

# The identity of *Zamia katzeriana* and *Z. verschaffeltii* (Zamiaceae)

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**Abstract.** The morphological variation of recently described species (also the older taxa) of *Zamia* distributed within southeastern Mexico that have wide, coriaceous leaflets is analyzed. The complex is designated as the *Z. katzeriana* species complex in reference to an historic collection of this name, which is also the earliest named species in the complex. The complex consists of *Z. cremnophila*, *Z. lacandona*, *Z. splendens* and *Z. purpurea*. During the 1990's, *Z. splendens* was separately synonymized under *Z. katzeriana* and *Z. verschaffeltii*, both collected in Mexico by German collectors during the 18th century, but the precise locality is unknown. Information concerning the incomplete holotype of *Z. verschaffeltii* is particularly ambiguous, and the possible type locality suggested by Schuster, Socorro, is imprecise, thus generating taxonomic confusion. Morphometric characterization and discriminant analysis of the contemporary and historic collections (i.e., *Z. katzeriana* and *Z. verschaffeltii*) included all the known populations (11) and individuals (115) of the complex throughout its range. The results show that *Z. verschaffeltii* is not morphometrically related to any of the species in the complex and that *Z. splendens* should be considered a synonym of *Z. katzeriana*.

**Key Words:** Cycads, discriminant analysis, holotype, Mexico, morphometry.

**Resumen.** En este artículo se caracteriza la variación morfológica de las especies de un complejo de *Zamia*, que presentan folíolos anchos y coriáceos con distribución en el sureste de México, la mayoría de reciente descripción. El complejo es denominado *Z. katzeriana*, por una colección histórica de este nombre, y consiste de *Z. cremnophila*, *Z. lacandona*, *Z. splendens* y *Z. purpurea*. *Zamia splendens* fue sinonimizada separadamente bajo dos colecciones históricas *Z. katzeriana* y *Z. verschaffeltii*, de las cuales se desconoce con exactitud su lugar de procedencia, excepto que fueron colectadas en México por botánicos alemanes del siglo XVIII. La información, en especial sobre el holotipo incompleto de *Z. verschaffeltii* es muy ambigua y la posible localidad tipo mencionada por Schuster, Socorro, es imprecisa, lo cual ha generado confusiones taxonómicas. La caracterización de la variación morfométrica incluyó a todas las poblaciones (11) e individuos (115) conocidas actualmente para el complejo en todo su rango de distribución en México. El análisis discriminante incluyendo a las colecciones históricas, determina que *Z. verschaffeltii* no está relacionado morfométricamente con ninguna especie del complejo y *Z. katzeriana* está estrechamente correlacionada con *Z. splendens*.

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There are approximately 58 known species of *Zamia* L. (Hill et al., 2004a, b, c) and it is the most widespread cycad genus in the neotropics, ranging between latitudes 30° N

and 18° S. It occurs in Georgia and Florida in the United States, throughout the Greater Antilles, Mexico, Central America, and in South America (Balduzzi et al., 1982; Sabato,

1990; Norstog & Nicholls, 1997; Stevenson, 2001a). *Zamia* also has the greatest variation within the cycads in such features as leaflet shape and size, habitat and life form, as well as a wide range of karyotypes and chromosome numbers (Vovides, 1983; Moretti & Sabato, 1984; Moretti, 1990; Vovides & Olivares, 1996; Norstog & Nicholls, 1997).

The last complete taxonomic treatment for the neotropical species of *Zamia* was by Schuster (1932). Later works (Sabato, 1990; Stevenson, 1987, 1991a, b, 2001a, b, 1993, 2004; Norstog & Nicholls, 1997), including the typification of valid names (Stevenson & Sabato, 1986), have provided data concerning the nomenclatural and taxonomic errors of this treatment, mainly due to insufficient field work and collections, notably, the destruction of all cycad specimens and types in Berlin.

Various regional treatments on the neotropical Zamiaceae have since appeared (see Vovides, 1983; Stevenson, 1987, 1991a, b, 2001a, b, 1993, 2004). However, none of these treatments has dealt with the problem of the identity of *Zamia katzeriana* (Regel) E. Rettig (Fig. 1), *Z. verschaffeltii* Miq., and *Z. splendens* Schutzman. The binomial *Z. verschaffeltii* was published in 1870. More recently, *Z. verschaffeltii* appears in the published World List of Cycads (Hill & Stevenson, 1998), although Stevenson et al. (1995) and Osborne et al., (1999) placed this taxon under synonymy of *Z. muricata* Willd. Later, Hill & Stevenson (1998) placed *Z. splendens* and *Z. katzeriana* under synonymy of *Z. verschaffeltii* (see Hill et al., 2004a, b, c). The existing information on the geographic origin of *Z. verschaffeltii*, as reported by both Miquel (1870) and Schuster (1932), and the sterile holotype consisting of an incomplete leaf and leaflets are very ambiguous. According to Schuster (1932) the type locality is Socorro, Mexico and the material used for the description was probably cultivated. There are eight localities with the name Socorro in Mexico, of which only two are within the climatic and elevational range for *Zamia*. In the case of *Z. katzeriana*, although no locality is mentioned other than Mexico, the holotype, though sterile, is in excellent condition, and there is a published photograph of a fertile living plant (Rettig, 1896).



FIG. 1. Holotype of *Zamia katzeriana* (E. A. Regel s.n., LE).

In the publication of the World Cycad List by Hill & Stevenson (1998), *Zamia katzeriana* and *Z. splendens* are included as synonyms of *Z. verschaffeltii*, the status of which has been upheld by the Cycad Specialist Group (Hill et al., 2004a, b, c). The main discussion has been centered on the synonymy of *Z. splendens* under *Z. verschaffeltii* as discussed and refuted by Schutzman (2004) whose argument is based solely on the fragmentary nature of the *Z. verschaffeltii* holotype and ambiguity of where it was collected.

Because there is no revision that corroborates the taxonomic and nomenclatural status of these entities, the goal of this research has been aimed at defining the identities of *Zamia katzeriana*, *Z. verschaffeltii*, and *Z. splendens*. In doing so, the study also included *Z. cremnophila* Vovides, Schutzman and Dehgan, *Z. purpurea* Vovides, J. D. Rees and Vázq. Torres, and *Z. lacandona* Schutzman and Vovides. The latter species have been included in the analysis because

these taxa are morphologically similar and they also share the same distribution in southeastern Mexico (Fig. 2), especially in the arc floristic refuge of Wendt (1987), which is an area consisting of relict species of ancient floristic affinities that range from northern Oaxaca and southern Veracruz to northern Tabasco and Chiapas. *Zamia variegata* Warsz., though not within the geographical range of the taxa under study, was included because of the similarity of its habitat to the taxa under study, i.e., evergreen tropical rainforest with similar edaphic conditions and altitudinal range in southeastern Mexico. *Zamia paucijuga* Wieland was included because of certain morphometric similarities to the *Z. verschaffeltii* holotype.

### Materials and Methods

#### POPULATION SELECTION

A total of 115 individuals from 11 known populations of the *Zamia katzeriana* complex were studied as presented in Table I, which represents the total number of populations and individuals currently known to occur in Mexico. Also, specimens held in the living cycad collection at the Jardín Botánico Fco.

Javier Clavijero, Instituto de Ecología, A. C., were examined as well as herbarium specimens from the following herbaria: B, CHIP, ECOSUR, ENCB, FLAS, FTG, HEM (Universidad de Ciencias y Artes de Chiapas, México), IBUG, IEB, K, LE, MEXU, NY, U, and XAL. Measurements used only for the discriminant analysis were taken directly from the types of *Z. katzeriana* and *Z. verschaffeltii*, and other characters were taken from the original descriptions.

#### CHARACTER SELECTION

Twelve quantitative vegetative morphological characters were selected (Table II). Measurements were made manually using calipers or a ruler. These variables represent a suite of characteristics that have been used for diagnosing species of *Zamia*. The emphasis on vegetative characters was necessary because specimens represented in herbaria are often sterile and taxonomic treatments have placed major emphasis on foliar characters (Miquel, 1861; de Candolle, 1868; Schuster, 1932; Eckenwalder, 1980; Vovides et al., 1983; Newell, 1986; Stevenson, 1993, 2001a, b, 2004; Schutzman & Vovides, 1998). Additionally, 28 qualitative morphological charac-

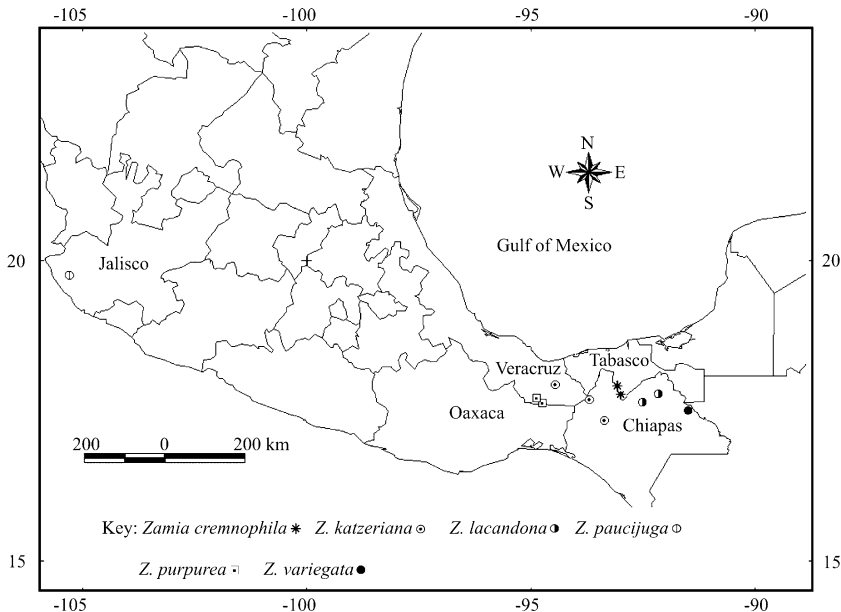


FIG. 2. Distribution of natural populations in Mexico of the *Zamia* species used in this study.

TABLE I  
THE NATURAL POPULATIONS AND THE NUMBER OF INDIVIDUALS OF *ZAMIA* SPECIES FROM MEXICO USED IN THIS STUDY

Species	State of Mexico	No. of populations	No. of individuals
<i>Z. cremnophila</i> <sup>a</sup>	Tabasco	2	20
<i>Z. lacandona</i> <sup>a</sup>	Chiapas	2	20
<i>Z. katzeriana</i> <sup>a</sup> (= <i>Z. splendens</i> )	Chiapas, Veracruz	3	32
<i>Z. purpurea</i> <sup>a</sup>	Oaxaca, Veracruz	2	20
<i>Z. paucijuga</i>	Oaxaca	1	12
<i>Z. variegata</i>	Chiapas	1	11
TOTAL		11	115

<sup>a</sup> Species of the *Z. katzeriana* species complex.

ters from foliar and reproductive structures as well as habit were coded as binary or multistate characters (Table III).

#### ANALYSES

Univariate, principal component and discriminant analyses were conducted using Statistica for Windows (StatSoft®, 1998). The final discriminant graphic was obtained using Statgraphic Plus® ver. 4.1, (1994) then edited in Photoshop® ver. 6 for Macintosh.

An exploratory univariate analysis was performed using a Student's *t* test with the aim of assessing the variation of individuals within and between species.

A principal component analysis (PCA) was done to identify which variables and the percentage that each contributes to the variation within the species complex (eigenvectors and eigenvalues from the correlation matrix after linear standardization of the

original data, see Table IV). The analyses were based on two different data sets: (1) quantitative characters, (2) both quantitative and qualitative characters. Correlation matrices were generated for matrix 1 to evaluate the variance of the new factors extracted successively and to explain the percentage of variance each component describes. A PCA was done on matrix 2 to evaluate grouping patterns of the species defined a priori, a scenario that could not be observed with matrix 1. The factors that explained most of the variation, and their contribution, were extracted from the correlation matrix for each variable. All quantitative variables were log<sub>10</sub> transformed because they were not normally distributed.

Finally, to explore and corroborate the position of *Zamia katzeriana* and *Z. verschoffeltii* (where only historical information on origin and vegetative characteristics defining them as taxonomic entities exists), a discriminant analysis was applied where all the data including those from Miquel (1870), Rettig (1896), and the existing holotypes were considered in the analysis.

## Results

#### UNIVARIATE ANALYSES

Leaflet length measurements (Table V) of *Zamia lacandona* show high variation between individuals of the same population and between populations of the species. With respect to this variable, *Z. cremnophila* and *Z. purpurea* are homogenous within and between populations, whereas *Z. katzeriana* (including *Z. splendens*) and *Z. variegata* are consistent within their populations but exhibit slight variation between their populations.

TABLE II  
QUANTITATIVE MORPHOLOGICAL CHARACTERS AND THEIR ABBREVIATIONS USED IN THIS STUDY

Character	Code
Number of leaves per plant	NL
Leaf length	LL
Petiole length	PL
Number of leaflets per leaf	NLF
Length of leaflets at leaf base	LLB
Length of leaflets at leaf median	LLM
Length of leaflets at leaf apex	LLA
Width of leaflets at leaf base	WLB
Width of leaflets at leaf median	WLM
Width of leaflets at leaf apex	WFA
Distance between leaflets	DL
Leaflet articulation width	AW

TABLE III  
QUALITATIVE MORPHOLOGICAL CHARACTERS USED IN THIS STUDY

Character	State of character
Habit (seedling)	(0) Hypogeal; (1) semi-hypogeal
Cataphyll apex	(0) Aristate; (1) acuminate
Cataphyll texture	(0) Chartaceous; (1) membranaceous
Cataphyll persistence	(0) Semi-deciduous; (1) deciduous
Leaf orientation	(0) Adpressed; (1) ascending; (2) descending
Petiole shape	(0) Terete; (1) subterete
Bulbose petiole base	(1) Present; (0) absent
Petiole color in adult plants	(0) Green; (1) brown; (2) purple
Rachis prickles	(0) Absent; (1) present
Leaflet texture	(0) Coriaceous; (1) chartaceous
Adaxial leaf cuticle	(0) Lustrous; (1) non-lustrous
Leaflet shape in adult leaves	(0) Oblong-elliptic; (1) elliptic; (2) linear-lanceolate
Leaf venation	(0) Conspicuous; (1) inconspicuous
Leaflet base	(0) Cuneate; (1) attenuate; (2) cuneate to attenuate
Leaflet apex	(0) Acuminate; (1) acute
Sinuuous leaflet margin	(0) Present; (1) absent
Leaflet variegation	(0) Present; (1) absent
Leaflet imbricate	(0) Present; (1) absent
Megastrobilus shape	(0) Ellipsoid; (1) conical; (2) cylindrical
Megastrobilus peduncle habit	(0) Descending; (1) erect
Megastrobilus color	(0) Brown; (1) purple; (2) green; (3) yellow
Distal face of megasporophyll	(0) Truncate; (1) scutiform; (2) protuberant
Megastrobilus apex	(0) Aristate; (1) acute; (2) apiculate; (3) mucronate
Megastrobilus shape	(0) Barrel-shaped; (1) conical; (2) conical-cylindrical; (3) cylindrical
Microstrobilus color	(0) Creamy; (1) purple; (2) brown
Microstrobilus apex	(0) Mucronate; (1) acute; (2) truncate
Microstrobilus peduncle habit	(0) Descending; (1) erect; (2) decumbent
Sarcotesta color (ripe seeds)	(0) Red; (1) orange

Leaflet width at the base, median, and leaf apex separate *Zamia katzeriana* from the rest of the species in the complex; these values are constant between populations 2 and 3 but not so in population 1 of *Z. katzeriana*. *Zamia lacandona*, *Z. cremnophila*, *Z. purpurea*, and *Z. variegata* show little variation for this

variable within and between their populations, with the exception of one individual of *Z. variegata* with a leaflet width of up to 9 cm. *Zamia paucijuga* shows narrower leaflets.

The maximum leaf length (30–220 cm) is greater in *Zamia lacandona* than the rest of

TABLE IV  
SUMMARY OF THE PRINCIPAL COMPONENTS ANALYSIS

Component Number	Eigenvalue	Percent of variance	Cumulative percentage
1	4.42557	36.880	36.880
2	3.25819	27.152	64.031
3	1.7489	14.574	78.606
4	0.787914	6.566	85.171
5	0.476508	3.971	89.142
6	0.390987	3.258	92.401
7	0.24894	2.075	94.475
8	0.238251	1.985	96.461
9	0.213003	1.775	98.236
10	0.117933	0.983	99.218
11	0.059461	0.496	99.714
12	0.0343366	0.286	100.000

TABLE V  
 MEDIAN LEAFLET LENGTH AND WIDTH MEASUREMENTS FROM NATURAL POPULATIONS OF *ZAMIA* SPECIES IN MEXICO

Species	Leaflet length (cm)	Leaflet width (cm)
<i>Z. cremnophila</i> <sup>a</sup>	22–38	3.1–4.4
<i>Z. lacandona</i> <sup>a</sup>	15–37	3.2–6
<i>Z. katzeriana</i> <sup>a</sup> (incl. <i>Z. splendens</i> )	18–35	4.5–12
<i>Z. purpurea</i> <sup>a</sup>	20–24	4.7–7.2
<i>Z. paucijuga</i>	15–25	2.2–3.8
<i>Z. variegata</i>	12–21(35)	3.5–5.8

<sup>a</sup>Species of the *Z. katzeriana* species complex.

the species; *Z. cremnophila* and *Z. katzeriana* have individuals with leaf lengths not greater than 180 cm, and a third group, *Z. purpurea* and *Z. paucijuga*, has leaves up to 75 cm long.

#### PRINCIPAL COMPONENTS ANALYSIS (PCA)

According to the correlation matrix, 36.9% of the total variation is explained by the leaflet articulation width, and basal, median, and apical leaflet lengths, represented by component 1. Component 2, representing number of leaflets and the width of basal and median leaflets, contributes 27.2%. Finally component 3, representing number of leaves, leaf length and petiole length contributes 14.6%. Collectively, the three components explain 78.6% of the observed morphological variation of the complex (Tables IV and VI). The combined matrix analysis (qualitative and quantitative characters) resulted in better-resolved groupings (Fig. 3), which permitted us to easily characterize the species included in this study using

the first two components. Six variables explained 55% of the total variation of the following qualitative characteristics for component 1: cataphyll persistence, petiole type, adult plant leaflet shape, megastrobilus peduncle type, microstrobilus color, and microstrobilus peduncle type, and for component 2: cataphyll apex shape, leaf orientation with respect to the rachis, petiole color in adult plants, leaflet arrangement along the rachis, ripe sarcotesta color, and habit.

#### DISCRIMINANT ANALYSIS

Figure 4 shows the configuration of the groups derived from the discriminant analysis. Four discriminant functions contribute significantly ( $p < 0.01$ ) to the separation of three groups (Tables VII, VIII). Clusters of three groups of the four species representing the *Zamia katzeriana* complex form one large group in which overlap is observed according to the variables analyzed. *Zamia paucijuga* does not overlap with the complex, but is only shortly separated from it and *Z. variegata* also forms

TABLE VI  
 SUMMARY OF PRINCIPAL COMPONENT WEIGHTS

Character <sup>a</sup>	Component 1	Component 2	Component 3
NH	-0.0752502	-0.164739	-0.441456
LH	0.304574	0.108935	-0.484207
LP	0.246457	0.0197849	-0.553604
NF	0.100931	0.487297	-0.0823356
LFB	0.369359	0.19868	0.158082
LFM	0.359071	0.238206	0.152202
LFA	0.341607	-0.407671	0.265383
AFB	0.275796	-0.422145	0.140114
AFM	0.283815	-0.389967	0.104798
AFA	0.286783	-0.389967	0.166342
IF	0.302971	-0.197849	-0.275905
AA	0.343425	0.189332	0.0664224

<sup>a</sup>See Table 2.



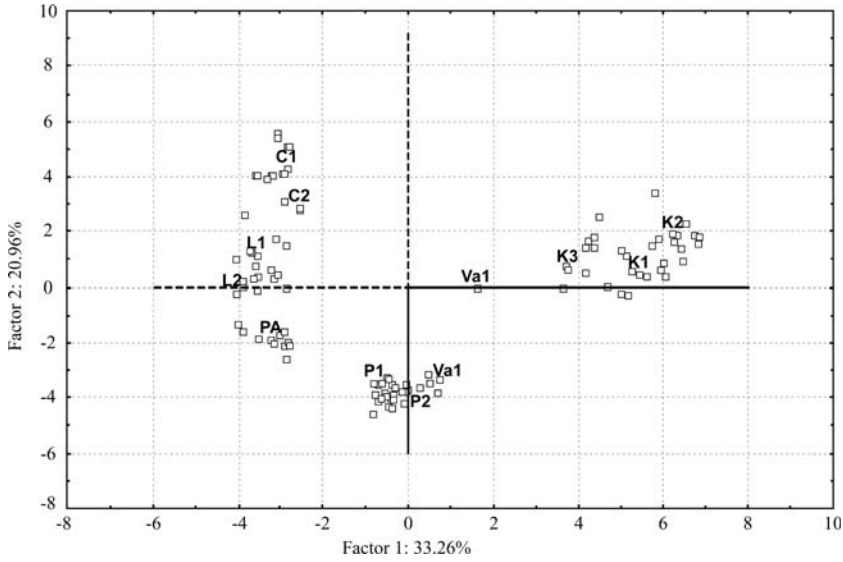


FIG. 3. Plot of principal components analysis using the qualitative and quantitative data matrix on all living material studied. Key: *Zamia cremnophila* (C1, C2); *Z. katzneriana* (K1, K2, K3); *Z. lacandona* (L1, L2); *Z. paucijuga* (PA); *Z. purpurea* (P1, P2); *Z. variegata* (Va1).

a group isolated from the rest of the species analyzed. The analysis placed the type of *Z. verschaffeltii* among individuals of *Z. paucijuga* and *Z. splendens* among populations of *Z. katzneriana*.

**Discussion and Conclusions**

According to our morphological analyses, the quantitative characters from the living and herbarium specimens examined show slight overlap between the species analyzed (Fig. 4).

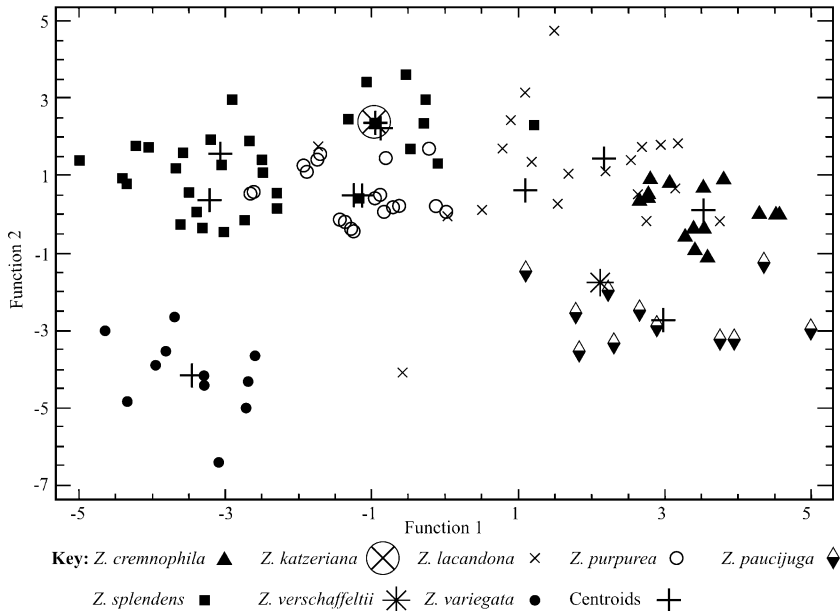


FIG. 4. Scatter plot of the *Zamia katzneriana* species complex, *Z. variegata* and *Z. paucijuga* on function scores derived from discriminant analyses.

TABLE VII  
SUMMARY OF THE DISCRIMINANT FUNCTION VALUES

Discriminant function	Eigenvalue	Relative percentage	Canonical correlation
1	7.40869	54.75	0.93866
2	3.51754	25.99	0.88241
3	1.33662	9.88	0.75633
4	0.659817	4.88	0.63049
5	0.340681	2.52	0.50409
6	0.173926	1.29	0.38491
7	0.0625471	0.46	0.24262
8	0.0270593	0.20	0.16232
9	0.00501395	0.04	0.07063
10	0.0000590585	0.00	0.00768

However, the combined quantitative and qualitative character analysis, excluding the two holotypes, shows a separation between the species of the complex, with the exception of some *Z. variegata* associated with *Z. purpurea* (Fig. 4). The consistent occurrence of yellow spots on the leaves of *Z. variegata* is distinctive and makes the species unmistakable. *Zamia katzeriana* is morphologically similar to the populations of *Z. splendens* (sensu Schutzman, 1984), especially to the San Fernando, Chiapas population, whose morphometric parameters are constant and consistent with the attributes of the *Z. katzeriana* holotype. Based on the evidence presented here, we conclude that *Zamia splendens* is a synonym of *Z. katzeriana*, with the latter having nomenclatural priority.

Despite that morphometrically the *Zamia verschaffeltii* holotype lies within the *Z. paucijuga* area (Fig. 4), both Miquel's (1870) and Schuster's (1932) descriptions of *Z. verschaffeltii* do not coincide with that of

*Z. paucijuga*, which is confirmed by our field observations.

Socorro, the locality mentioned by Schuster (1932) for Miquel's type of *Zamia verschaffeltii* opens up the possibility of finding an extant population for the species. However, of the eight localities with this name in Mexico, only two are in suitable cycad habitats: La Ruta del Socorro in southern Veracruz and El Socorro in Tabasco. The other six are in northern Mexico in arid zones where no cycads have ever been reported.

In the case of the Veracruz locality, no species of *Zamia* have been found there. It is important to note that the whole area and surrounding regions have been converted into vast sugar cane plantations so that historically *Zamia* could have been present but would now be extirpated. However, 20 km west of this locality in the vicinity of the city of Tuxtepec, Oaxaca, plants with an affinity to *Z. sylvatica* Chamb., of the *Zamia loddigesii* Miq. complex were located, but these plants

TABLE VIII  
SUMMARY OF THE DISCRIMINANT ANALYSIS OF POPULATIONS OF *ZAMIA* USED IN THIS STUDY

Functions derived	Wilks lambda	Chi-square	df	P value
1	0.003932	576.0152	110	0.0000
2	0.0330629	354.5716	90	0.0000
3	0.149363	197.7430	72	0.0000
4	0.349005	109.4775	56	0.0000
5	0.579285	56.7799	42	0.0635
6	0.776636	26.2894	30	0.6603
7	0.911714	9.6126	20	0.9747
8	0.968739	3.3031	12	0.9930
9	0.994952	0.5263	6	0.9975
10	0.999941	0.0061	2	0.9969



bear very little resemblance to the type of *Z. verschaffeltii*. In the case of El Socorro, Tabasco, all the adjacent areas have been converted into immense pasturelands, and no remaining relict forest nor cycads were found in the scarce secondary vegetation of the region. At El Socorro ranch, a cultivated *Z. loddigesii* was found growing in the rancher's garden, which we suspect came from the Macuspana region to the west of El Socorro, a known locality for this species.

We can confidently say that no species of *Zamia* were found in or near the two localities of the name Socorro, and no other locality of this name was located within the distribution range of the species examined in this study. Also, no individuals or populations of *Zamia* studied here conform to the original description of *Z. verschaffeltii*. We therefore agree with Schutzman (2004) that *Z. verschaffeltii* and *Z. splendens* are distinct. Because we were unable to find another record of *Z. verschaffeltii* since its publication in 1870, we believe that this species is extinct.

### Taxonomic Treatment

***Zamia katzeriana*** (Regel) E. Retting, *Gartenflora* 45: 148. 1896. *Ceratozamia katzeriana* Regel, *Acta Horti Petrop.* 4: 298. 1876. (Type: ex Horto Katzer, *E. A. Regel s.n.* lectotype: LE, designated by Stevenson & Sabato, 1986).

*Zamia splendens* Schutzman, *Phytologia* 55 (5): 299. 1984. Type: Cultivated in Fairchild Tropical Garden, Miami, accession no. FTG 76-1046, *J. Watson s.n.* (holotype: NY; isotypes: FLAS, FTG, MEXU).

Dioecious plant up to 1.6 m tall; trunk subterranean up to 25 cm long, 7 cm in diameter. Cataphylls chartaceous, semi-deciduous, base triangular, apex aristate, 1.4 cm wide, 5.3 cm long, with yellowish indument. Leaves 1 or 2 (3), adpressed, about 180 × 36–70 cm wide, juvenile leaves bright pink; petiole terete with simple prickles; rachis 35–75 cm long, unarmed, with three to seven leaflet pairs. Leaflets coriaceous, oblong-lanceolate, opposite to subopposite, median leaflets 18–35 × 4.5–12 cm wide, venation inconspicuous, adaxial surface with brilliantly shining cuticle, sessile, base cuneate, apex acuminate, asymmetric, margin denticulate along the distal half, sub-

revolute; articulation 0.6–1.6 cm wide. Microstrobili 1–5, conical, 3.9 cm long, 1.1 cm in diameter, brown tomentulose, apex acute; microsporophyll cuneiform, distal end hexagonal-truncate; peduncle 3.8 cm long, descending, yellowish tomentose. Megastrobilus usually solitary, 8–12 cm long, 4.5–6 cm in diameter, elliptic, brown tomentulose, apex aristate up to 0.8 cm; megasporophylls about 2.6 × 1.5 cm, cuneate-peltate, distal end hexagonal-truncate; peduncle 11–14 cm long, descending, tomentose. Seeds obovoid, 1.2 cm long, 1.8 cm in diameter, sarcotesta pink when immature, red upon maturity.

**Distribution and habitat.** Geographically, the widest distributed species of the complex, occurring in Chiapas, Veracruz, and Tabasco, at elevations of 200 to 700 m in evergreen tropical rain forest. The populations are poorly conserved in their natural state, owing to deforestation for agricultural and pastureland expansion.

### Representative specimens examined. MEXICO.

**CHIAPAS:** San Fernando, *Nicolalde and Pérez Farrera 1420* (XAL), *Palacios 383* (CHIP), *Pérez-Farrera s.n.* (XAL), *Vovides et al. 1266* (XAL), *Walters s.n.* (FTG accession 23-2, XAL); Malpaso, *Gómez-Pompa 705* (MEXU), *Nicolalde et al. 1453* (XAL), *1454* (XAL), *1455* (XAL), *1456* (XAL), *1457* (XAL), *1458* (XAL), *1459* (XAL), *1460* (XAL); Ocozocoautla, *Pérez-Farrera 29* (CHIP, MEXU); Tila, *Vovides et al. 1340* (XAL), *1341* (XAL), *1343* (XAL). **TABASCO:** Macuspana, *Vovides et al. 1344* (XAL), *1345* (XAL); Teapa, *Hernández-Najarro 622* (CHIP), *Pérez-Farrera s.n.* (XAL), *Pérez-Farrera 899* (HEM, MEXU), *Walters s.n.* (FTG accession 12-2, XAL). **VERACRUZ:** Las Choapas, *Martínez & Martínez 825* (HEM), *Nicolalde et al. 1436* (XAL), *1437* (XAL).

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### Appendix 1. Specimens examined

*Zamia cremnophila* Vovides, Schutzman & Dehgan, **MEXICO**. **TABASCO**: *Magaña & Zamudio 343* (MEXU, MO); *Teapa, Pérez-Farrera 900* (HEM, MEXU).

*Zamia lacandona* Schutzman & Vovides, **MEXICO**. **CHIAPAS**: *Palenque, Schutzman 510, 511(XAL), 512 (XAL), 513 (XAL), 514 (XAL), 515 (XAL), 516 (XAL), 517 (XAL), 518 (XAL), 519 (XAL), 520 (XAL), Nicolalde & Martínez 1418 (XAL), Pérez-Farrera 890* (HEM, MEXU), *Walters s.n.* (FTG accession 14-2, XAL); *San Jerónimo Tulija, Chavelas et al. ES=315* (ENCB, MEXU), *Schutzman 521 (XAL), 522 (XAL), 524 (XAL), 523 (XAL), 525 (XAL)*.

*Zamia paucijuga* Wieland, **MEXICO**. **GUERRERO**: *Jose Azueta, Vovides et al. 1426 (XAL); Petatlan, Vovides et al. 1427 (XAL), 1428 (XAL), 1429 (XAL), 1430 (XAL), 1431 (XAL), 1432 (XAL), 1433 (XAL), 1434 (XAL)*; *Unión de Isidro Montes De Oca, Vovides et al. 1416 (XAL), 1417 (XAL), 1418 (XAL), 1420 (XAL), 1421 (XAL)*; *Zihuatanejo, Castillo et al. 6633 (XAL)*. **JALISCO**: *El Arenal, Castillo et al. 9822 (XAL)*; *Cabo Corrientes, Castillo et al. 10147 (XAL), 11733 (XAL), 10280 (XAL), 10466 (XAL)*; *Cuautitlán, Pérez de la Rosa 1039* (IBUG, XAL), *1040* (IBUG, XAL), *1518* (IBUG, XAL); *Nayarit, Vovides et al. 1487, 1488 (XAL), 1489 (XAL), 1490 (XAL), 1491 (XAL), 1493 (XAL)*; *San Sebastián, Nicolalde et al. 1422 (XAL), 1423 (XAL), 1424 (XAL), 1425 (XAL), 1426 (XAL), 1427 (XAL), 1429 (XAL)*, *Pérez de la Rosa 1084* (IBUG, XAL), *1097* (IBUG, XAL), *1098* (IBUG, XAL). **OAXACA**: *Loxicha, Nicolalde et al. 1422 (XAL), 1423 (XAL), 1424 (XAL), 1425 (XAL), 1426 (XAL), 1427 (XAL), 1429 (XAL)*; *Pochutla, Schutzman 544 (XAL), 543*

*(XAL), 545 (XAL), 546 (XAL), 547 (XAL), 548 (XAL), 550 (XAL), 551 (XAL), 552 (XAL), 553 (XAL), 554 (XAL), 555 (XAL), 556 (XAL), 557 (XAL), 558 (XAL), 560 (XAL), 561 (XAL), 562 (XAL), 563 (XAL), 565 (XAL)*; *Puerto Escondido, Walters s.n.* (FTG accession 7-14, XAL).

*Zamia purpurea* Vovides, J. D. Rees & Vázquez-Torres, **MEXICO**. **OAXACA**: *Santa María Chimalapa, Sánchez et al. 40* (B, MEXU); *Santa María Lachixio, Cerón et al. 266 (XAL)*; *San Juan Guichicovi, Walters s.n.* (FTG accession 10-1, XAL). **VERACRUZ**: *Vovides 743 (XAL), Rees et al. 1654 (IEB)*; *Hidalgotitlán, Calzada 8374 (XAL-MEXU)*; *Carranza, Vázquez et al. V-2532 (CHAPA, XAL)*.

*Zamia variegata* Warsz **MEXICO**. **CHIAPAS**: *Ocosingo, Castillo et al. 3884 (XAL), 3885 (XAL)*; *Margaritas, Nicolalde et al. 1443 (XAL), 1444 (XAL), 1445 (XAL), 1447 (XAL), 1448 (XAL), 1449 (XAL), 1451 (XAL) 1452 (XAL)*.

*Zamia verschaffeltii* Miq., **MEXICO**. *Miquel s.n.* (U)

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