimens examined: PANAMA. Colon: J. Cowell 165 (MO); R. Drexler 5153 (MO, PMA); S. Klem & N. Norstog s.n. (FTG). Cuna Yala (Comarca de San Blas): B. Herrera 204 (PMA); G. de Nevers 4711, 4786, 5034 (MO, PMA).

5. *Zamia faichildiana* L. D. Gomez (Fig. 1B)


Stem arborescent, 0.5–1 m tall, 5.6–5 cm diam. Leaves 3–10, 0.7–2.5 (2.5) m long; petiole densely pricked, 0.3–0.5 (0.8) m long; rachis with prickles in lower third, 10–30 pairs of leaflets. Leaflets oblong, subulate basally, acutely apically, sparsely serrulate apically, the larger median ones 20–40 cm long, 2.4–4 cm wide. Pollen strobili cream to yellow, cylindrical, 10–40 cm long, 2.5–6 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 diam.

*Zamia faichildiana* may be the most common 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 1200 m, but is most common with the largest pop-
Fig. 3. Zamia dressleri (Stevenson & Valdés 1143). A. Habit. B. Median leaflet. C. Ovulate strobilus.

Representative specimens examined: PANAMA-Chiquita: Croot 35048 (MO); E. Leigh s.n. (PMA); Uppiay 5808 (MO). Colon: Correa & Dressler 621; Dodge & Alpin 17100 (MO); Dodge et al. 10933 (J), MICH, MO, NY, P, UC; Dressler 4997 (MO, MA). Cuna Yela (Comarca de San Blas): de Nevers 1066, 4897, 4994, 5497 (MO, PAMA); Stevenson et al. 1155 (PTG, k, NY, PMA, U). Panama: Baptol 16153 (MO), Berg & Dressler 2722 (MO); Dressler 4644 (F, MO, PMA, US); Folsom 4652 (MO); Moris 1655 (MO); Moris & Gallucci 1782 (MO); de Nevers 4943 (MO, PMA), Stevenson et al. 1146 (FTG, K, MO, NY, PMA, US). Systema 2958 (MO); R. & A. Tryon 5470 (MO); G. Wilder s.n. (MO).

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

ta, paucifoliolata; foliola mediana oblonga, acuminata, acuminata serrulata; microporophylla microporophylla adaxialibus et abaxialibus; strobili feminei fuscifurcigenae; 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; petiole 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-
Zamia mancata Linder ex Regel (Fig. 1E)


Stem subterranean, globose to subcylindrical, 2–3 cm long. Leaves 3–10, 0.5–2 m long, petiole 0.2–1 m long, slightly to dense-
ly prickled; rachis often with prickles in lower third, with 10–30 pairs of leaflets. Leaflets with distinct petiolo and abaxial gland-like
collar at the juncture of the lamina, oblong to long-elliptic, margins serrate in upper third, cuneate basally, acute to acu-
minate apically, the larger median ones 15–35 cm long, 3–7 cm wide. Polleniferous strob-
bi creamy 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 petiolo and gland-like collar (Fig. 4E) occur among cycads only in Z. mancata (Stevenson, 1990). However, they are not present in seedling leaves, only diminutive-
ly 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. mancata with Z. obliqua and placed the former in synonymy with the latter. Schus-
ter’s description is a mixture of the two spe-
cies. However, Braum (1875) described Z. obliqua with sessile elliptic to ovate-elliptic (“obelliptic”) leaflets and trunks to 2.5 m and never mentioned petiololes or gland-like collars because these characters do not occur in Z. obliqua. In fact Schuster’s con-
cept of Z. obliqua was a plant with the trunks and strobili of Z. obliqua and the leaves of Z. mancata. Moreover, he described the pet-
ioles as unarmed when in fact anyone who has collected either of these species can at-
test to the numerous prickles. In contrast, Gomez’s concept of Z. obliqua is in fact that of Z. mancata. Because of the confusion instigated by Schuster (1932), Schultes (1958) redescribed Z. mancata as Z. madu-
da and the description of Z. obliqua by Gomez (1942b) is that of Z. mancata with both Z. mancata and Z. madida listed in synonymy. Besides the presence of petio-
ules and gland-like collars in Z. mancata and their absence in Z. obliqua, salient differ-
ences between these two species are sub-
terranean 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. mancata. In contrast, Z. ob-
liqua 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 microspo-
rangia on both the adaxial and abaxial sur-
faces, and tan to light brown ovulate stro-
bili.

Zamia mancata occurs in rainforest and secondary forest from 100 m to 1000 m in the Darien of Panama and contiguous Col-
ombia.
Zamia nevadillilata D. Stevenson, sp. nov. (Fig. 5)


Zamia skinneri affinis sed truncus 5 (loc. 10) den altu diversa; foliola elliptica, 12-20 cm lata, 5-8 cm longa; stipulae 15-25 cm longa; semina 1 cm unique long.

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; ra- chis 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, acuminated apica- lly, margins serrulate in upper third, the larger median ones 12-20 cm long, 6-10 cm wide. Polleniferous strobili cream to tan, cylin- drical to elongate-cylindrical, 5-8 cm long, 1-2 cm diam. Ovalate 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 nevadillilata appears to be a smaller version 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 diminu- tive size as adult reproductive plants for nearly thirty years. Thus, Z. nevadillilata appears to be a distinct local endemic spe- cies related to Z. skinneri.

Zamia nevadillilata, endemic to Pan- ama, occurs from 100 to 200 m in rainforest that is occasionally flooded.

Representative specimens examined: PANAMA. Bocas del Toro: Dressler & Kennedy (NY); Greeny 2140 (MO, PMA). Han 179 (US). New & Hansen 14079 (MO, H. Smith s.n. (US).

9. ZAMIA OBQUIA A. Braun (Fig. 1C)


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 ob- ovate, obliquely cuneate basally, acuminated apically, margins serrulate in upper third, the median ones 5-10 cm long, 3-6 cm wide. Polleniferous strobili cream to tan, cylin- drical 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. Ovalate 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. (28=18). Z. obquia 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. manicana, Z. obquia has been confused with that species but there is no close re- semblance between them other than the fact that they both belong to the same genus.

Zamia obquia occurs in primary and sec- ondary rainforests from near sea level to 500 m in southern Panama to the southern Choco in Colombia.


10. ZAMIA PSEUDOPARASTICA Yates in See- mann (Fig. 1A)


Plants epiphytic. Stem arborescent, to 1
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, oblongate, subacute basally, acute apically, margins entire, the mesi- dian ones 30–50 cm long, 2–4 cm wide. Polifenérosa strobilus cream to tan, cylin- drical, 25–30 cm long, 2–4 cm diam. Ovalate 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, 1.1–1.5 diam. (D=1.6)

Zamia pseudoparasitica is the only truly epiphytic cycad and is not formed as a ter- restrially 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, epi- cads, 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, coaloid roots are produced but unlike other cycads the coa- loid 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 the plants or seedlings have been found growing on the forest floor under trees with ovulate plants even though old undegraded seeds have been found. Thus, it ap- pears as if *Z. pseudoparasitica* is dispersed by animals, most likely frugivorous bats. *Zamia pseudoparasitica*, endemic to Pan- ama, 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. A. Churchill 6720 (MO); Steven- son et al. 1149 (FTG, K, MO, NY, PMA, U). Cule.
Problematic Species of Zamia in Panama

There is one specimen of a partial leaf of *Z. roezlii* K. at 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 traveled 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) subulate, oblanceolate leaves with acute tips and an entire margin as opposed to the elliptic, wider (12-15 cm) leaves 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. lindeyi* Warszewicz ex A. Dietrich from the same source. As noted by Stevenson and Sabato (1986), none of the specimens have survived so *Z. lindeyi* 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. lindeyi* resembles most closely *Z. chigua* but differs in having only one-third to one-half as many leaves, which are neither imbricate nor subacute. In other respects, *Z. lindeyi* resembles *Z. roezlii* but lacks the characteristic grooves on the adaxial leaflet surface of the latter. Thus, *Z. lindeyi* must remain a species dubium.

Finally, it should be noted that *Z. pseudomonocotila* 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 leaves.

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 delineation of the species and their distribution patterns in Central and South America makes possible some tentative 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. farichildiana*, and *Z. skinneri*, reach the southern limits of their distribution in central Panama. In fact, *Z. farichildiana* 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. farichildiana* appear to form an unresolved clade, based upon leaflet and reproductive morphology, with *Z. pseudomonocotila*, a relict 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, leaf and reproductive morphology, *Z. skinneri* is most closely related to the Panama endemic *Z. neurophyllidio* 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 strobilius, 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 disjoint 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 northern limit of distribution in Panama. This species is commonly found from southern Central 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. cunara*, *Z. dresleri*, *Z. iptenon*, *Z. neurophyllidii*, and *Z. pseudoparaphysa* represent differing patterns of distribution and relationship from the previous discussion. The most bizarre and enigmatic species of all cycads is *Z. pseudoparaphysa*, 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. pseudoparaphysa* 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. pseudoparaphysa* 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. pseudoparaphysa*, which leaves open to conjecture any ancestral relationship based upon morphlogy given the number of autapomorphies in this species. The most plausible relationship would appear to be with *Z. farchnoides* based upon leaflet anatomy and distribution.

*Zamia neurophyllidii* is almost certainly a sister species to *Z. skinneri* based upon morphology and distribution. *Zamia neurophyllidii* occupies a specialized lowland
wet habitat within a restricted portion of the southern part of the distribution of Z. skinneri. However, this morphological pattern was interpeted as a local endemic derived from habitat specialization within the more general habitats of its sister species.

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

The other two species endemic to Panama, Z. cuenana and Z. petipotensis, 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. leocinctorium Deutz which is found in the Rio Negro water-shed of Venezuela and Colombia. I would also include Z. ular 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 cyclic genus Zamia because it is the northern limit of South American species and/or sister taxa of these species, it is the southern limit of more widespread Central American species of Zamia, and it is an area of localized endemism. 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 (Sa-bato, 1990), this name endemic pattern of species of Zamia fits well with the concept of neotropical refugia (France, 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 Dresler 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, Heralcio Herrera, and Greg de Nevers were extremely helpful in the fieldwork. I thank Maria Lucas Kawasaki for help with Latin, Knut Norstog who instigated this research on my part, Lisa Camp-bell for editorial expertise, and James Eckenwalder and Thomas Zanoni for constructive reviews.

Literature Cited

Mavrova, A. 1990. Karyotypic data on North and Central American Zamia (Cycadaceae) and their
phylogenetic implications. Amer. J. Bot. 77: 1016–
1038.
Nursing, K. 1980. Chromosome numbers in Zami
(Cycadales). Caryologia 33: 419-428.
—. 1981. Karyotypes of Zamiopsis cycad (Cyc-
—. 1986. Zamiopsis cycad, a case of mistaken iden-
Francis, G. 1982. Forest regeneration evidence from woody
versity Press, New York.
Sabin, S. 1990. West Indian and South American
Schultes, R. 1958. Plantae Asotri-Americanae X.
Cycadaeeae. Bot. Mus. Leafl. Harvard Univ. 18:
114-115.
Engler. Das Pflanzenreich IV. 1 (Heft 99).
Stevenson, D. 1988. Subfamily oncorea in the Cyca-
daeae. Pages 205-244. In P. Lewis, S. Tucker &
P. Endress, editors. Aspects of floral development.
—. 1990. Morphology and systematics of the
—. 1991. The Zamiaeeae in the Southeastern
United States. J. Arnold Arbor., Suppl. Series 1:
367-384.
—. 1992. A formal classification of the extant
— & S. Sabin. 1986. Taxonomy and systematics of
Zamiaceae. Pages 1-134. In D. J. P. Quattrocchi &
M. Vazquez Torres. 1986. A new species of American (Zamiaceae) from Ve-
zuela. Mexico with comments on species relation-
ships, habitats, and vegetative morphology in Con-
Woodon, R. 1943. Flora of Panama. Part II. Cyca-

SYSTEMATIC BOTANY MONOGRAPHS
Volume 37. Biogeography and Systematics of Poacea (Leguminosae), Matt Lavin, 87

Terms: Payment in US currency must precede shipment. Not available as exchange.
No discounts allowed on single orders. No refunds. Price is postpaid. Check payable to American Society of Plant Taxonomists and send with order to: Systematic Botany Monographs, University of Michigan Herbarium, North University Building, Ann Arbor, MI 48109-1057 USA.

Standing order customers receive a 10% discount beginning with the current volume and are billed with shipment. Information about previously published volumes and instructions for contributors may be obtained by writing to the editor, Christiane An-
derson, at the above address.