Aldo Moretti* Sergio Sabato*

Mario Vázquez Torres**

The distribution of *Ceratozamia* Brongn. (Zamiaceae)

The Cycadales, representated today by ten genera found in the tropics of both hemispheres, are a relict group of ancient spermatophytes. Only four of the genera are American: *Ceratozamia* Brongn., *Dioon* Lindl., *Microcycas* A. DC. and *Zamia* L., all of the family Zamiaceae. The distribution of these genera was hitherto little known, except for *Microcycas* endemic to Cuba, probably on account of their localized and/or scattered stations. In this connection, however, ECKENWALDER (1980), NORSTOG (1981) and DE LUCA, MORETTI & SABATO (1980) have given recently additional information on *Zamia* and *Dioon* distribution.

The purpose of this paper was to examine the geographical distribution of *Ceratozamia* and to discuss in a preliminary manner the distributional correlations among the American Cycadales.

HISTORY OF THE GENUS

The genus *Ceratozamia* is composed of five recognized species. The genus *Ceratozamia* and the species *C. mexicana* were described by BRONGNIART (1846) from material collected in a

* Istituto di Botanica della Facoltà di Scienze dell'Università di Napoli, via Foria 223, Napoli, Italy.

** Facultad de Ciencias Biológicas, Universidad Veracruzana, Xalapa, Veracruz, México.

not stated locality of Mexico by Ghiesbreght. Later CHAMBERLAIN (1909) bounded the species in the vicinity of Jalapa (Veracruz) and Tuxtepec (Oaxaca) in Mexico and STANDLEY & STEYERMARK (1958) recorded it in the Department of Huehuetenango in Guatemala.

REGEL (1857) described *Ceratozamia kuesteriana* from a plant introduced in cultivation by Karwinski from a not stated locality of Mexico. Following its publication this species was never recorded in the field.

A comprehensive treatment for the genus was published by SCHUSTER (1932), who recognized *Ceratozamia mexicana, C. kuesteriana* and five varieties of the former species.

Since monograph of SCHUSTER three new species from Mexico were added: *Ceratozamia matudai* Lundell (Mt. Ovando, Chiapas) (LUNDELL, 1939); *C. zaragozae* Medellin (Pico El Agujon, San Luis Potosì) (MEDELLIN LEAL, 1963) and *C. hildae* Landry & Wilson (in the vicinity of Xilitla, San Luis Potosì) (LANDRY & WILSON, 1979).

GEOGRAPHICAL DISTRIBUTION OF CERATOZAMIA

The results of our studies on the distribution of *Ceratozamia* are shown in Fig. 1. These data are based on field observations made, in 1971, 74, 79 and 80, in the course of botanical expeditions to Latin America and on localities recorded in herbarium specimens (ARIZ, BH, BM, C, DUKE, ENCB, GH, INIF, LE, M, MEXU, MICH, MO, NY, TENN, TEX, UC, US, WIS, XAL, XALUV and Colegio Superior de Agricultura Tropical, Cárdenas, Tabasco). Herbarium acronyms are defined by HOLMGREN & KEUKEN (1974).

Herbarium specimens examined: MEXICO. CHIAPAS: mt. Ovando, 1 Jan 1937, *E. Matuda s.n.* (UC); mt. Ovando, Dec 1937, *E. Matuda 2087* (MICH); mt. Ovando, Jul 1938, *E. Matuda 2509* (ENCB); northern slopes in broadleaf zone, mt. Ovando, elev. 1000 m, Feb 1939, *E. Matuda 2645* (MICH); mt. Ovando, Feb 1939, *E. Matuda 2646* (GH, MEXU); mt. Ovando, Feb 1939, *E. Matuda 2659* (MICH); Barranca Honda, Siltepec, elev. 1500 m, Oct-Nov

1940, *E. Matuda 4032* (GH, MEXU, MICH, NY); Finca Liquidambar, cerca de Palestina, Sierra de Soconusco, 8 Nov 1945, *E. Hernández X. & A. J. Sharp s.n.* (ENCB); in steep canyon at west end of Laguna Ocotal Grande, Mpio of Ocosingo, elev. 3000 ft, 14 Apr 1967, *D. E. Breedlove 15687* (ENCB, MICH, TEX); steep heavily wooded slope near the Rancho Viejo of the Finca Prusia, Mpio of Angelo Albino Corzo, elev. 2400 ft, 23 Jan 1968, *Alush Shilom Ton 3554* (DUKE, ENCB, TEX, WIS); moist gradual slope with *Quercus, Pinus, Nyssa* and *Liquidambar*, in the paraje of Mahosik, Mpio of Tenejapa, elev. 4800 ft, 24 Apr 1968, *D. E. Breedlove 16173* (MICH). HIDALGO: west slopes of mountain near km 278 on highway north of Jacala, Mpio of Jacala, elev. 1500 m, 29 Oct 1946, *H. E. Moore Jr. 1788* (BH); steep slopes and ledges near km 340-341 on highway below Chapulhuacán, District of Jacala, elev. 2600 ft, 28 Apr 1947, *H. E. Moore Jr. 2718* (BH, GH); steep slopes at Hidalgo-S.L.P. border, km 343-344 on highway below Chapulhuacán, elev. 2100 ft, 19 May 1947, *H. E. Moore Jr. 2888* (BH), (GH); wooded slopes and ledges of calcareous rock above La Placita Nera, km 260 on highway between Zimapán and Jacala, elev. 1600-1700 m, 10 Jul 1948, *H. E. Moore Jr. & C. E. Wood Jr. 3889* (BH); Durango, Mpio Jacala, Eichenwaldgürstel, elev. 2000 m, 3 Apr 1954, *C. Troll s.n.* (M). OAXACA: steep mountain sides ca. 80 km SW of Sola de Vega, seaward side of the pass 25 km above S. Gabriel Mixtepec, Mpio de Juquila, and ca. 30 km S of the Rio Verde crossing at Juchatengo, elev. 1450-1750 m, 11 Feb 1965, *R. McVaugh 22346* (ENCB, MICH); Juquila, 13 Apr 1965, *L. Vela 1574* (*INIF*). PUEBLA: sierras, vicinity of Puebla, 8 Dec 1907, *Bro. G. Arsene 3556* (US). SAN LUIS POTOSÍ: Tamazunchale, in forest hillside, elev. 300 m, Jul 1937, *C. L. Lundell & A. A. Lundell 7235* (MICH); Tamazunchale, on forest on hillside, elev. 300 m, Jul 1937, *C. L. Lundell & A. A. Lundell 7239* (MICH); about 30 mi W of Antiguo Morelos, along highway 80, elev. 4000 ft, 7 Nov 1951, *Mr. & Mrs. Morris Clint M-144* (US); vicinity of Tamazunchale, elev. 2000-5000 ft, Jul 1952, *Mrs. Morris Clint M-273* (US); near Xilitla, elev. 3500-4500 ft, 1954, *Mr. & Mrs. Morris Clint M-517 C* (US); 8 mi W of El Naranjo, oak woods in limestone slopes, elev. 3000 ft, 13 Feb 1960, *M. C. Johnston 5114 A* (MICH, TEX); Potrero del Carnero, Mpio de Rayon, 30 Jun 1962, *F. Medellín Leal 1330* (ENCB, INIF); 19 mi SW of turnoff to El Refugio, 22 Jul 1962, *Elwood Molseed 34* (MEXU, MICH, UC); Pico el Agujon, Sierra de la Equiteria, ca. 30 km SW de Rio Verde, Mpio de Rio Verde, elev. 1800 m, 22 Jul 1962, *F. Medellín Leal 1451* (ENCB, GH, INIF); Pico el Agujón, Sierra de la Equiteria, ca. 30 km SW de Rio Verde, Mpio de Rio Verde, elev. 1300 m, 22 Jul 1962, *F. Medellín Leal 1452* (ENCB, MEXU, MICH); 12 km SE de Tamasopo, 11 Sep 1967, *J. Rzedowski 25471* (ENCB); Canoa, Mpio de Cárdenas, 12 Sep 1967, *J. Rzedowski 24746* (ENCB); Cerro El Agujón, cerca de El Zapote, ca. 30 km SSW de Rio Verde, elev. 1250 m, 13 Apr 1968, *J. Rzedowski 25568* (ENCB, MICH); cascada de Tamasopo, 2 Jun 1968, *F. Medellín Leal s.n.* (ENCB, INIF); Ciudad del Maiz, Ejido Las Abritas, 13 Oct 1968, *H. Puig 3420* (ENCB); San Rafael, Mpio de Aquismon, 10 Feb 1969, *H. Puig 3979* (ENCB); 36.7 mi E of Rio Verde on north side of highway 70, Dec 1977, *N. F. McCarten & R. L. Bittman 2552* (ARIZ). TABASCO: km 36

a Francisco Rueda, Mpio Huimanguillo, elev. 25 m, 22 Feb 1972, *H. Puig 638* (Col. Agr. Trop., Tabasco); km 3 Oeste de Chontalpa, Mpio Huimanguillo, elev. 20 m, 2 Mar 1972, *H. Puig 657* (Col. Agr. Trop., Tabasco); km 3 Ejido Tierra Nueva, Mpio Huimanguillo, elev. 20 m, 4 Mar 1972, *H. Puig 752* (Col. Agr. Trop., Tabasco); km 3 Ejido Tierra Nueva, Mpio Huimanguillo, elev. 20 m, 4 Apr 1972, *H. Puig 751* (Col. Agr. Trop., Tabasco); 3 km Norte Balancan, Mpio Balancan, elev. 25 m, 11 Apr 1972, *H. Puig 788* (Col. Agr. Trop., Tabasco). TAMAULIPAS: Gómez Farías - Ocampo, 30 Apr 1961, *P. S. Martin & C. Saravia 1170* (ENCB); Rancho del Cielo above Gómez Farías, elev. 3600 ft, 5 Dec 1965, *A. J. Sharp, Z. Iwatsuki, S. Sohmer, F. H. Harrison s.n.* (TENN). VERACRUZ: Colipa, Mar 1841, *Liebmann s.n.* (C); Mirador, Nov 1841, *Liebmann 2* (C, MO, UC); Colipa, 1841, *Karwinski 1031* (LE); Paso del Correo - Papantla, Mesa Chica - Paso del Correo, 1841, *Karwinski 1031* (LE); Zacuapam, Apr 1913, *C. A. Purpus 6362* (BM, GH, MO, NY, UC, US); Huatusco, 14 Aug 1932, *C. A. Purpus s.n.* (US); moist shaded rocks, Barranco del Fortin, Zacuapam, Feb 1933, *C. A. Purpus 16225* (C); Zacuapam, May 1935, *C. A. Purpus 16466* (GH); Region of San Andres Tuxtla, near Tapalapan, NW of Santiago Tuxtla, 11 Aug 1953, *R. L. Dressler & Q. Jones 42* (GH); Peak of Cerro Blanco, 2.5 mi W of Tapalapan, elev. 2350 ft, 23 Aug 1962, *R. F. Andrle 64* (US); 2 mi N Ocotal Grande, oak Liquidambar forest, elev. 3000 ft., 21 Jun 1963, *G. M. Ross s.n.* (US); Monte Blanco, Santiago Tuxtla, 12 May 1965, *M. Sousa 2420* (MEXU); El Salto, a S de Chiconquiaco, 13 Apr 1967, *R. Hernández 385 A* (MEXU); cerro El Vigia, Santiago Tuxtla, 29 Aug 1967, *M. Sousa 3201* (MEXU); Sierra de Santa Marta, Santiago Tuxtla, 17 Mar 1968, *M. Sousa 3645* (MEXU); 6.5 km al W de Tlapacoyan, camino a Teziutlán, elev. 900 m, 20 Jun 1970, *Nevling & Gómez-Pompa 1083* (GH); El Esquilón, Mpio de Jilotepec, elev. 1350 m, 7 Dec 1970, *F. Ventura A. 2936* (ENCB, MICH); El Esquilón, Mpio de Jilotepec, elev. 1300 m, 22 Jan 1971, *F. Ventura A. 3014* (ENCB, NY); 5 km NW del Campamento Hermanos Cedillo por el Rio Solosúchil, Hidalgotitlán, 17°16' N. 94°36' W, elev. 150 m, 16 Jan 1975, *Brigada Vázquez 1760* (MEXU, MO, XAL, XALUV); Carretera 22 km de Colipa a Palma Sola, 21 Sept 1976, *J. Rees & A. Bovides, s.n.* (XAL); Tzimentey, Mpio de Huayacocotla, 13 Mar 1980, *J. Palma s.n.* (XAL); BELIZE. DISTRICT OF TOLEDO: vicinity of Sapote Camp, ca. 6.5 mi due W of Medina Bank, on wooded rocky limestone hilltop, elev. 800-1200 ft, 23-27 Apr 1976, *G. R. Proctor 35985* (MO). GUATEMALA: San Andrés, 30 May 1906. *O. F. Cook 51* (US); along road between Chajmayc and Sebol, Dept. Alta Verapaz, elev. 300-500 m, 17 Apr 1942, *J. A. Steyermark 45734* (US); wooded slopes opposite river from Finca Soledad, 5 mi SE of Barillas, Sierra de los Cuchumatanes, Dept. Huehuetenango, elev. 1150 m, 26 Jul 1942, *J. A. Steyermark 49506* (GH, MO, NY, TEX, UC, US); along Rio Amelco, Sierra de los Cuchumatanes below Finca San Rafael, Dept. Huehuetenango, 27 Jul 1942, *J. A. Steyermark 49682* (GH, NY); trail between Catarina and San Andres, Sierra de Los Cuchumatanes, Dept. Huehuetenango, elev. 900-1300 m, 3 Sep 1942, *J. A. Steyermark 51818* (GH, MICH, NY, US).

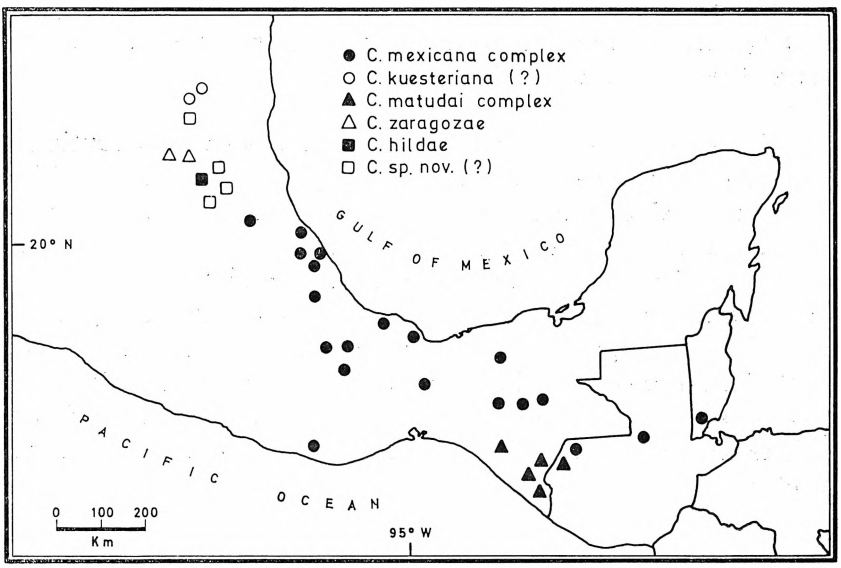

Fig. 1 - Geographical distribution of *Ceratozamia*

Our data point out that distribution of *Ceratozamia* is continuous along a not much wide band from Tamaulipas, San Luis Potosì, Hidalgo, Puebla, Veracruz and Oaxaca which extends, with a hiatus at level of the Isthmus of Tehuantepec, through Chiapas, Tabasco and Guatemala into Belize. The arrangement of the *Ceratozamia* distribution now known reflects that of the mountain systems that run in these regions with prevalently north and south orientation. The only disjunct localities are in the isolated Sierra de los Tuxtlas (Veracruz) near the Gulf of Mexico coast and in the area of Mpio of Juquila (Oaxaca) on the Sierra Madre del Sur near the Pacific coast.

Ceratozamia grows in the understorey of the forest in steep slopes and/or in moist shade rocks at an altitude of 150-2000 m.

The greatest part of the *Ceratozamia* distribution, ranging from Veracruz into Belize, can be referred in gross morphology to the *C. mexicana* complex. Along this area, *Ceratozamia* does not show a considerable range of morphological variation even if the Chiapas, Tabasco and central America populations are well geographically isolated from those of Oaxaca and central Mexico.

The southern part of the distribution is occupied by the *Ceratozamia matudai* complex which centers in southern Chiapas and western Guatemala.

The northeastern part of the *Ceratozamia* distribution is characterized by the occurrence of a high number of taxa. Here, in the inner side of the Sierra Madre Oriental, *C. zaragozae* and *C. hildae* occur. In this area, in southern Tamaulipas, we collected in the vicinity of Tula on the road to Guadalupe, at 1300 m, *Ceratozamia* specimens which, upon examination of types deposited at Leningrad and Utrecht, revealed to be very similar to *C. kuesteriana.* Furthermore we found in San Luis Potosì *Ceratozamia* populations characterized by little size of fronds, leaflets and cones and which we think to be a putative new species.

Discussion and conclusions

Ceratozamia is a more frequent and widespread genus than might have been expected from its initial discovery. Its distribution, even if scattered, is continuous. The disjunct localities of the Sierra de los Tuxtlas (Veracruz) and of the Sierra Madre del Sur (Pacific Oaxaca) suggest that the distribution of *Ceratozamia* was more wide in the past, even if the only one recorded locality in Pacific Oaxaca could be imputed to incomplete collecting in this area.

Irrispective of its wide distribution *Ceratozamia* is a relatively little variable genus. The higher number of taxa, however, observed in the northern part of its distribution could be related to the changed ecological conditions.

In its range *Ceratozamia* overlaps considerably *Dioon* distribution (De Luca, Moretti & Sabato, 1980). Both occur on the Mexico and central America mountains and are confined to the north of the Depression of Nicaragua. *Ceratozamia,* however, does not occur on Sierra Madre Occidental and its distribution on Pacific side northwards does not get over the Oaxaca re-

gion. This seems in close relation to the less moist conditions which occur in north Pacific side of Mexico (RZEDOWSKI, 1978). From an ecological point of view, *Ceratozamia* differs from *Dioon*; the former grows in the understorey of the forest or in moist shade habitat while the latter prefers more open areas and occurs also in xeric habitats.

Ceratozamia and *Dioon* evolved probably from tertiary ancestors distributed in this part of the continent. In particular, as regard *Ceratozamia*, its occurrence in these territories dates from lower Miocen as stated by pollen analysis of sediments in Chiapas (RZEDOWSKI & PALACIOS CHÁVEZ, 1977).

Ceratozamia and *Dioon* show a restricted distribution and probably a different centre of origin in respect of *Zamia*. *Zamia* occurs in both tropics ranging from Florida to Perù and keeps its most primitive specie, *Zamia chigua* (NORSTOG, 1981), distributed in the southern hemisphere (Colombia).

ACKNOWLEDGMENTS

We are very grateful to Prof. Ruggero Tomaselli of the Istituto e Orto Botanico, University of Pavia (Italy), who led us in 1971 and 1980 during botanical expedition to Mexico. Special thanks are due to Dr. K. Norstog of the Fairchild Tropical Garden (Miami, U.S.A.) and Dr. J. Rzedowski of the Escuela Nacional de Ciencias Biólogicas, IPN, Mexico D. F. (Mexico), who gave us precious suggestions for this work. We are also indebted to the following herbaria and institutions for their courtesy in providing specimens or photograph: ARIZ, BH, BM, C, DUKE, ENCB, GH, INIF, LE, M, MEXU, MICH, MO, NY, TENN, TEX, UC, US, WIS and XAL. Thanks are due also to Colegio Superior de Agricultura Tropical, Cárdenas, Tabasco. This research has been supported by Accademia Nazionale dei Lincei (Italy).

SUMMARY

The distribution of *Ceratozamia*, an American cycad, is provided. The distribution ranges from Tamaulipas, San Luis Potosì, Hidalgo, Puebla, Veracruz and Oaxaca and it extends, with a hiatus at level of the Isthmus of Tehuantepec, through Chiapas, Tabasco and Guatemala into Belize. *Ceratozamia* grows in the understorey of the forest in steep slopes at an altitude of 150-2000 m. A preliminary discussion on distributional correlations among the American cycads is given. *Ceratozamia* and *Dioon* overlap to a great extent their distribution and southwards do not get over the Depression of Nicaragua. *Zamia*, on the contrary, occurs in both tropics and *Microcycas* is endemic to Cuba.

RIASSUNTO

Gli Autori hanno studiato l'areale di *Ceratozamia*, un genere americano di Cycadales. L'areale di *Ceratozamia* è risultato molto più ampio di quanto ritenuto finora, estendendosi dal Messico (Tamaulipas, San Luis Potosì, Hidalgo, Puebla, Vcaerurz, Oaxaca, Chiapas e Tabasco) fino al Guatemala e Belize. L'areale si presenta continuo, con l'eccezione di stazioni disgiunte della Sierra de los Tuxtlas (Veracruz) e della Sierra Madre del Sur (Oaxaca). La distribuzione riflette l'andamento dei principali rilievi di questi territori. L'habitat è quello di sottobosco di foreste umide tra i 150-2000 m di altezza. Il confronto con la distribuzione degli altri generi di Cycadales americani ha mostrato che l'areale di *Ceratozamia* coincide in gran parte con quello di *Dioon*; entrambi hanno distribuzione limitata alla fascia tropicale a nord della Depressione del Nicaragua. La distribuzione di *Zamia*, invece, riguarda le fasce tropicali di entrambi gli emisferi e quella di *Microcycas* è ristretta all'isola di Cuba.

LITERATURE CITED

BRONGNIART M. A. D., 1846. *Note sur un nouveau genre de Cycadées du Mexique.* Ann. Sci. Nat., troisieme series: 5-9.

CHAMBERLAIN C. J., 1909. *Morphology of Ceratozamia.* Bot. Gaz., **53** (1): 1-19.

DE LUCA P., MORETTI A., SABATO S., 1980. *Distribuzione e tassonomia del genere Dioon* (*Zamiaceae*). Giorn. Bot. It., **114** (3-4): 129-130.

ECKENWALDER J. E., 1980. *Taxonomy of the West Indian cycads.* J. Arnold Arbor., in press.

HOLMGREN P. K., KEUKEN W., 1974. *Index Herbariorum, Ed. 6.* Oosthoek, Scheltema and Holkema, Utrecht.

LANDRY C. P., WILSON M. C., 1979. *A new species of Ceratozamia* (*Cycadaceae*) *from San Luis Potosì.* Brittonia, **31** (3): 422-424.

LUNDELL C. L., 1939. *Cycadaceae.* In: *Studies of Mexican and Central American plants - VII.* Lloydia, **2** (2): 75-76.

MEDELLIN LEAL F., 1963. *A new species of Ceratozamia from San Luis Potosì.* Brittonia, **15**: 175-176.

NORSTOG K., 1981. *Chromosome numbers in Zamia* (*Cycadales*). Caryologia, in press.

REGEL E., 1857. *Zwei neue Cycadeen.* Bull. Soc. Nat. Mosc., **30**: 187.

RZEDOWSKI J., PALACIOS CHÁVEZ R., 1977. *El bosque de Engelhardtia* (*Oreomunnea*) *mexicana en la region de la Chinantla* (*Oaxaca, Mexico*). *Una reliquia del Cenozoico.* Bol. Soc. Bot. Mex., **36**: 93-118.

RZEDOWSKI J., 1978. *Vegetacion de Mexico.* Editorial Limusa, Mexico.

SCHUSTER J., 1932. *Cycadaceae.* In: *Das Pflanzenreich. IV, 1.* (*99*). Engelmann, Leipzig, 1-168.

STANDLEY P. C., STEYERMARK J. A., 1958. *Flora of Guatemala.* Fieldiana, Bot., **24** (1): 11-20.