

## TWO NEW SPECIES OF *ZAMIA* (ZAMIACEAE, CYCADALES) FROM SOUTHERN MEXICO<sup>1</sup>

BART SCHUTZMAN,\* ANDREW P. VOVIDES,† AND BIJAN DEHGAN\*

\*Horticultural Systematics Laboratory, Department of Ornamental Horticulture, University of Florida, Gainesville, Florida 32611; and †Instituto Nacional de Investigaciones Sobre Recursos Bióticos, Apartado Postal 63, Xalapa 91000, Veracruz, Mexico

Two new species of the genus *Zamia* (Zamiaceae, Cycadales) from southern Mexico are described. *Zamia soconuscensis*, an arborescent species from the state of Chiapas, seems most closely related to *Z. inermis*. *Zamia cremnophila*, a cliff-dwelling, pendent-leaved species from Tabasco, appears to belong to a species group including *Z. purpurea* and *Z. splendens*. We have endeavored to utilize an Adansonian approach to species delimitation in *Zamia* by employing as many characteristics as possible. Our concept of species is compared to the extremes of fine splitting and extreme lumping of taxa used in the past. Both new species exhibit relatively symmetrical karyotypes with a diploid chromosome number of 16; *Z. cremnophila* has a symmetry index of 1.65, and that of *Z. soconuscensis* is 2.08. The species of *Zamia* thus far studied appear to support the hypothesis that asymmetrical, high-numbered karyotypes, concomitant with reduced vegetative and reproductive structures, are common in inhospitable environments, but discrepancies exist.

### Introduction

*Zamia* is a wide-ranging Neotropical cycad genus of ca. 40 species distributed from southern coastal Georgia in the United States to Peru, Brazil, and Bolivia in South America. It is a highly complex taxon that exhibits many ecological adaptations, including epiphytic, subterranean-stemmed, and large arborescent life forms. Some species form natural hybrid populations, such as the *Z. furfuracea* L.f./*Z. loddigesii* Miq. complex (SCHUTZMAN 1982, 1987; SCHUTZMAN and VOVIDES 1985; NORSTOG 1987). Hybridization in cycads was mentioned by CHAMBERLAIN (1926a), who performed viable artificial crosses in *Zamia*. JOHNSON (1963) identified hybrid swarms in the Australian cycad *Macrozamia communis* Johnson. The processes of ecological adaptation and hybridization in this archaic plant group through relatively recent geological time make the genus *Zamia* one of the most complex of the living cycads. These facts, in concert with confused taxonomy and nomenclature of the last century, urgently call for a modern biosystematic revision of the group. CHAMBERLAIN (1926b) was aware of these problems; he noted that species descriptions could degenerate into a description of individuals and that caution should therefore be exercised. He qualified his comments, stating that there were "doubtless many new species of this family waiting to be discovered and described."

With our present-day concern for conservation of this highly endangered and biologically signif-

icant plant group, the necessity to find and document new taxa, as well as promote their conservation, cannot be overstated. Here, we describe two striking species previously unknown. In the absence of a recent biosystematic revision of *Zamia*, a chromosomal study has also been included as a contribution toward our collaborative research for a biosystematic monograph and for the Flora Mesoamerica project of the Missouri Botanical Garden. We present our karyotypic studies of the two species described here and discuss their evolutionary status in the light of previous work by others.

### *Zamia soconuscensis*

When EIZI MATUDA made his comprehensive study of the Soconusco district of Chiapas, Mexico, he discovered but failed to recognize a remarkable *Zamia* as distinct, sympatric with *Ceratozamia matudai* Lundell, named in his honor. The two species were superficially similar enough in vegetative characteristics to cause confusion between sterile specimens from an area of sympatry (MATUDA 2087); the *Zamia* was later relabeled 2087-A. On the second of two expeditions to southern Chiapas, in January 1985, we rediscovered the plant that MATUDA had identified as *Zamia* sp. or *Z. loddigesii*. The collection is distinct from all its Mesoamerican congeners.

### SYSTEMATIC DESCRIPTION

*Zamia soconuscensis* Schutzman, Vovides et Dehgan, sp. nov. (figs. 1-3). *Affinis* *Z. inermis* Vovides, Rees et Vázquez-Torres a qua differt foliis emergentibus albis tomentosis, foliolis plus falcatis et minus coreaceis, petiolis spinosis et parce pubescentibus, caudicibus epigaeis, gracilibus, et decumbentibus, strobilis brunneis, seminibus ovoid-eis, grandibus, subtiliter exaratis, angulatis et ordinate formatis.

Plants dioecious, palmiform, 0.3-0.5 m tall; trunk

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Address for correspondence and reprints: B. SCHUTZMAN, Horticultural Systematics Laboratory, Department of Ornamental Horticulture, 2522 W. M. Fifiel Hall, University of Florida, Gainesville, Florida 32611.

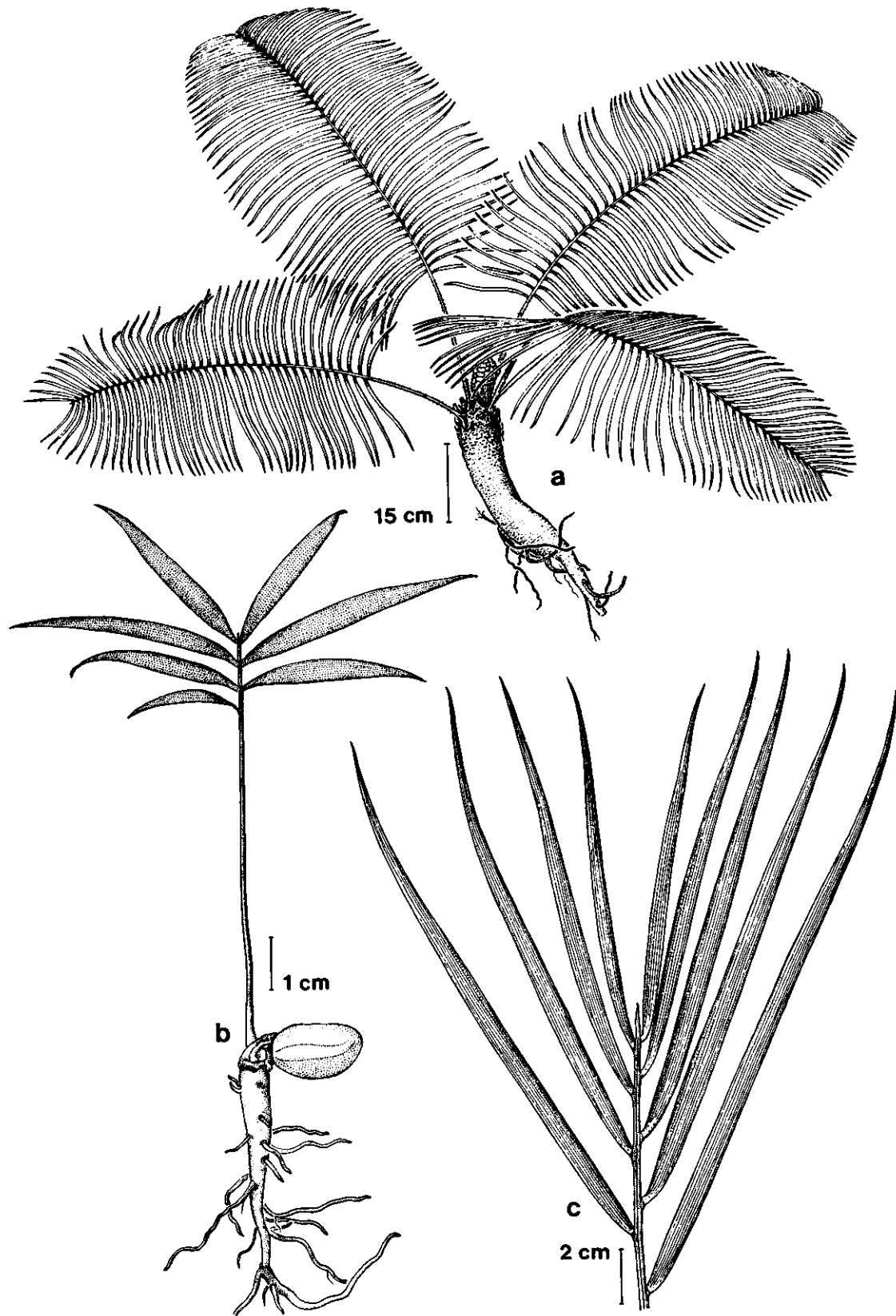


FIG. 1.—*Zamia soconuscensis*. a, Habit of plant. b, Seedling. c, Detail of leaf apex. Drawn by EDMUNDO SAAVEDRA.

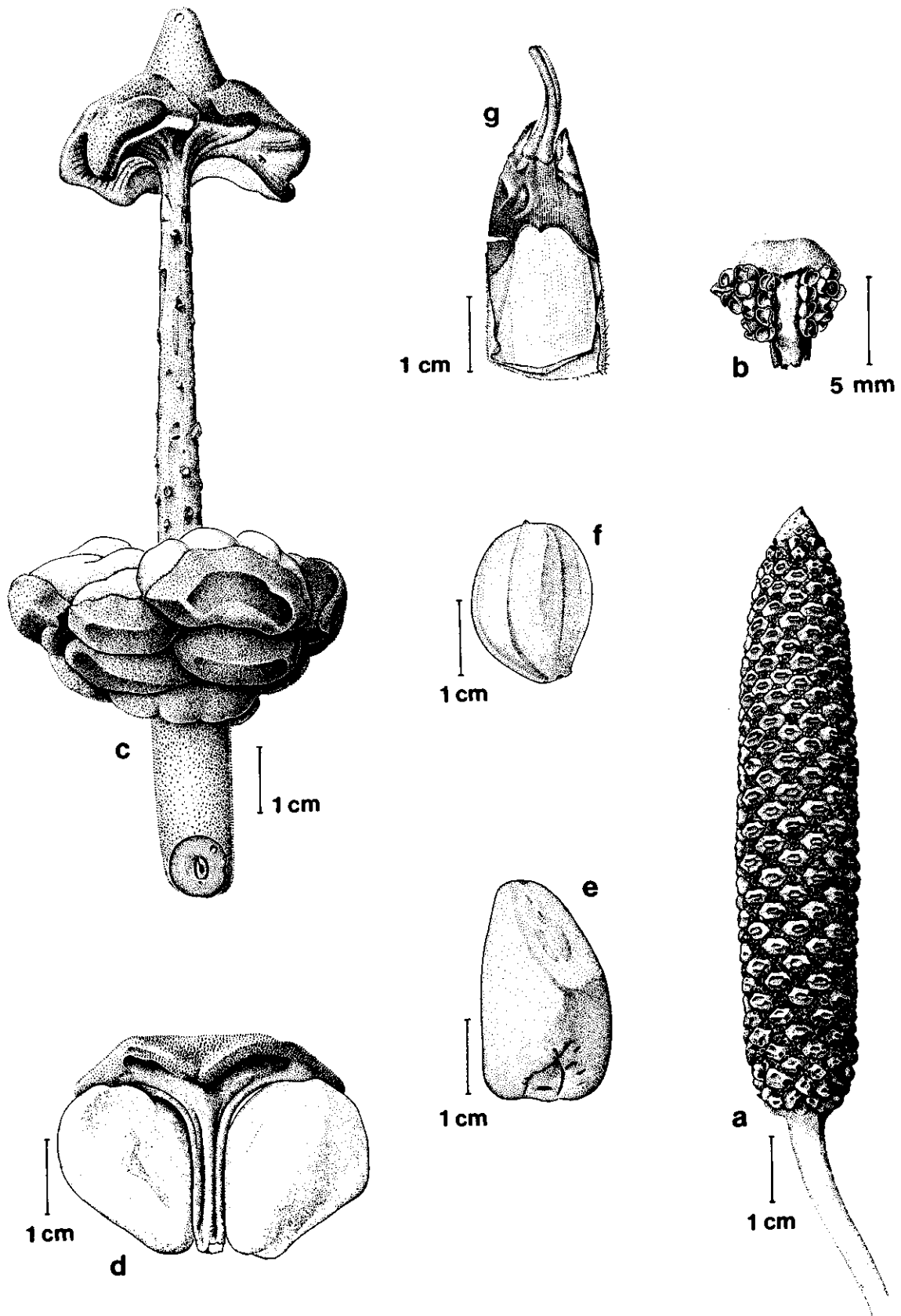


FIG. 2—*Zamia soconuscensis*. *a*, Microsporangiate strobilus. *b*, Microsporophyll showing microsporangia. *c*, Megasporangiate strobilus. *d*, Megasporophyll with two ovules. *e*, Ripe seed with fleshy sarcotesta. *f*, Seed showing details of sclerotesta. *g*, Cataphyll. Drawn by EDMUNDO SAAVEDRA.

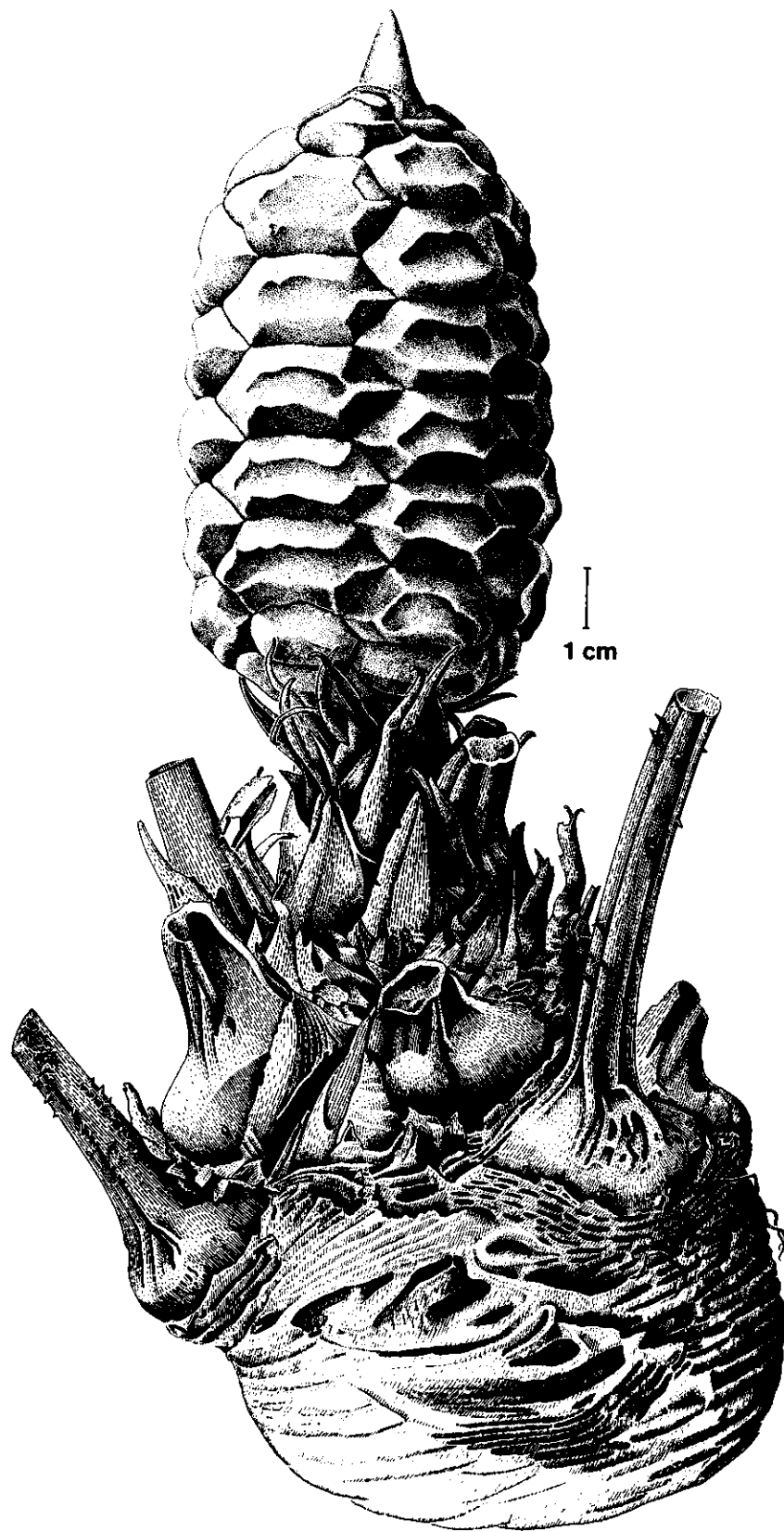


FIG. 3.—*Zamia soconuscensis*. Detail of megasporangiate strobilus, leaf bases and trunk. Drawn by EDMUNDO SAAVEDRA.

pachycaulous, arborescent, erect when small, becoming decumbent, branching infrequently, 5–25 cm diameter. Leaves one to many depending on size and condition of the plant, spreading, 0.4–1.9 m long, 0.25–0.64 m wide; leaflets opposite to subopposite on a single leaf, long-lanceolate, falcate to subfalcate, 14–33 cm long, 0.6–1.4 cm wide; margin entire, subrevolute; apex acute; base attenuate, white tomentulose while emerging, at maturity green, coriaceous, and glabrous; articulation with rachis 2.5–4.3 mm wide; petiole and rachis variably spinose, especially closer to the petiole base, 14–28 cm long, 0.4–1.0-cm diameter; spines terete, 0.5–4.0 mm long; petiole base massive and spineless; cataphylls elongate-triangular, stipulate, tomentose, 4.5 cm long, 1.5 cm wide. Microsporangiate strobilus cylindrical to conic, deep brown, 9.5 cm long, 2.1 cm diameter; microsporophylls cuneiform, distal ends hexagonal-truncate, long axis 0.44–0.5 cm, short axis 0.26–0.39 cm, proximal to distal ends 0.80–0.86 cm, fertile portion occupying  $\frac{1}{2}$ – $\frac{2}{3}$  its length; microsporangia spheroidal, 16–24 per sporophyll, aggregated into sori of two microsporangia each, dehiscing by longitudinal sutures, 1.2–1.6 mm long, 0.9–1.2 mm wide; peduncle puberulent, 5.5 cm long, 0.6-cm diameter. Megasporangiate strobilus cylindrical, barrel-shaped with an acuminate apex, deep brown tomentulose, 12–21 cm long, 7–10-cm diameter; peduncle puberulent, 3.4 cm long, 1.3-cm diameter; megasporophylls cuneiform, the distal ends hexagonal-truncate with a short hexagonal-truncate protuberance, long axis 3.2–4.8 cm, short axis 1.8–2.4 cm, proximal to distal end 3.1 cm; ovules two per megasporophyll. Seeds ovoid, regular to angular; sarcotesta white when immature, becoming salmon-pink when mature; sclerotesta light beige, smooth with 6–8 light furrows running longitudinally and sometimes dichotomizing, 2.2–2.6 cm long, 1.4–1.9 cm diameter.  $2n = 16$ .

TYPE.—Chiapas, February 1939, *Matuda 2659*. Holotype: F; Isotypes: MICH, CR.

OTHER SPECIMENS EXAMINED.—Chiapas, June 1938, *Matuda 2535* (MICH); Chiapas, July 1938; *Matuda 2590* (MICH); Chiapas, December 1937, *Matuda 2087* (MEXU); Chiapas, February 2, 1985, *Schutzman 673–694* (XAL, FLAS); Chiapas, February 5, 1986, *Vovides 1062* (XAL).

ETYMOLOGY.—The species is named after the Sierra del Soconusco, also called Sierra Madre de Chiapas, where it is native.

DISTRIBUTION AND ECOLOGY.—*Zamia soconuscensis* occupies an understory niche in the transition zone between “selva alta perennifolia” and “bosque mesófilo de montaña” of RZEDOWSKI (1978) and grows in an organic clay soil. Precise locality information is withheld because of the taxon’s endangered status and because subsequent collecting by commercial interests would lead to its eventual

extinction in the wild. It is probably narrowly endemic, known only from small, localized areas in the Soconusco mountain range. Further fieldwork may substantiate undocumented reports of additional localities in this mountain range. TOLEDO (1982) postulated that the Soconusco range is one of five primary Mexican refugia. Habitat study there has been cut short because of recent conversion of the land for coffee and maize cultivation, and rescue attempts have been under way for some time to obtain representative living samples for cultivation in the botanical gardens and biological station at INIREB and elsewhere. We hope that discovery of additional localities can proceed before they suffer a fate similar to other floristically unique areas in Mexico such as the Lacandon and Uxpanapa rain forests, where other rare and endangered cycads are found.

*Zamia soconuscensis* has affinities with *Z. inermis*, found several hundred kilometers to the northwest in the state of Veracruz, *Z. tuerckheimii* Donn. Sm. from Guatemala and Honduras, and *Z. monticola* Chamb. Plants labeled *Z. monticola* from Guatemala and Honduras may be included in a broader concept of *Z. tuerckheimii*, the populations of which, when taken together, exhibit a continuum in leaflet morphology (SCHUTZMAN 1982). These species are all arborescent, bear large cones, have falcate or subfalcate leaflets with margins untoothed or sparingly toothed, and  $2n = 16$ . *Zamia soconuscensis* has long, narrow lanceolate, relatively papyraceous leaflets that lack marginal denticulation, whereas those of *Z. tuerckheimii* (sensu lato) have wider elliptic to oblanceolate leaflets that are slightly toothed at their apices; those of *Z. inermis* are linear, untoothed, and coriaceous. Cones of *Z. inermis* are yellowish-brown or beige; those of *Z. soconuscensis* and *Z. tuerckheimii* (sensu lato) are coffee colored to dark brown at maturity.

### *Zamia cremnophila*

In January 1985, we examined an unusual *Zamia* specimen at INIREB in Mérida, Yucatán. After a visit to the locality and subsequent systematic investigation, we determined that this unique plant was indeed distinct and previously undescribed.

#### SYSTEMATIC DESCRIPTION

*Zamia cremnophila* Vovides, Schutzman et Dehgan, sp. nov. (figs. 4, 5). Affinis *Z. splendens* Schutzman a qua differt foliis plantarum maturorum pendentibus et aculeatissimus, foliolis lanceolatis et imbricatis, strobilis erectis.

Plants dioecious, palmiform, 1.2 m; trunk pachycaulous, hypogeous, erect to decumbent, 10–25 cm long or more, 3–9-cm diameter. Leaves one to many depending on size and condition of the plant, pendent, 0.45–2.0 m long, 41–72 cm wide; leaflets up to 15–25 pairs per leaf, opposite to sub-

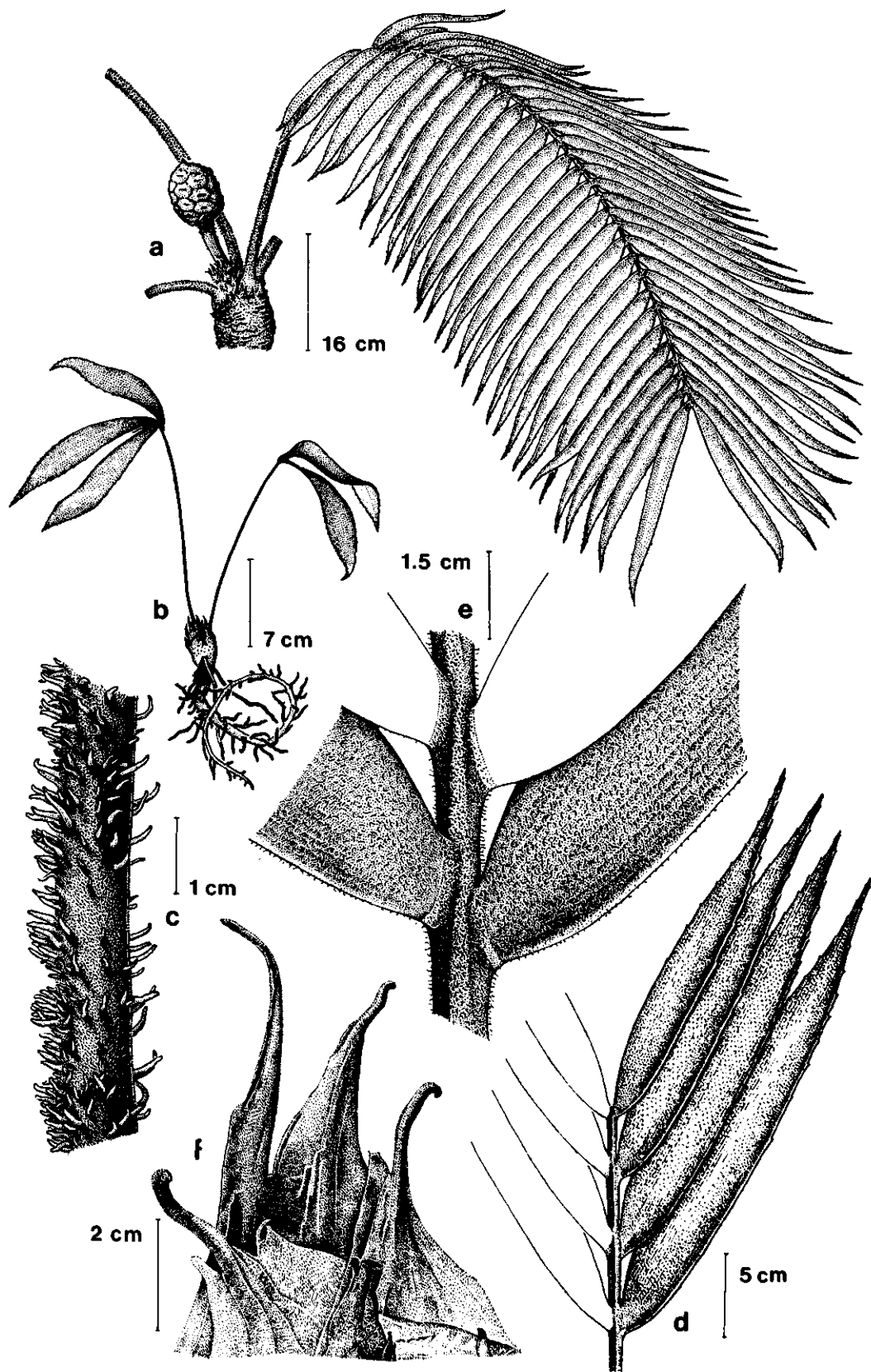


FIG. 4.—*Zamia cremnophila*. *a*, Habit of plant with megasporangiate strobilus. *b*, two-year-old seedling (note leaf with three leaflets, first leaves always with two leaflets). *c*, Detail of petiole. *d*, Detail of leaf apex. *e*, Detail of median leaflets. *f*, Cataphylls. Drawn by EDMUNDO SAAVEDRA.

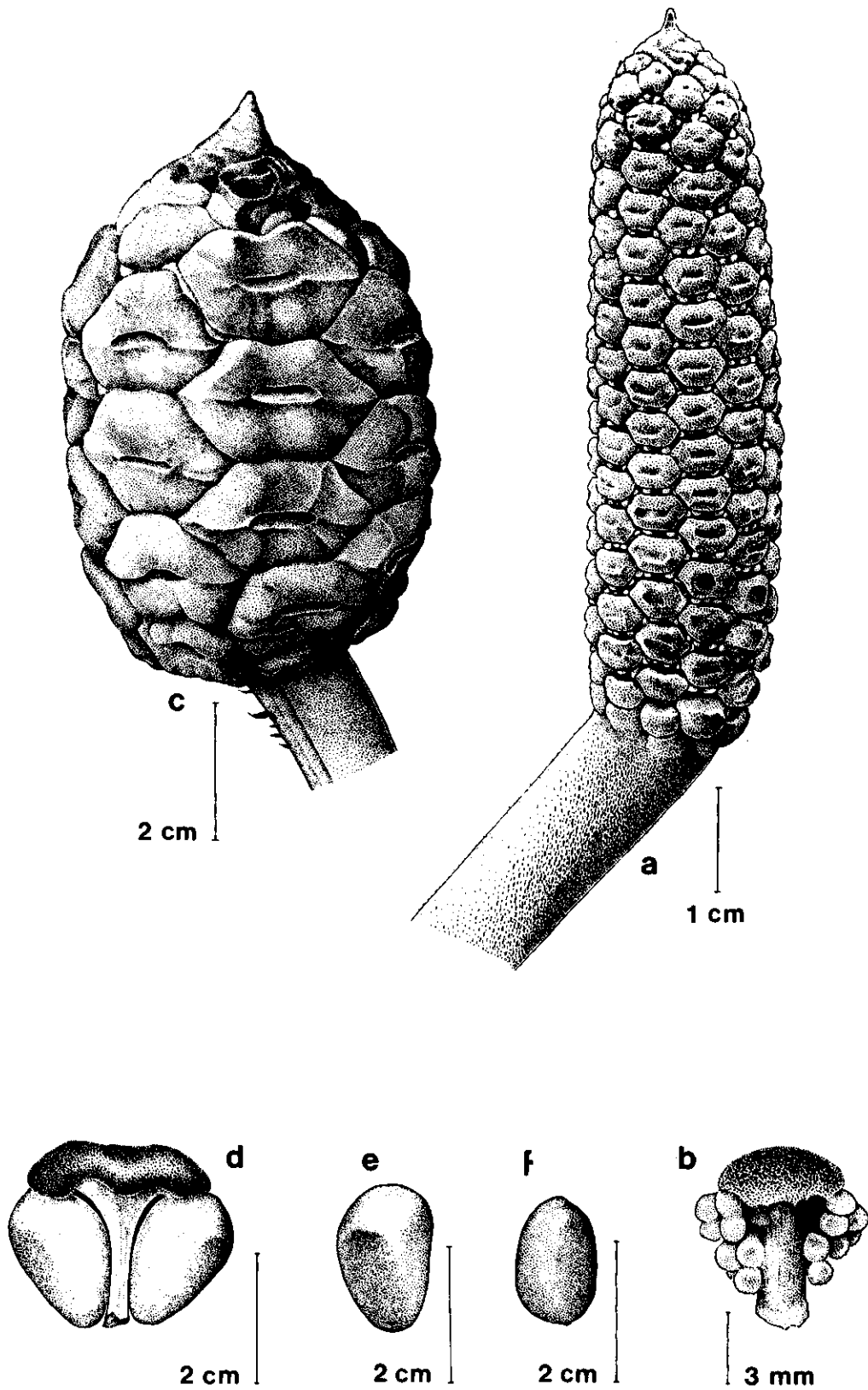


FIG. 5.—*Zamia cremnophila*. a, Microsporangiate strobilus. b, Microsporophyll showing microsporangia. c, Megasporangiate strobilus. d, Megasporophyll with two ovules. e, Ripe seed with fleshy sarcotesta. f, Seed with fleshy sarcotesta removed. Drawn by EDMUNDO SAAVEDRA

opposite, long-lanceolate to oblong, deep purplish-red during and for some time after emergence, at maturity green, coriaceous, and glabrous, imbricate in all but deep shade; apex acute; base attenuate, amphistomatic, with small numbers of stomata on adaxial surface, 10–36 cm long, 2–4 cm wide; articulation with rachis 0.8–1.2 cm long; petiole and rachis extremely spinose, especially closer to the petiole base, adaxial surface of the rachis with few spines; spines terete, often branched, 0.5–4.0 mm long; petiole base relatively spineless, bulbous, puberulent to glabrous, ca. 2.2 cm wide; cataphylls elongate triangular, stipulate, tomentose, 3.7–4.3 cm long, 1.2–1.4 cm wide at base. Microsporangiate strobilus cylindrical to conic, light brown; peduncle puberulent, 2.5 cm long, 0.8-cm diameter; microsporophylls cuneiform, distal ends hexagonal-truncate, long axis 0.43–0.52 cm, short axis 0.29–0.35 cm, distal to proximal ends 0.6 cm, fertile portion covering  $\frac{1}{2}$  to  $\frac{2}{3}$  its length; microsporangia 14–18 per sporophyll, aggregated into sori of two microsporangia each, spheroidal, dehiscing by longitudinal sutures, 0.65–0.78-mm diameter. Megasporangiate strobilus cylindrical, barrel-shaped with an acuminate apex, deep brown, tomentulose, ca. 8.5 cm long, 5.5-cm diameter; megasporophylls cuneiform-peltate, distal end hexagonal-truncate with a horizontal longitudinal depression or slit, wide axis 1.6–2.6 cm, short axis 1.1–1.6 cm, slit 0.69–1.04 cm long, 0.19–0.33 cm wide; ovules two per sporophyll; seeds ovoid, regular; sarcotesta white when immature, bright scarlet when mature, sclerotesta light beige, smooth, 1.5–1.7 cm long, 0.9–1.0-cm diameter.  $2n = 16$ .

TYPE.—Tabasco August 18, 1981, *M.A. Magaña 343*, collected by M. A. MAGAÑA and S. ZAMUDIO, Holotype: MEXU; Isotype: XAL.

OTHER SPECIMENS EXAMINED.—Tabasco January 29, 1985: *Schutzman 617–637*, *Vovides 897* (XAL).

ETYMOLOGY.—The species epithet is derived from the Greek word for cliff, “cremnos,” and highlights the unusual habitat of this species.

DISTRIBUTION AND ECOLOGY.—This hypogeous stemmed species from the state of Tabasco occupies rocky cliff-sides of calcareous hills (mogotes), bearing striking pendent leaves up to 2 m long. Precise locality data is withheld owing to the taxon's endangered status and because commercial collecting would lead to its eventual extinction in the wild. The vegetation type is the “selva alta perennifolia” of RZEDOWSKI (1978). This plant appears to belong to a complex of similar, closely related species in northern Chiapas, bordering areas of Tabasco, Oaxaca, and southern Veracruz. The first of these to be described was *Z. purpurea* (VOVIDES et al. 1983). *Zamia splendens* was subsequently described (SCHUTZMAN 1984).

Juvenile plants of *Z. splendens* and *Z. cremnophila* are similar, but distinctions between mature

plants are more readily apparent. Eophylls (first seedling leaves) of *Z. purpurea* and *Z. splendens* are distinct from those of *Z. cremnophila*, the former two having four leaflets, the latter consistently with two leaflets. The leaf-habit distinction between *Z. cremnophila* and the other two species appears ontogenetically early, leaves of even the smallest plants beginning to arch. This appears to be genetically controlled, as altering its environment does not produce any change in leaf habit. The three species also differ in emergent leaf color. *Zamia splendens* and *Z. purpurea* have pinkish red emergent leaves; those of *Z. cremnophila* are purplish red; *Z. splendens* may also exhibit bright green emergent leaves. *Zamia purpurea* is the only member of the complex or any other Mexican zamia with visibly elevated veins on adaxial leaflet surfaces. In addition, the predominant number of microsporangia on median microsporophylls is distinctly different in the three species: median microsporophylls of *Z. purpurea* have four or eight; those of *Z. splendens*, 20; and those of *Z. cremnophila*, 16.

#### Chromosomal studies

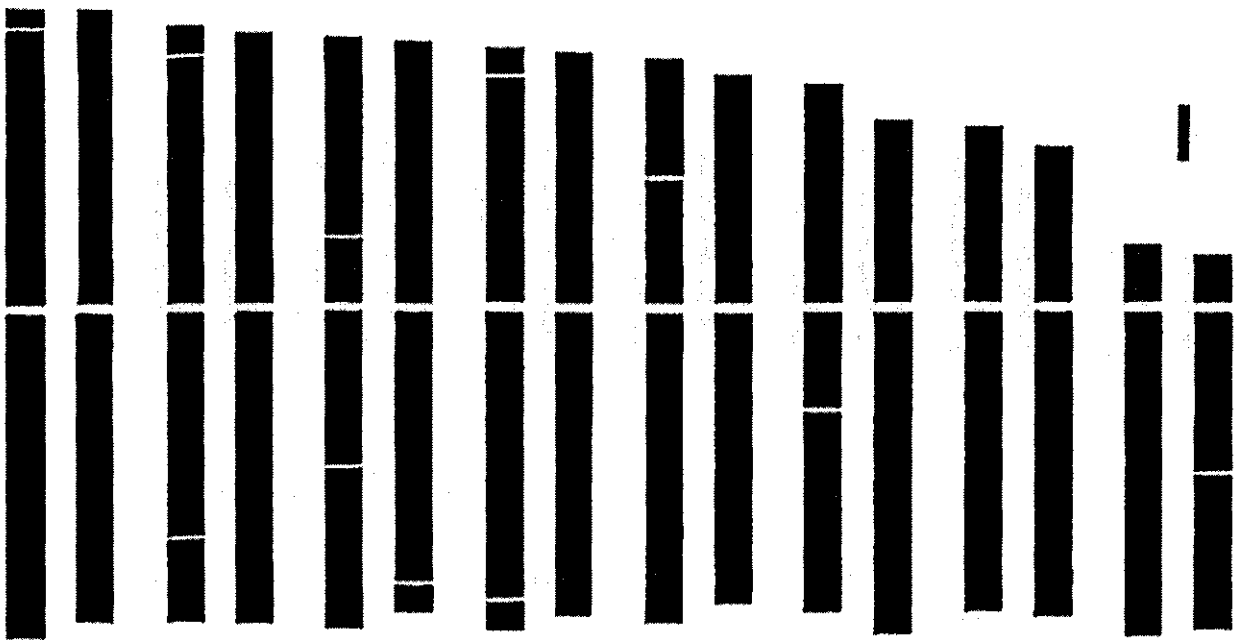
A wide range of chromosome numbers has been reported in *Zamia*:  $2n = 16$  to  $2n = 28$  (MARCHANT 1968; NORSTOG 1980a, 1980b; VOVIDES 1983; MORETTI and SABATO 1984; SCHUTZMAN 1984).

#### MATERIAL AND METHODS

Diploid chromosome counts and karyotypes were obtained by the method of VOVIDES (1983). Vouchers of the karyotyped plants have been made and deposited at XAL and FLAS. Softening of cell walls was achieved by incubating root tips in 0.02% pectinase solution for 30 min in a 37 C water bath. With chilling, good metaphase configurations were obtained, and squashes were facilitated by the pectinase treatment because the application of excessive pressure on preparations was avoided. A 2% acetic-orcein solution was used for staining.

Measurements of the chromosomes were taken from those metaphase cells in which chromosomes had reached maximum contraction with minimal overlapping. Metaphase cells with overlapping chromosomes were used only when the centromere and telomere portions could be clearly distinguished. Measurements were taken from scaled camera lucida drawings using a calibrated compass and “walking” the compass along the long and short arms of each chromosome. Kinetochores and putative heterochromatic regions were excluded in the measurements. Photomicrographs of metaphase configurations (figs. 6A, 7A) were made on a Zeiss Fotomicroscope III using a X63 planapochromatic objective in conjunction with an achromatic-aplan-





**B**

FIG. 6.—*Zamia soconuscensis*. *a*, Mitotic metaphase cell. *b*, Diploid idiogram. Scale lines = 2  $\mu$ m.

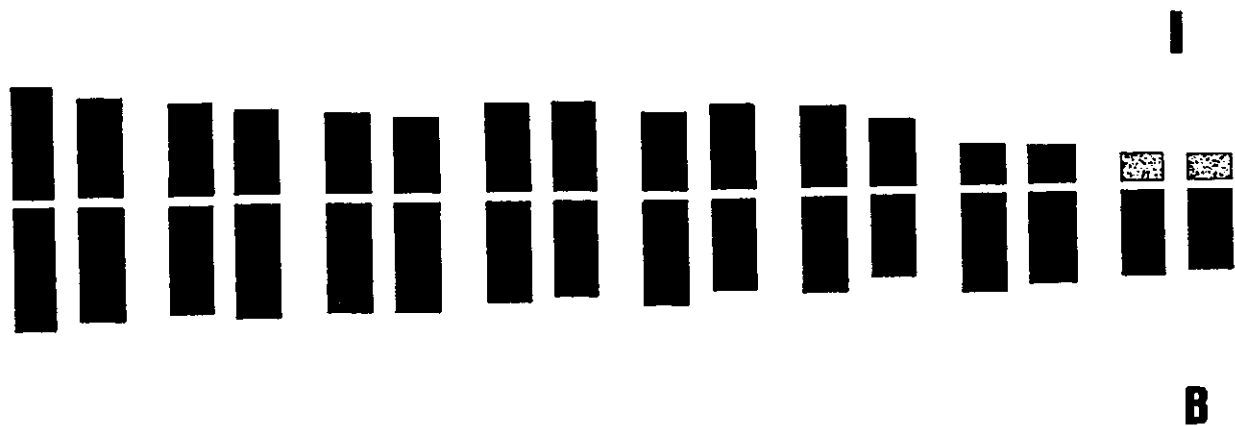
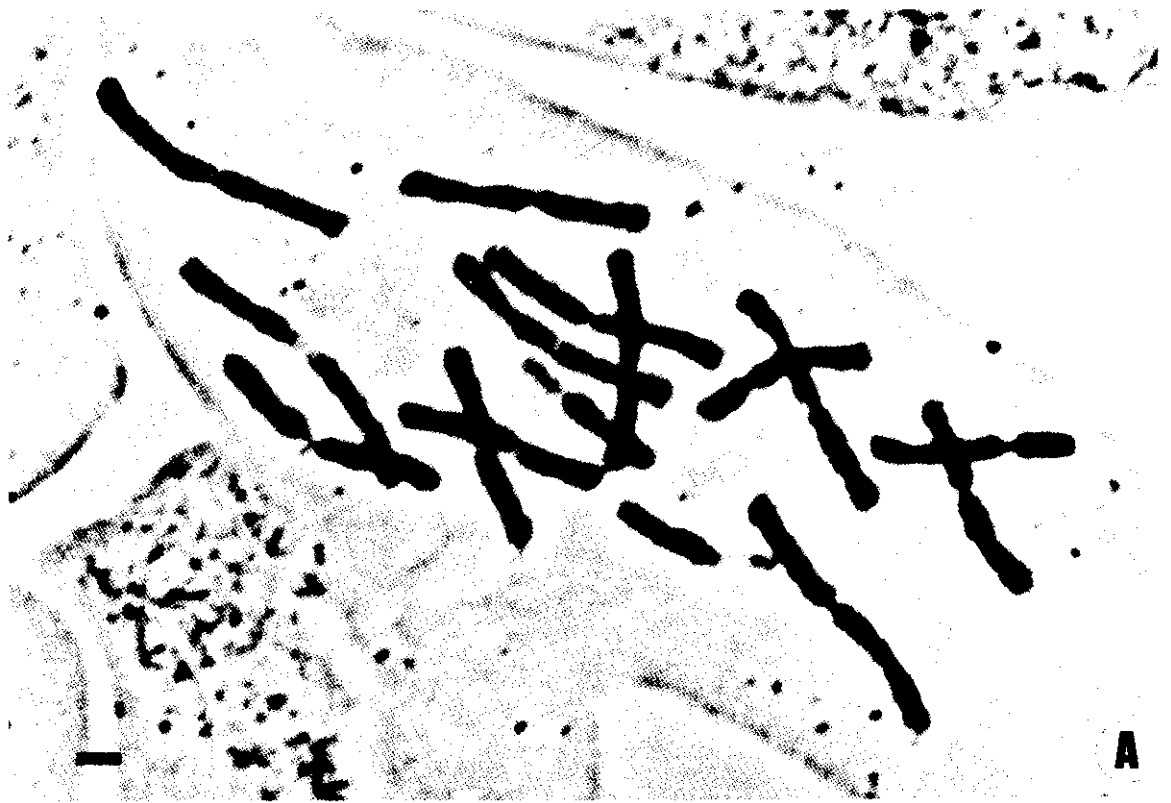


FIG. 7.—*Zamia cremnophila*. *a*, Mitotic metaphase cell. *b*, Diploid idiogram. Scale lines = 2  $\mu$ m.

atic condenser. The film used was Kodak panchromatic Plus-X, ASA 125.

For *Z. soconuscensis*, the idiogram was constructed by taking the average arm lengths of the best four metaphase cells examined. Arm lengths, total chromosome length, chromosome index (short arm divided by long arm), and a symmetry index (length of longest pair divided by length of shortest

pair) were computed using measurements of the average arm lengths from the four metaphase cells (table 1). For *Z. cremnophila*, the mean arm lengths of six good metaphase cells were used for the idiogram, and the best metaphase cell was used to compute the karyotypic data (table 2). Chromosomes are arranged in putative pairs in order of decreasing total length (figs. 6*B*, 7*B*). The chromo-

TABLE 1  
KARYOTYPIC DATA AT METAPHASE IN ROOT-TIP MITOSIS OF *ZAMIA SOCONUSCENSIS*

CHROMOSOME PAIR	ARM LENGTH ( $\mu\text{m}$ )			INDEX (S/L)	<i>r</i> value	KINETOCHORE POSITION <sup>a</sup>
	Short (S)	Long (L)	Total			
1 .....	11.43	12.25	23.68	.93	1.07	m
	11.18	11.75	22.93	.95	1.05	m
2 .....	10.62	11.68	22.30	.91	1.10	m
	10.50	11.68	22.18	.90	1.11	m
3 .....	10.00	11.93	21.93	.84	1.19	m
	9.81	12.00	21.81	.82	1.22	m
4 .....	8.93	12.31	21.24	.73	1.38	msm
	9.75	11.12	20.87	.88	1.14	m
5 .....	9.37	11.31	20.68	.83	1.21	m
	8.50	10.87	19.37	.78	1.28	m
6 .....	8.12	11.18	19.30	.73	1.38	msm
	6.87	12.00	18.87	.57	1.75	sm
7 .....	6.43	11.18	17.61	.58	1.74	sm
	5.75	11.37	17.12	.51	1.98	sm
8 .....	2.18	12.25	14.43	.18	5.62	st
	1.81	11.86	13.67	.15	6.55	st
Total			317.99			

NOTE.—Vouchers: S-676, 678, 685, 694 (XAL, FLAS).

<sup>a</sup> m = median, msm = median-submedian, sm = submedian, st = subterminal. Average chromosome index = 0.70. Symmetry index = 1.66.

some classification used was that of LEVAN et al. (1964), modified by SCHLARBAUM and TSUCHIYA (1984).

#### RESULTS

While no difficulties were encountered in obtaining *Z. cremnophila* chromosomes sufficiently contracted for reliable counts, the chromosomes of *Z. soconuscensis* appeared to have "sticky" telo-

meres and formed what seemed to be chains of two or more chromosomes end to end. Further confusion was caused by the relative ease with which these large chromosomes fragmented during treatment. Modifying the technique by the addition of a 12-h cold treatment of 0 C after the 0.2% colchicine pretreatment solved these problems. A diploid chromosome number for *Z. soconuscensis* of 16 was observed (fig. 6A), with 9 median (m), 2

TABLE 2  
KARYOTYPIC DATA AT METAPHASE IN ROOT-TIP MITOSIS OF *ZAMIA CREMNOPHILA*

CHROMOSOME PAIR	ARM LENGTH ( $\mu\text{m}$ )			INDEX (S/L)	<i>r</i> value	KINETOCHORE POSITION <sup>a</sup>
	Short (S)	Long (L)	Total			
1 .....	5.00	5.40	10.40	.93	1.08	m
	4.50	5.00	9.50	.90	1.11	m
2 .....	4.20	4.80	9.00	.88	1.14	m
	3.80	5.00	8.80	.76	1.32	msm
3 .....	3.60	4.80	8.40	.75	1.33	msm
	3.50	4.80	8.30	.73	1.37	msm
4 .....	4.00	4.20	8.20	.95	1.05	m
	4.00	4.10	8.10	.98	1.03	m
5 .....	3.50	4.60	8.10	.76	1.31	msm
	3.80	4.00	7.80	.95	1.05	m
6 .....	3.60	4.20	7.80	.88	1.17	m
	3.00	3.50	6.50	.86	1.12	m
7 .....	1.80	4.30	6.10	.42	2.39	sm
	1.75	4.00	5.75	.44	2.29	sm
8 .....	1.20	3.75	4.95	.32	3.13	st
	1.10	3.50	4.60	.31	3.18	st
Total			122.30			

NOTE.—Vouchers: S-619, 622, 625, (XAL, FLAS).

<sup>a</sup> m = median, msm = median-submedian, sm = submedian, st = subterminal. Average chromosome index = 0.74. Symmetry index = 2.08.

median-submedian (msm), 3 submedian (sm), and 2 subterminal (st) chromosomes. The chromosomes appear to show numerous secondary and tertiary constrictions, knobs, and satellites shown as light bands in the idiogram (fig. 6B). The appearance of these constrictions varied greatly between cells, and the maximum number seen in any single metaphase cell has been recorded. This "banding" effect is probably caused by allocyclus or differential activity prior to staining, an effect perhaps enhanced by the cold treatment; this causes differential supercontraction of the euchromatin, as mentioned by DARLINGTON and LA COUR (1976).

Chromosome lengths in the complement ranged from an average of 14.1  $\mu\text{m}$  in the smallest pair to 23.3  $\mu\text{m}$  in the largest pair. Even with an observable asymmetry, this is the most symmetrical *Zamia* karyotype we have thus far observed.

A diploid chromosome number for *Z. cremnophila* of 16 was observed (fig. 7A), with 8 median (m), 4 median-submedian (msm), 2 submedian (sm), and 2 subterminal (st) chromosomes (fig. 7B).

The chromosome complement of *Z. cremnophila* (fig. 7A) shows what appear to be large centromere regions in the longer median chromosomes, probably caused by multiple kinetochores in the centromere, the length of which varied from cell to cell. Also, the subterminal pair appears to have differentially staining short arms or possibly tandem duplication in satellites associated with extremely small short arms (A. KENTON, personal communication). This was observed in several cells.

Chromosome length in the complement varies from a mean of 9.95  $\mu\text{m}$  in the longest pair to 4.78  $\mu\text{m}$  in the smallest. Symmetry index of the karyotype is 2.08.

### Discussion

#### SPECIES CONCEPTS IN ZAMIA

There appear to be varying approaches in the literature to the problem of species delimitation in *Zamia*. Early taxonomic work in the genus was mostly based on gross leaflet morphology, exemplified by the works of MIQUEL (1861), DE CANDOLLE (1868), and SCHUSTER (1932). STANDLEY (1923) used leaflet shape, vein number, leaflets per leaf, and apex shape to key the Mexican zamias. NEWELL (1985) pointed out the early predominance of leaflet morphology in taxonomic treatments and demonstrated that leaflet morphology can be environmentally influenced. These differences were likely responsible for much of the earlier splitting, evidenced by 128 binomials in Index Kewensis (some of which were later moved into other genera, mostly *Encephalartos*).

ECKENWALDER (1980) statistically analyzed leaflet length, width, and vein number of the West Indian zamias and found a continuum in leaflet width throughout the West Indies and a correlation be-

tween vein number and leaflet width. Using these criteria, he reduced the group to two subspecies of a single endemic species, *Z. pumila* L. (ssp. *pumila* and ssp. *pygmaea* [Sims] Eckenwalder). He did not take into account other characteristics such as leaflet denticulation and shape, strobilus color and form, and seeds, not to mention karyotypic data. As STEVENSON (1987) pointed out, had he done so, he would probably have arrived at different conclusions. A view unacceptable to us is that of STEWARD (vide ECKENWALDER 1980), who regards *Zamia* as a monotypic genus. These are clearly two extremes of the species problem in *Zamia*. Although we are cognizant of a number of synonymies in the group, we do not agree with either extreme but advocate an Adansonian approach to the problem of species delimitations, examining as many characters as is reasonably possible. A key to the Mexican species of *Zamia* is presented in table 3.

#### CHROMOSOME MORPHOLOGY

*Zamia* exhibits a wide range of chromosome numbers as well as variation in karyotype symmetry. Centromeric fission was reported by MORETTI and SABATO (1984) in *Z. paucijuga* Wieland, resulting in chromosome numbers from  $2n = 23$  to  $2n = 28$ , with more telocentric chromosomes in the higher-numbered karyotypes. This species most likely has its origins in the *Z. loddigesii*  $2n = 18$  complex from the Mexican Gulf Coast and Isthmus of Tehuantepec. According to MORETTI and SABATO, the evolution of more asymmetric and high-numbered karyotypes may have favored its adaptation to more xeric conditions along the northwest Pacific coast of Mexico.

The asymmetrical, high-numbered karyotypes, concomitant with reduced vegetative and reproductive structures and subterranean caudex, support KHOSHOO's (1969) hypothesis that karyotypes of derived taxa are asymmetric and those of less morphologically advanced taxa are more symmetric. Certain species, however, are antithetic to KHOSHOO's concepts. *Zamia roezlii* (previously known as *Z. chigua*), a relatively unspecialized, arborescent species growing in unstressful environments in Colombia, was studied by NORSTOG (1980a, 1980b). Like *Z. paucijuga*, this taxon has a large-numbered and highly asymmetric karyotype. Conversely, the two species with the most highly reduced vegetative and reproductive structures, *Z. pygmaea* Sims and *Z. purpurea*, have highly symmetrical karyotypes and  $2n = 16$  and are native to stable, unstressful environments. *Zamia pygmaea* is found on moist forest ravines on limestone outcroppings (mogotes) or in open limestone or serpentine communities (ECKENWALDER 1980). *Zamia purpurea* is native to moist tropical rain forests.

The solution to these apparent contradictions may

TABLE 3  
KEY TO MEXICAN SPECIES OF ZAMIA L.

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1. Plants arborescent, leaflets with entire margins:
    2. Petiole/rachis always unarmed, emerging leaves sparingly pubescent  
..... *Z. inermis* Vovides, Rees & Vázquez-Torres
    2. Petiole/rachis spinulose, emerging leaves white tomentulose  
..... *Z. soconuscensis* Schutzman, Vovides & Dehgan
  1. Plants not arborescent, leaflets with denticulate margins:
    3. Plants partly hypogeous, partly epigeous, leaflet apices obtuse to acute  
..... *Z. furfuracea* L.f.
    3. Plants entirely hypogeous, leaflet apices acute to long acuminate:
      4. Leaves pendent..... *Z. cremnophila* Vovides, Schutzman & Dehgan
      4. Leaves erect to arching:
        5. Strobili decumbent..... *Z. splendens* Schutzman
        5. Strobili erect:
          6. Petiole/rachis unarmed, leaflets shorter than 10 cm ..... *Z. fischeri* Miq.
          6. Petiole/rachis usually armed, leaflets longer than 10 cm:
            7. Leaflets < 7 mm wide ..... *Z. spartea* A.D.C.
            7. Leaflets > 7mm wide:
              8. Veins slightly protruding on adaxial leaflet surface  
..... *Z. purpurea* Vovides, Rees & Vázquez-Torres
              8. Veins not protruding:
                9. Leaflets papyraceous ..... *Z. herrerae* Calderon & Standley
                9. Leaflets coriaceous ..... *Z. loddigesii* Miq.

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perhaps be found in the vegetational history of their environments. GRAHAM (1976) showed that lowland moist tropical rain forest habitats have been disrupted since the upper Miocene in Veracruz. His fossil pollen evidence from the Paraje Solo formation of Coatzacoalcos showed "that a warm-oak community would likely replace the rain-forest disrupted by lower temperatures." These present-day warm-oak communities, though not entirely xeric, are subject to seasonal brush fires. Changes to these types of communities probably have exerted selection pressures on *Zamia* that resulted in chromosomal change. Conversely, species occupying refugia such as the Sierra del Soconusco would find themselves in a relatively more stable environment, most likely with fewer selection pressures. This seems to be reflected in the relatively unspecialized, arborescent species *Z. soconuscensis*, which also has a low chromosome number and symmetrical karyotype, although morphological specialization need not always coincide with chromosome morphology (EHRENDORFER 1976).

The Florida coontie, *Z. floridana* L.f., exemplifies this discrepancy between chromosomal and vegetative specialization. It grows in one of the most inhospitable habitats colonized by this genus, where periodic severe drought and freezing temperatures are not uncommon, and has a subterranean caudex and relatively reduced vegetative body. As NORSTOG (1980b) found, however, it has a symmetric karyotype of  $2n = 16$ . Examples of both morphologically specialized and unspecialized plants with symmetrical, low-numbered karyotypes may indicate this to be a symplesiomorphic, or shared prim-

itive, feature. JONES (1977) mentioned that the process of fusion and fission in Robertsonian changes may have produced cycles of karyotype symmetry and asymmetry over a span of evolutionary time. According to STEBBINS (1971), highly asymmetrical karyotypes in modern gymnosperms are not truly primitive but archaic and specialized, and their less specialized, extinct ancestors probably had relatively symmetrical karyotypes.

Recent knowledge of climatic and vegetational changes of the geologic past will be useful in understanding speciation and biological diversity of the lowland tropics (PRANCE 1982). This evidence will be especially important for the understanding of archaic groups such as cycads.

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