



# Karyotype polymorphism in the cycad *Zamia loddigesii* (Zamiaceae) of the Yucatan Peninsula, Mexico

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The cycad *Zamia loddigesii* Miq. forms a morphologically variable complex on the Yucatan peninsula, Mexico. Several diploid chromosome numbers have been found in the species:  $2n = 17, 24, 25, 26$  and  $27$ . Differing karyotypes and chromosome numbers were found in individuals of the same population and the karyotypes differ widely in numbers of metacentric and telocentric chromosomes present. Centrometric fission as well as pericentric inversions and unequal translocations are suggested to be the probable mechanisms for this karyotype variation. There appears to be a correlation between high chromosome number and increasing dryness of the habitats. Coupled with the strongly asymmetrical karyotypes, this suggests that karyotype evolution in *Z. loddigesii* is recent.

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ADDITIONAL KEY WORDS:—Centric fusion/fission – chromosomes – cycads – karyotype evolution.

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## INTRODUCTION

The variability in the chromosome numbers reported for *Zamia* (Norstog, 1980, 1981; Vovides, 1983; Moretti & Sabato, 1984; Moretti, 1990; Moretti *et al.*, 1991), with  $2n = 16–28$ , is unsurpassed by any other cycad genus studied so far. *Zamia* is a neotropical genus of cycads that is distributed from Florida through the Greater Antilles, Mexico, Central America south to Bolivia and Brazil. *Z. loddigesii* Miq. forms a variable complex thought to be of hybrid derivation, with its possible point of origin somewhere on the isthmus of Tehuantepec (Schutzman, 1987; Schutzman, Vovides & Dehgan, 1988). It is distributed throughout most of tropical Mexico and into Guatemala, Belize and Honduras (Anonymous, 1989). We consider this complex to include *Zamia* sp. nov. of Moretti *et al.* (1991) from the Yucatan peninsula. *Z. loddigesii*

has been reported from the Yucatan peninsula by Flores, Narave & Vovides, (1992). Vovides (unpublished) and Norstog (1980) reported *Z. loddigesii* from the Valladolid area of Yucatan with a chromosome number of  $2n = 27$ . Moretti & Sabato (1984) reported centric fission in the related *Zamia paucijuga* along the Pacific coast of Mexico, with the chromosome numbers  $2n = 23, 25, 26, 27, 28$  and strongly asymmetric karyotypes. They suggested that increasing climatic dryness may be a factor influencing chromosome change in *Z. paucijuga*.

During botanical expeditions to the Yucatan peninsula living specimens of *Z. loddigesii* were collected and established at the Jardín Botánico Francisco Javier Clavijero of Xalapa, Veracruz for further study.

#### MATERIAL AND METHODS

Eleven individuals of *Z. loddigesii* from seven localities from the Yucatan peninsula covering the states of eastern Tabasco, Campeche, Yucatan and Quintana Roo were used to obtain karotypes from root-tip mitosis (Fig. 1). Pre-treatment, staining, squash and permanent preparations were done according to Vovides (1983). Scaled

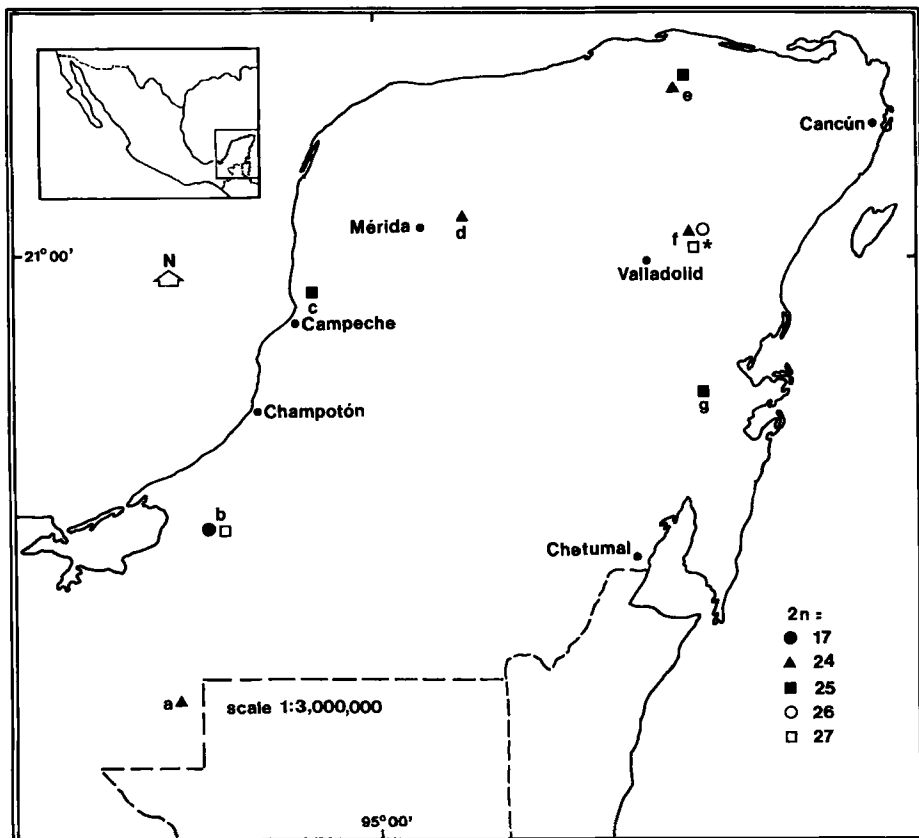


Figure 1 Map of the Yucatan peninsula showing localities of *Zamia loddigesii* studied; (a) Balancán, (b) Champotón, (c) Campeche, (d) Oxcutzab, (e) Xuilub, (f) Valladolid, (g) Chetumal. \*  $2n = 27$  reported by Norstog (1980).

TABLE 1. Locality, Garden accession numbers, voucher numbers and diploid chromosome counts of *Zamia loddigesii* from the Yucatan peninsula, Mexico

State	Garden accession	Voucher	2n
Tabasco (a)	75-005	MO-001	24
Campeche (b)	84-265	MO-008	17
Campeche (b)	84-264	MO-007	27
Campeche (c)	84-222	AV-1254	25
Quintana Roo (g)	80-178	MO-002	25
Yucatan (d)	81.009.02	AV-1255	24
Yucatan (f)	84-262	AV-1253	24
Yucatan (f)	84-263	MO-006	26
Yucatan (e)	85-008.01	MO-009	26
Yucatan (e)	85-008.02	MO-010	25
Yucatan (e)	85-008.03	MO-011	24

a-g, localities (a) Balancán, (b) Champotón, (c) Campeche, (d) Oxcutzcab, (e) Xuilub, (f) Valladolid, (g) Between Chetumal and Cancún.

camera lucida drawings were made from the best metaphase cells obtained using a Zeiss microscope equipped with a 63× planapochromatic objective. The drawings were digitized by the computer program Sigma Scan version 4 and idiograms generated by a non-commercial program developed at the Instituto de Ecología (Fig. 2). Arm length relationships and nomenclature for chromosome morphology were classified according to Levan, Fredga & Sandberg (1964). Vouchers were made from the specimens studied and deposited at XAL (Table 1).

## RESULTS

Table 2 and Figure 2 summarize the findings of this investigation. The distribution of the cytotypes is shown in Figure 1. The eleven specimens of *Zamia loddigesii* studied presented chromosome counts of  $2n = 17, 24, 25, 26$  and  $27$  (Figs 3-7). Two plants from the Champotón area were found to have  $2n = 17$  and  $27$  with karyotypes consisting of  $10M + 4sm + 1st + 2T$  and  $2M + 3sm + 2st + 1t + 19T$  chromosomes respectively (Fig. 2.1, 2.2), where M = metacentric, sm = submetacentric, st = subtelocentric, t = acrocentric, T = telocentric (Levan *et al.*, 1964). One plant from eastern Tabasco in the Balancán area had  $2n = 24$ , the karyotype consisting of  $5M + 4sm + 4st + 4t + 7T$  chromosomes (Fig. 2.3). An individual from Yucatan, municipality of Oxcutzcab had  $2n = 24$ , the karyotype consisting of  $5M + 3sm + 2st + 14T$  chromosomes (Fig. 2.4). Two plants from the municipality of Valladolid, Yucatan presented  $2n = 24$  and  $26$ , with karyotypes consisting of  $5M + 7sm + 1st + 1t + 10T$  and  $9M + 3sm + 2st + 1t + 11T$  chromosomes respectively (Figs 2.5 and 2.6). Three plants from the Xuilub area, Yucatan presented  $2n = 24, 25$  and  $26$ , with karyotypes consisting of  $5M + 1sm + 2st + 1t + 15T$ ;  $4M + 3st + 4t + 14T$  and  $3M + 4st + 4t + 15T$  chromosomes respectively (Figs 2.7-2.9). One plant from Campeche state in the Campeche area presented  $2n = 25$ , the karyotype consisting of  $4M + 2sm + 3st + 1t + 15T$  chromosomes (Fig. 2.10). Finally one plant from Quintana Roo between Cancún and Chetumal presented  $2n = 25$ , the karyotype consisting of  $7M + 4sm + 4st + 1t + 9T$  chromosomes (Fig. 2.11).

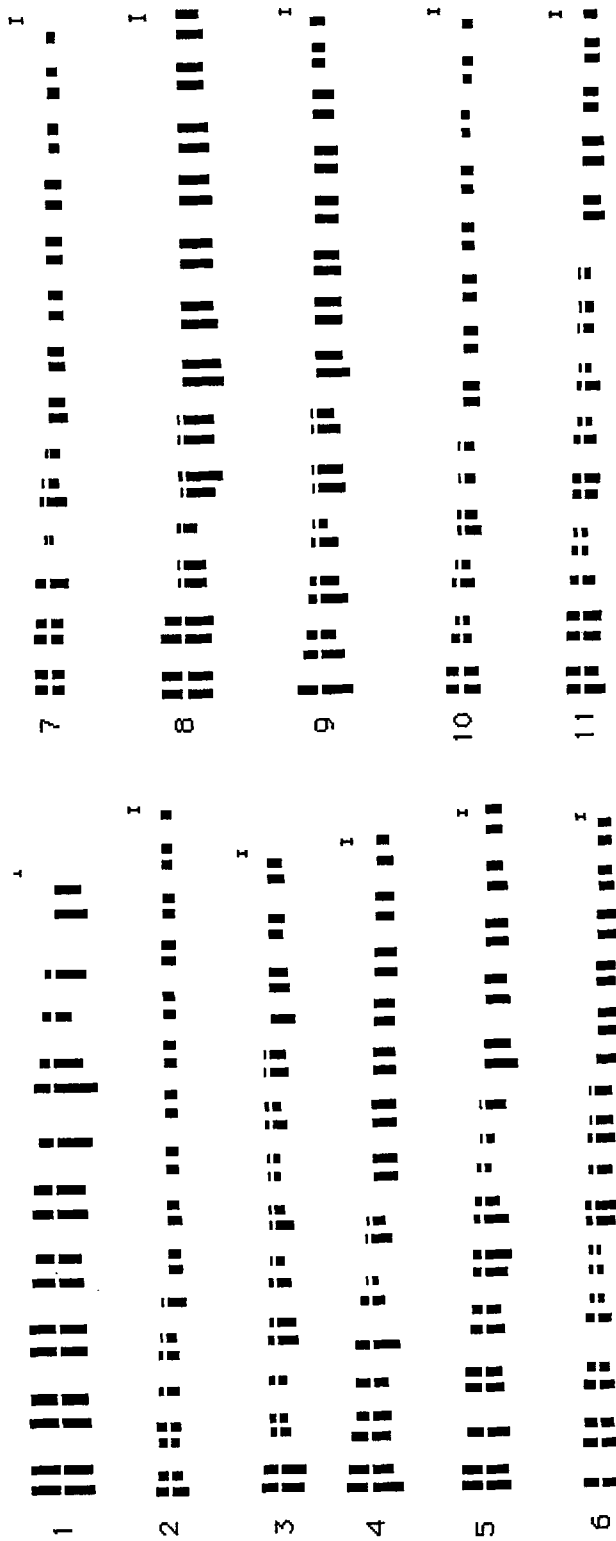


Figure 2. 1-11. Idiograms of *Zamia loddigesii* from different localities on the Yucatan peninsula: 1, Champotón area  $2n = 17$ ; 2, Champotón area  $2n = 27$ ; 3, Balancán  $2n = 24$ ; 4, Oxcutzab  $2n = 24$ ; 5, Valladolid  $2n = 26$ ; 6, Valladolid  $2n = 26$ ; 7, Xutilub  $2n = 25$ ; 8, Xutilub  $2n = 25$ ; 9, Xutilub  $2n = 25$ ; 10, Campeche  $2n = 25$ ; 11, between Cancún and Chetumal  $2n = 25$ . All scale bars = 2  $\mu\text{m}$ .

TABLE 2. Chromosome constitution of *Zamia loddigesii* cytotypes

Metacentrics	Submetacentrics	Subtelocentrics	Acrocentrics	Telocentrics	Total arm No.	2n
10	4	1	—	2	31	17
2	3	2	1	19	35	27
5	4	4	4	7	41	24
5	3	2	—	14	34	24
5	7	1	1	10	38	24
9	3	2	1	11	41	26
5	1	2	1	15	33	24
4	—	3	4	14	36	25
3	—	4	4	15	37	26
4	2	3	1	15	35	25
7	4	4	1	9	41	25

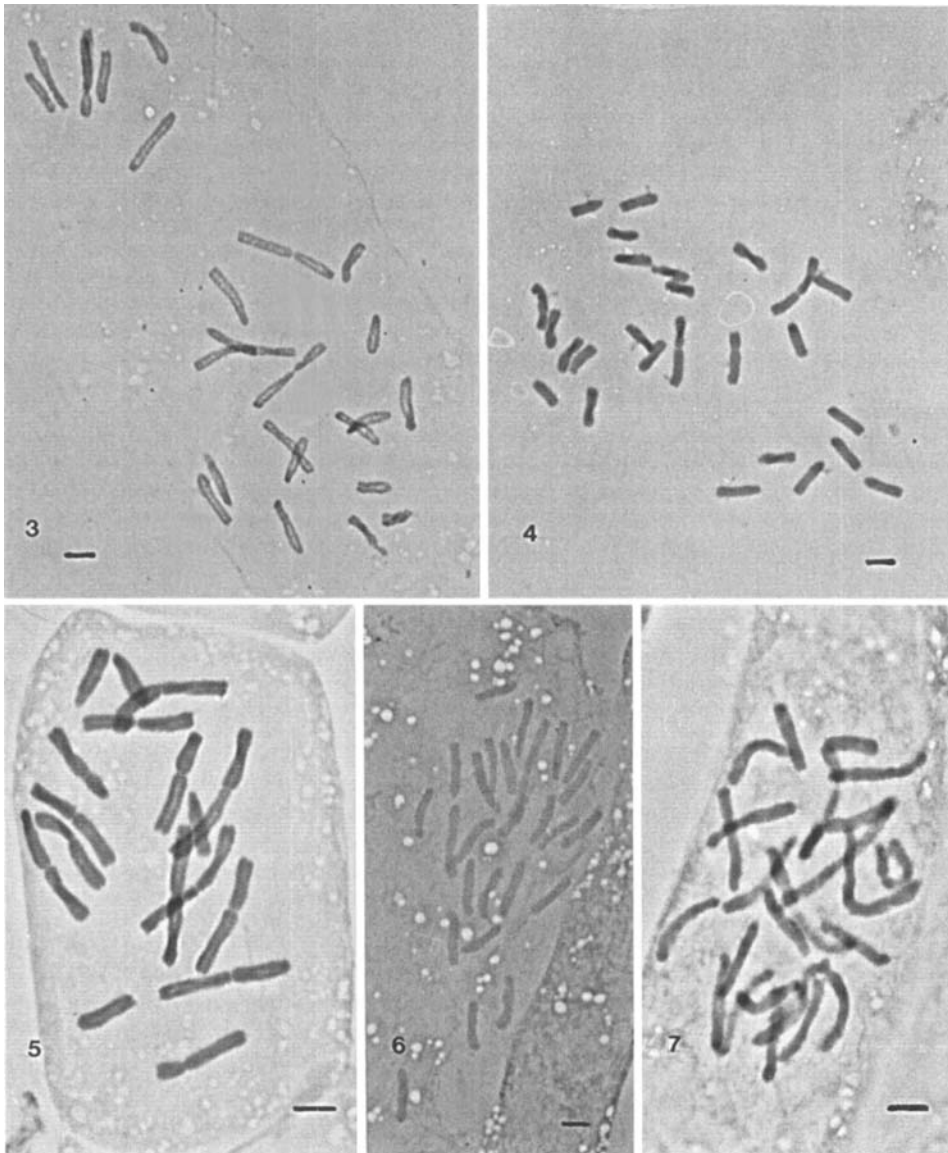
## DISCUSSION

The karyotypes of *Zamia loddigesii* from the Yucatan peninsula are similar to those of *Z. paucijuga* reported by Moretti & Sabato (1984), with  $2n = 23, 25, 26, 27, 28$ , also to those of *Z. roezlii* from Colombia, with  $2n = 22, 24, 25, 26$  (Moretti *et al.*, 1991; Norstog, 1980 [as *Z. chigua*]) and 21, 24, 25 (Vovides unpubl.). They differ from those of *Z. loddigesii*, *Z. furfuracea* (Moretti & Sabato, 1984) and *Z. sparteae* (*Z. loddigesii* var. *angustifolia* of Vovides, 1983) by their higher number of telocentric chromosomes accompanied by a lower number of metacentrics. *Z. loddigesii* on the Yucatan peninsula is morphologically very diverse, especially in leaflet morphology, but no apparent correlation was found between karyotype and external morphology among the differing karyotypes reported from individuals from the same population. True Robertsonian changes (centric fission and fusions) cannot be entirely attributed to the karyotype polymorphism found in the *Z. loddigesii* complex of the Yucatan peninsula, since the total number of chromosome arms was found to be variable, ranging from 31 to 41 (Table 2). Pericentric inversions and unequal translocations probably have been involved as well as Robertsonian changes in this karyotype evolution. Pericentric inversions tend to alter the 'fundamental number' of chromosome arms, since they are capable of moving centromeres to terminal positions, whereas centric fission consists in the transfer of whole arms leaving the 'fundamental number' of arms unchanged (Stebbins, 1971). The importance of inversion heterozygosity in adaptation and evolution has been discussed by Stebbins (1971) and by Rees & Jones (1977).

The present day distribution of chromosome races of the shrew *Sorex araneus* in Great Britain is interpreted to be a product of colonizing radiations and retreats to refugia associated with climatic changes. The number of metacentric chromosomes in the grasshopper *Caledia captiva* was found to be favoured on one side of the hybrid zone of chromosome races of this species during mesic years and the number of acrocentrics favoured during dry years (King, 1993).

We suggest that in *Z. loddigesii* studied, the karyotypes of high diploid numbers confer adaptive advantages in drier localities. This is in agreement with Moretti & Sabato (1984) who suggested that karyotypes with  $2n = 27$  and 28 are of advantage in these localities. Both *Z. loddigesii* and *Z. paucijuga* are found in vegetation types adapted to long dry periods (annual precipitation less than 1500 mm), viz. tropical deciduous forest, tropical thorn forest, as well as in secondary succession states of

these vegetation types and also in nearby areas of subsistence agriculture. The hypogeous and contractile stems of both of these species protect them from fire as well as human-caused disturbance. Graham (1976) reported that near xeric habitats have replaced rain-forests in Veracruz, Mexico since the late Miocene. The onset of drier ecological conditions could have exerted selective pressures resulting in chromosomal changes in some zamias and it is also interesting to note that chromosome numbers in *Zamia soconuscensis* and *Z. cremnophila* are  $2n = 16$  with symmetrical karyotypes (Schutzman *et al.*, 1988). These two species are found in conditions that are ecologically more stable and mesic, their localities coinciding with



Figures 3-7. Representative mitotic metaphase cells of *Zamia loddigesii* from the Yucatan peninsula: Fig. 3,  $2n = 24$ ; Fig. 4,  $2n = 26$ ; Fig. 5,  $2n = 17$ ; Fig. 6,  $2n = 27$ ; Fig. 7,  $2n = 25$ . All scale bars =  $4 \mu\text{m}$ .

the Pleistocene refugia identified by Toledo (1982). There are contrasting reports to this trend in cycads. For example, *Z. roezlii* with chromosome numbers of  $2n = 21, 22, 24, 25$  and  $26$  is from the Chocó district of Colombia with a very high rainfall, and Norstog (1981) related this to primitive characters such as arborescence and equatorial rain-forest habitat. *Zamia inermis*, with  $2n = 16$  and a symmetrical karyotype (Vovides, 1983), is from deciduous tropical forests in central Veracruz subject to long dry periods with average annual rainfall well below 1500 mm. Studies of meiosis would throw more light on the subject of chromosome rearrangements in *Zamia*, but this, coupled with infrequency of production of cones, has been found very difficult to achieve in cycads. This makes inference of ecological relations among cycad species at the karyotypic level a difficult task. Changing climatic conditions may be one of many factors influencing chromosomal changes in *Zamia*, as suggested here.

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#### REFERENCES

- Anonymous.** 1989. Perfil de una planta Salvadoreña: una cica poco conocida *Zamia herrerae* Calderón & Standl. Boletín Informativo Jardín Botánico La Laguna **8**: 4–5.
- Flores JS, Narave H, Vovides AP.** 1992. Gymnospermae. *Etnoflora Yucatanense* **5**: 49. Universidad Autónoma de Yucatán, Mexico.
- Graham A.** 1976. Late Cenozoic evolution of tropical lowland Vegetation in Veracruz, Mexico. *Evolution* **29**: 723–735.
- King M.** 1993. *Species evolution: the role of chromosome change*. Cambridge University Press, New York.
- Levan A, Fredga K, Sandberg AA.** 1964. Nomenclature for centromeric position on chromosomes. *Hereditas* **52**: 201–220.
- Moretti A.** 1990. Cytotaxonomy of cycads. *Memoirs of the New York Botanical Garden* **57**: 114–122.
- Moretti A, Caputo P, Gaudio L, Stevenson DW.** 1991. Intraspecific chromosome variation in *Zamia* (Zamiaceae, Cycadales). *Caryologia* **44**: 1–10.
- Moretti A, Sabato S.** 1984. Karyotype evolution by centromeric fission in *Zamia* (Cycadales). *Plant Systematics and Evolution* **146**: 215–223.
- Norstog K.** 1980. Chromosome numbers in *Zamia* (Cycadales). *Caryologia* **33**: 401–409.
- Norstog K.** 1981. Karyotypes of *Zamia chigua* (Cycadales). *Caryologia* **34**: 255–260.
- Rees H, Jones RN.** 1977. *Chromosome genetics*. London: Edward Arnold.
- Schutzman B.** 1987. Mesoamerican zamias. *Fairchild Tropical Garden Bulletin* **42**: 16–19.
- Schutzman B, Vovides AP, Dehgan B.** 1988. Two new species of *Zamia* (Zamiaceae, Cycadales) from southern Mexico. *Botanical Gazette* **149**: 347–360.
- Stebbins GL.** 1971 *Chromosomal evolution in higher plants*. London: Edward Arnold.
- Toledo VM.** 1982. Pleistocene changes of vegetation in tropical Mexico. In: Prance GT ed. *Biological Diversification in the tropics*. New York: Columbia University Press, 93–111.
- Vovides AP.** 1983. Systematic studies on the Mexican Zamiaaceae. I. Chromosome numbers and karyotypes. *American Journal of Botany* **70**: 1002–1006.