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A phytogeographical approach to the New World cycads

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Riassunto

Sono presentate la distribuzione e l'ecologia delle Cycadales americane. *Dion* è distribuito in Messico e in Honduras; *Ceratozamia* è distribuita in Messico, Guatemala e Belize; *Microcycas* è endemica di Cuba; *Zamia* è distribuita in Georgia e Florida (U.S.A.), Grandi Antille, Bahamas, Messico, America centrale, Colombia, Venezuela, Ecuador, Perù, Brasile e Bolivia.

L'attuale distribuzione, le affinità tra *Ceratozamia, Microcycas* e *Zamia,* i reperti fossili e la storia geologica dell'America suggeriscono che i progenitori dei moderni generi di Cycadales americane furono isolati in Nord America nel tardo Mesozoico. *Zamia* fu probabilmente isolata nelle Indie occidentali mediante migrazione verso est della catena di isole vulcaniche presenti durante il Cretaceo tra il Nord e Sud America. Questo arco di isole vulcaniche rese possibile la diffusione di *Zamia* in Sud America durante il medio ed il tardo Cretaceo. *Microcycas* rimase isolata in Cuba probabilmente per gli stessi eventi che isolarono *Zamia* nelle Indie occidentali.

INTRODUCTION

The cycads (Cycadales) are an ancient group of seed plants confined to the tropics and subtropics of both Hemispheres. The present cycads are considered to be a monophyletic group by their anatomy, morphology and chemistry. In particular, cycasin, a MAM (methylazoxymethanol) glycoside, is characteristic of, and exclusive, to the cycads (DE LUCA *et al.*, 1980).

Key Words: *Cycadales* of the New World, distribution, origin.

The order Cycadales may be classified into four families (STEVENSON, 1981): Boweniaceae, with *Bowenia* (2 sp.) endemic to Australia; Cycadaceae, with *Cycas* (approx. 20 sp.) distributed from Madagascar and throughout south-east Asia and tropical Australia to the western Pacific; Stangeriaceae, with *Stangeria* (1 sp.) endemic to southern Africa; and Zamiaceae, further subdivided into three tribes: Dioeae, with *Dion* (10 sp.) distributed in America, Encephalarteae, with *Encephalartos* (approx. 40 sp.) endemic to Africa, *Lepidozamia* (2 sp.) and *Macrozamia* (14 sp.) endemic to Australia, Zamieae, with *Ceratozamia* (9-10 sp.), *Microcycas* (1 sp.), and *Zamia* (approx. 30 sp.) distributed in America.

In the last 15 years, we have spent considerable time in Latin America, in particular in Mexico, in order to study the distribution and ecology of New World cycads. One of us paid special attention to the vegetational features of Mexico and mapped the more important vegetational formations (BALDUZZI & TOMASELLI, 1978).

In the present paper, we report on the distribution of the New World cycads and present some observations on the ecology of the Mexican taxa. The classification of the vegetational formations is based both on the one proposed by BALDUZZI & TOMASELLI (1978) and on the one proposed by RZEDOWSKI in his Vegetación de México (1978). However, we emphasized the latter because it is more familiar, at the present, to the students of Mexican vegetation. The vegetational types by BALDUZZI & TOMASELLI are listed parenthetically.

Finally we discuss the origin of the New World cycads on the basis of the fossil record and continental drift.

DISTRIBUTION AND ECOLOGY

The results of our studies on the distribution of *Dion, Ceratozamia, Microcycas,* and *Zamia* are shown in Figs. 1-4. These data are based primarily on field observations made in 1969, 71, 74, 79, 80, 81, 83, in the course of botanical expeditions to Latin America. The South American and Central American data

on the distribution of *Zamia* are based mostly on localities recorded from herbarium specimens.

Dion (Fig. 1)

The genus *Dion* Lindley includes 10 species and is distributed between the 15° and 29° latitude in Mexico and Honduras. Despite its wide distribution, *Dion* plants are generally very scattered and form small communities which rarely if ever play an important role in the vegetation. Only in some regions, such as San Luis Potosí, Tamaulipas and Nuevo León does it sometimes become common and abundant. However, the bulk of the genus is concentrated in communities of primary vegetation and is generally restricted to rocky, steep hillsides with poor soils.

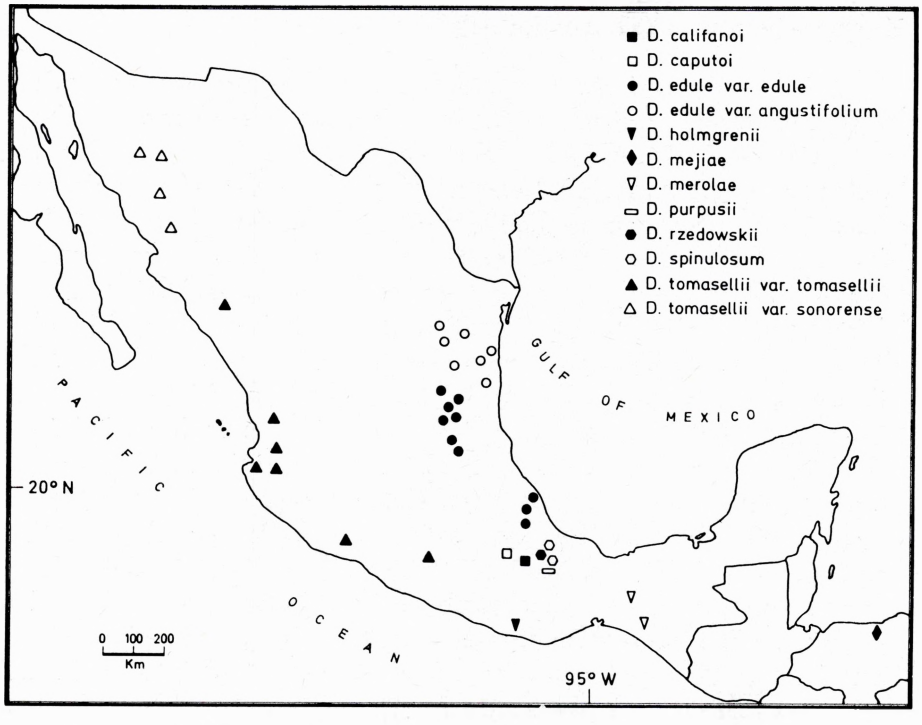

Fig. 1. - Distribution of *Dion*.

Dion edule Lindley with two varieties is endemic to eastern Mexico where it is distributed through the Sierra Madre Oriental from Veracruz to Nuevo León and in disjunct stations in Tamaulipas (De Luca *et al.*, 1982a). Var. *edule* is distributed in the south and middle of the range and is centered in two areas: central Veracruz; and northern Hidalgo, Querétaro, San Luis Potosí and southern Tamaulipas. It occurs primarily in habitats transitional between Bosque Tropical Subcaducifolio (Evergreen Broad-Leaved Forest with 25-50% deciduous or semideciduous trees) and Bosque de *Quercus* (Oak Forest) at 500 to 1500 m. *Ceratozamia* and *Zamia* are often associated in Querétaro and San Luis Potosí. Var. *angustifolium* Miq. is distributed in the north of the range in Tamaulipas and Nuevo León and is centered in two areas: in the Sierra Madre Oriental; and in the Sierra de San Carlos, Sierra de Tamaulipas and low hills in the vicinity of Soto la Marina, Tamaulipas. It occurs between 200 and 1500 m in habitats transitional between Bosque Tropical Subcaducifolio and Bosque de *Quercus* (Oak Forest), and in Bosque Espinoso (Thorn Forest).

Dion tomasellii De Luca, Sabato & Vázquez Torres with two varieties is endemic to western Mexico and occurs in the Sierra Madre del Sur and in the Sierra Madre Occidental from Guerrero northwards to Sonora. Var. *tomasellii* ranges from Guerrero to Durango in habitats of Bosque de *Quercus* (Oak forest and Pine-Oak Forest) at 600 to 1850 m. *Zamia* occurs in the station of Cabo Corrientes, Jalisco. Var. *sonorense* ranges from northern Sinaloa to central Sonora in habitats transitional between Bosque Tropical Caducifolio (Deciduous Broad-Leaved Forest) and Bosque de *Quercus* (Oak Forest) at 600 to 1200 m. *D. caputoi* De Luca, Sabato & Vázquez Torres is localized in the Sierra Mixteca, southern Puebla, where it is restricted to a very small area in habitats transitional between Bosque Tropical Caducifolio and Bosque de *Quercus* (Oak Forest) at 1800 to 2000 m. *D. califanoi* De Luca & Sabato is distributed in the Sierra del Norte de Oaxaca at the border between Oaxaca and Puebla in habitats transitional between Bosque Tropical Caducifolio and Bosque de *Quercus* (Oak Forest) at 1800 to 2500 m. *D. purpusii* Rose is known only for Tomellin cañon in northern Oaxaca where it occurs in Bosque Tropical Caducifolio at 1350 m

(De Luca *et al.*, 1979). *D. holmgrenii* De Luca, Sabato & Vázquez Torres is localized in southern Oaxaca along the Pacific side of Sierra Madre del Sur and occurs in a very restricted area in Bosque de *Quercus* (Pine-Oak Forest) at 650 to 850 m. *D. merolae* De Luca, Sabato & Vázquez Torres occurs in northwestern Chiapas in the region of the Sierra Madre in habitats of Bosque Tropical Subcaducifolio and Bosque de *Quercus* (Pine-Oak Forest) at 900 to 1200 m. *D. spinulosum* Dyer is distributed in Atlantic side of Oaxaca and in Veracruz in lowlands and hills at the foot of the Sierra de Oaxaca (0-300 m) in Bosque Tropical Perennifolio (Evergreen Broad-Leaved Forest). *D. rzedowskii* De Luca, Moretti, Sabato & Vázquez Torres occurs in a very restricted area of the Sierra de Oaxaca in habitats of Bosque Tropical Subcaducifolio at 450-600 m. *Ceratozamia* and *Zamia* occur in the vicinity of *D. rzedowskii* in the station of San Bartolomé Ayautla. *D. mejiae* Standley & Williams occurs in northern Honduras where it has been found wild in a dry rocky canyon in the Departamento de Olancho (Standley & Williams, 1951).

Ceratozamia (Fig. 2)

The genus *Ceratozamia* Brongniart includes 9-10 species and is distributed between the 15° and 23° latitude in Mexico, Guatemala, and Belize. *Ceratozamia* is generally scattered and forms small communities commonly restricted to the understory of the forest in steep slopes and/or in moist shade rocks at 0 to 2000 m.

Ceratozamia mexicana Brongniart is the most widespread species of the genus. It is distributed in Mexico (San Luis Potosí, Hidalgo, Puebla, Veracruz, Oaxaca, Tabasco, and Chiapas), Guatemala and Belize (Moretti *et al.*, 1980). *C. mexicana* occurs in disjunct stations in the Sierra de los Tuxtlas, Veracruz, and in the Sierra Madre del Sur, Oaxaca. The latter locality represents the northern limit of the genus in the Pacific side of Mexico. The populations from southern Veracruz, Oaxaca, Chiapas, Guatemala, and Belize are often attributed to the var. *robusta* (Miq.) Dyer (Vovides *et al.*, 1983) because of the greater dimensions of their trunks, leaves and cones. The populations from the nor-

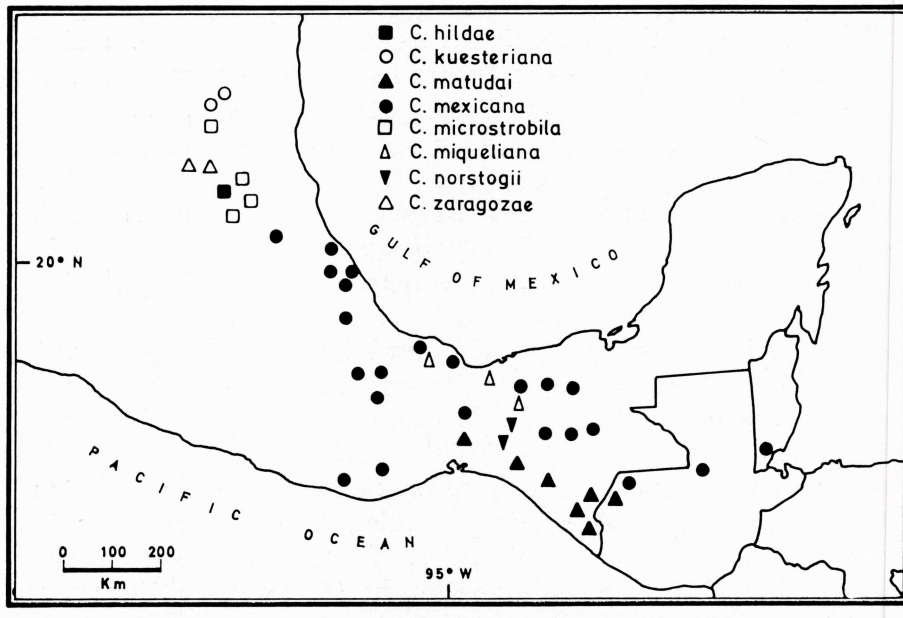

Fig. 2. - Distribution of *Ceratozamia.*

thern range of the distribution occur in habitats of Bosque Mesófilo de Montaña (Deciduous Broad-Leaved Cloud Forest) at 800 to 1850 m. The populations from the southern range occur in habitats of Bosque Tropical Perennifolio to Bosque Mesófilo de Montaña at 100 to 1300 m. *C. kuesteriana* Regel occurs in a very restricted area in southern Tamaulipas at the extreme northern portion of the range of *Ceratozamia* (MORETTI *et al.*, 1982). It occurs in the Sierra Madre Oriental in habitats transitional to the Bosque Mesófilo de Montaña at 1200 to 1800 m. *C. zaragozae* Medellín Leal is endemic to San Luis Potosí and occurs in the Sierra La Equiteria in habitats of Bosque de *Quercus* (Pine-Oak Forest) at 1250 to 1850 m. *C. microstrobila* Vovides & Rees is distributed in San Luis Potosí in habitats transitional between Bosque Tropical Caducifolio and Bosque de *Quercus* (Oak Forest) at 750 to 1300 m. *C. hildae* Landry & Wilson occurs in southern San Luis Potosí and eastern Querétaro; in Querétaro it has been found wild in habitat of Bosque de *Quercus* (Oak Forest) at 800-900 m (VOVIDES & REES, 1980). *C. miqueliana*

Wendland occurs in southern Veracruz and northern Chiapas in habitats of Bosque Tropical Perennifolio and in habitats transitional between Bosque Tropical Perennifolio and Bosque Tropical Caducifolio. *C. norstogii* Stevenson is localized at the border between Chiapas and Oaxaca in habitats of Bosque Mesófilo de Montaña. *C. matudai* Lundell is distributed in southern Mexico and northern Guatemala. It occurs in the Sierra Madre de Chiapas and in the Sierra de Chimalapa, Oaxaca, in habitats of Bosque Tropical Perennifolio, Bosque de *Quercus* (Pine-Oak Forest), and Bosque Mesófilo de Montaña at 450 to 1200 m.

Microcycas and *Zamia* (Figs. 3, 4)

Microcycas A.DC., a monotypic genus, is endemic to Cuba. It occurs in the Cordillera de los Organos in Western Cuba.

The genus *Zamia* L. is the most widespread cycad genus in America. It is distributed between the 30° parallel N and the 18° parallel S. *Zamia* occurs in Georgia, Florida (U.S.A.), the West Indies with the exception of the Lesser Antilles, Mexico, Central America, Colombia, Venezuela, Ecuador, Peru, Brazil and Bolivia. Its distribution is well known in Northern America, the West Indies, and Mexico whereas it is poorly known in the rest of Central and Southern America, especially in the Amazonia.

The taxonomy of *Zamia* is at best very confused. SCHUSTER (1932) lists 26 species, CHAMBERLAIN (n.d.) includes 29 species in the genus, NORSTOG (1980) estimates the species of *Zamia* to number ca. 30. Recently, ECKENWALDER (1980) has reduced 35 entities from the West Indies, accounting for about 40 percent of the names proposed in the genus, to synonymy with *Z. pumila* L.

Z. pumila with two varieties is the sole native cycad of the Greater Antilles, the Bahamas, Florida and southern Georgia (ECKENWALDER, 1980). *Z. pumila* subsp. *pygmaea* (Sims) Eckenwalder is endemic to western Cuba and Isla de Pinos. Ca. 20 species are distributed in Mexico and Central America; ca. 10 species are distributed in southern America. No species of *Zamia* extends its range beyond the limits of each American subcon-

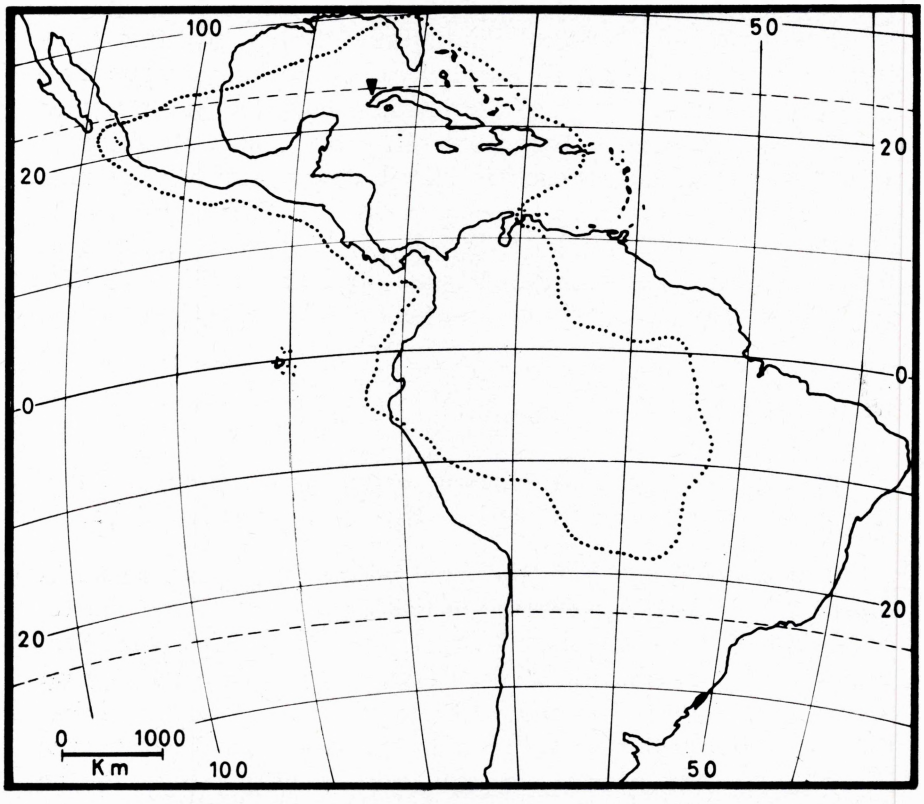

Fig. 3. - Distribution of *Microcycas* (triangle) and *Zamia* (dashed line).

tinent. According to NORSTOG (1980), *Z. chigua, sensu* NORSTOG, (= *Z. roezli* Regel ex Andrè) from Colombia is the most primitive member of the genus.

Zamia occurs in a variety of habitats ranging from open sea bluffs and sand dunes to closed tropical forests. *Z. chigua, sensu* NORSTOG (1980), a Colombian species, inhabits the low, swampy islands of the San Juan delta, where it grows just above the mangrove belt (NORSTOG, 1976). The ecological range is very wide, i.e. *Z. paucijuga* Wieland lives in dry habitats in western Mexico with average annual rainfall of about 1000 mm; *Z. madida* Schultes (= *Z. manicata* Linden ex Regel) lives in the extraordinarily humid forests of the Golfo de Urabá area of northwestern Co-

lombia, receiving between 4500 to 5400 mm of rain a year (SCHULTES, 1958).

As regards Mexico (Fig. 4), *Zamia* is distributed in southern and central regions. *Zamia* has its northern limit at southern Tamaulipas on the Atlantic side and at Nayarit on the Pacific side. *Zamia* occurs also on María Cleofas Island, one of the Tres Marías Islands, localized in the Pacicific Ocean off the coast of Nayarit. The systematics of Mexican *Zamia* spp. is incomplete, especially in southern Mexico.

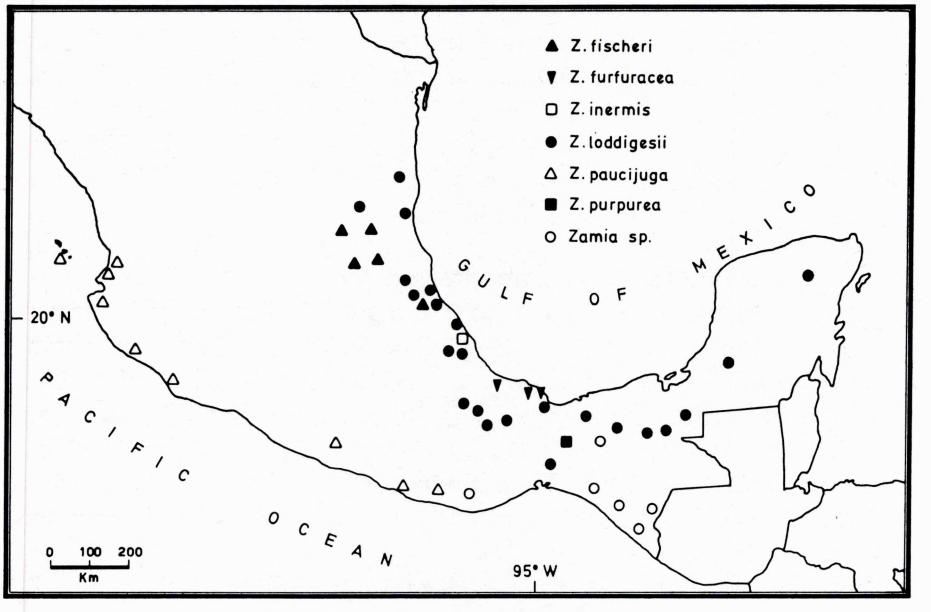

Fig. 4. - Distribution of *Zamia* in Mexico.

Zamia loddigesii Miq. is distributed on the Atlantic side from Tamaulipas southwards to Tabasco, and may occur in Chiapas, the Yucatán Peninsula and Central America. It occurs in habitats of Bosque Tropical Caducifolio, Bosque de *Byrsonima, Curatella* y *Crescentia* (Tropical Savanna with *Byrsonima, Curatella* and *Crescentia*) at sea level to 1000 m. *Z. paucijuga* is distributed from Oaxaca to Nayarit along the Pacific coast. It

occurs also in María Cleofas Island. It has been found in habitats of Bosque de *Quercus* (Pine-Oak Forest) (Nayarit, Jalisco, Guerrero, Oaxaca), Bosque Tropical Subcaducifolio (María Cleofas Island, Nayarit, Colima, Michoacán, Oaxaca). *Z. fischeri* Miq. is distributed in Querétaro, San Luis Potosí, and Veracruz. It occurs in habitats of Bosque de *Quercus* (Pine-Oak Forest) or transitional between Bosque Tropical Caducifolio and Bosque de *Quercus* (Pine-Oak Forest) at 750 to 900 m. in San Luis Potosí and Querétaro and in Bosque Tropical Perennifolio at 180 m in Veracruz (VOVIDES *et al.*, 1983). *Z. inermis* Vovides, Rees & Vázquez Torres is known only from one locality of Veracruz where it occurs in habitats of Bosque Tropical Caducifolio at 200-300 m. *Z. furfuracea* L. f. is distributed in the coastal region of southern Veracruz in habitats of Bosque Tropical Caducifolio, sand dunes, Palmar (Tropical Savanna with Palms) between a few meters above sea level to 50 m. *Z. purpurea* Vovides, Rees & Vázquez Torres is known only in southern Veracruz in habitats of Bosque Tropical Perennifolio at 100-150 m.

Despite the fact that *Dion*, *Ceratozamia* and *Zamia* are sympatric in Mexico, they occur in the same stations only in some regions (San Luis Potosí, Querétaro, Oaxaca). Moreover, their distribution is very different on the Pacific side of Mexico. On the Pacific side, *Ceratozamia* has its northern limit in Oaxaca, *Zamia* in Nayarit, *Dion* in central Sonora. On the Atlantic side, *Ceratozamia* and *Zamia* have their northern limits in southern Tamaulipas, whereas *Dion* extends its limit more northerly to Nuevo León.

The asymmetrical distribution of the Mexican cycads appears to be closely related to the climatic asymmetry occurring between the Pacific and Atlantic sides in Mexico (RZEDOWSKI, 1978). This is in large part due to the influence of the dominant winds (trade winds) and is connected to the occurrence of a notable increase in the aridity in Mexico along the direction SE to NW. Moreover the Sierra Madre Occidental, Eje Volcánico Transversal and Sierra Madre del Sur, which run N to S, represent a strong obstacle to the cold northern air masses. Thus, the Pacific side, more protected by these mountain systems, is generally warmer in the winter than the Atlantic side.

The distribution of *Dion, Ceratozamia* and *Zamia* in Mexico reflect their ecology. *Dion* has a wide ecological range but most of the species are restricted to arid or xeric habitats. *Zamia* is the more thermophilic genus and it is restricted in general, to the coastal belt in moist stations. *Ceratozamia* has a narrow ecological range and is restricted to stations where the moisture is high.

Most habitats of the Mexican cycads are included in the following formations:

a) Tropical Formations: Bosque Tropical Perennifolio, Bosque Tropical Subcaducifolio, Bosque Tropical Caducifolio (RZEDOWSKI, 1978) which are consistent with Evergreen Broad-Leaved Forest, Evergreen Broad-Leaved Forest with 25-50% deciduous or semideciduous trees, and Deciduous Broad-Leaved Forest (BALDUZZI & TOMASELLI, 1978).

b) Montane Formations: Bosque Mesófilo de Montaña (RZEDOWSKI, 1978) consistent with Deciduous Broad-Leaved Cloud Forest (BALDUZZI & TOMASELLI, 1978); Bosque de *Quercus* of RZEDOWSKI (1978) which includes both the Oak Forest and Pine-Oak Forest (with exclusion of the coldest localities) of BALDUZZI & TOMASELLI (1978).

Although these formations are very different from a physiognomic and floristic point of view, they have in the understory similar micro-environmental conditions. In particular, atmospheric moisture appears to be the principal ecological factor. This is especially significant in the typical formation of warm, xeric climates in bottom of canyons with steep sides and in rocky shaded areas.

THE FOSSIL RECORD

The fossil record for cycads in America can be traced back to the Permian and possibly into the upper Pennsylvanian (TAYLOR, 1981). For the Palaeozoic, MAMAY (1976) described two lower Permian megasporophylls that occur in Lower Leonardian rocks of Kansas and Texas: *Phasmatocycas* and *Archaeocycas* respectively. For the Mesozoic, DELEVORYAS & HOPE (1971) descri-

bed the new genus *Leptocycas* from Late Triassic deposits of the Pekin Formation of North Carolina. Although *Leptocycas* is the only attempt at reconstructing an entire American cycad, other remains are known from Mesozoic deposits. One of these is *Lyssoxylon gribsbyii* Daugherty, a petrified Triassic stem known from the Chinle Formation of Arizona and New Mexico (Gould, 1971). Another silicified Triassic stem that is believed to be a cycad is *Michelilloa waltonii* Archangelski & Brett (1963) from the Ischigualasto Formation in northern Argentina.

Among the taxa represented by leaves, *Mesodoscolea* Archangelski, from southern Argentina, appears of great phytogeographical interest because it has been included in the Stangeriaceae (ARCHANGELSKI & PETRIELLA, 1969) whose sole living member is *Stangeria,* a plant endemic to southern Africa.

Dion, Ceratozamia and *Zamia* are represented in the Cenozoic fossil flora of America, whereas there is no record for *Microcycas. Dion* and *Zamia* fossils consist of leaves while *Ceratozamia* consists of pollen grains. *Dion* has been found in Paleocenic deposits in Alaska (HOLLICK, 1932; WOLFE, 1972) and in Miocene of California (AXELROD, 1975). *Ceratozamia* has been found in Miocenic deposits of Mexico (RZEDOWSKI & PALACIOS, 1977). *Zamia* is reported from the Paleocene of Alaska, Lower Eocene of Tennessee, Louisiana, Mississippi, Upper Eocene or Oligocene of Porto Rico, Oligocene? of Colombia, Oligocene or Lower Miocene of Patagonia (Argentina), Lower (?) Miocene of Chile, and Late Tertiary (Pliocene?) of Brazil (HOLLICK, 1932).

Menucoa Petriella (1969) (Lower Tertiary) (?) and *Bororoa* Petriella (1972) (Paleocene) are two petrified trunks described from southern Argentina which for the polyxylic structure have been closely related to the Cycadaceae and Zamiaceae (Encephalarteae) respectively, rather than to the American Zamiaceae (PETRIELLA, 1969, 1972, 1981).

ORIGIN OF THE NEW WORLD CYCADS

In order to discuss the causes which determined the present distribution and origin of the New World cycads, it is useful

to outline the geological history of Mesoamerica and the Caribbean region from the initial breakup of Pangaea. In the Permian when the first Cycadales arose (MAMAY, 1976) until the Early Jurassic, the entire region of North America-South America-Africa was one landmass as part of the super-continent of Pangaea. During the Mesozoic, (by the Middle Jurassic time) the continents began to separate. By the Early Cretaceous North America and South America were separated. In the Middle to Upper Cretaceous, the gap between the North and South American subcontinents was beginning to diminish (CONEY, 1982) due to the formation of a series of volcanic islands which formed an Archipelago between Honduras and Colombia (Fig. 5). Beginning in the Turonian (90 million years BP) parts of these

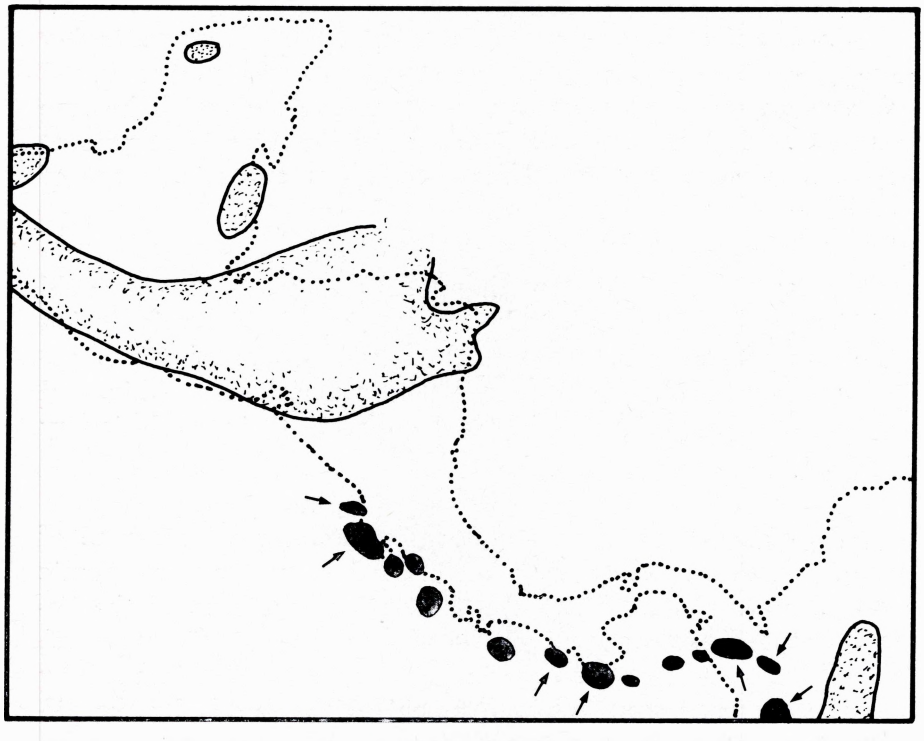

Fig. 5. - Palaeogeography of Central America during the Upper Cretaceous. Lines indicate the emerged lands. Solid areas represent volcanic islands, the arrows point to those still extant. (Redrawn from GOMEZ P., 1982).

islands were pushed eastwards and became the Greater Antilles (CONEY, 1982) which, by Eocene time, had achieved their present positions. It is considered unlikely that land ever connected North America and islands of the Greater Antilles after their initial separation (BROWN & GIBSON, 1983). The Lesser Antilles were, as they are today, more closely tied to South America during their development from Late Eocene to the present time. During the Cenozoic time Middle America grew subaerially southwards from North America as a complex volcanic arc-trench system, eventually forming the final land bridge by collision south of Panama in Pliocene time (4 million years BP).

In the New World, continental drift not only separated the American subcontinents from the palaeotropics but also separated North and South America, whose floras evolved in isolation. The separation of the two American subcontinents probably segregated, in North America, the ancestors of the present cycad genera. In South America, other cycads evolved which became extinct during the Cenozoic. Thus, South America is at present the only austral continental mass devoid of endemic genera of cycads.

It is most probable that the modern genera of cycads could be derived from ancestors who evolved in late Mesozoic during the Cretaceous. Unfortunately the existing genera of cycads appear in the fossil record at the beginning of the Cenozoic, and there is no previous information about their evolutionary history.

Evidence of isolation and early evolutionary divergence of the New World cycads may be inferred from their taxonomic isolation from the African and Australian members of the Zamiaceae and from recent chemical evidence. DE LUCA *et al.* (1982b), showed that the American genera of the Zamiaceae may be distinguished from other members of the family by the different monosaccharide composition of their mucilages. Moreover, the patterns of monosaccharide distribution of the mucilages of the American genera are different from those of the members of Boweniaceae, Cycadaceae and Stangeriaceae.

Dion represents the descendant of an ancient evolutionary line characterized by leaf-like megasporophylls, ovules usually borne on a stalk-like outgrowth of the sporophyll, and pinnae not articulate. *Ceratozamia, Microcycas* and *Zamia* appear closely related and originated from a distinct evolutionary line from which, however, *Ceratozamia* probably diverged earliest. These genera appear morphologically very similar. Their synapomorphies include very reduced sporophylls, ovules sessile, pinnae articulate, leaves stipuled (in *Microcycas* only in the seedling). *Ceratozamia,* however, has bicornuate sporophyll-ends and contain galactose only in traces in the mucilage (De Luca *et al.*, 1982b). *Microcycas* is scarcely discernable morphologically from *Zamia.* The only features that distinguish the two genera are the extreme proliferation of both archegonia and spermatozoids in *Microcycas* (Eckenwalder, 1980). Moreover, *Microcycas* has a high-numbered and asymmetrical karyotype (2M+2A+22T) that is equivalent to that of *Z. chigua* (4S+22T) (Norstog, 1980, 1981). *Zamia,* however, shows a wide range of chromosome numbers, from 2n= 16 to 2n= 28 (Norstog, 1980; Moretti & Sabato, 1984) with both symmetrical and asymmetrical karyotypes. On the other hand, the pattern of monosaccharide composition of the mucilage of *Microcycas* is very distinct from the pattern of *Zamia* (De Luca *et al.*, 1982b). Furthermore, the patterns of monosaccharide composition of the mucilage of both south and north American species of *Zamia* are very similar and do not support a distinct origin for the taxa of these continents and in fact support the close relationship of all species of *Zamia* (De Luca *et al.*, 1982b; unpublished).

The present distribution of American cycads, the close relationships among *Ceratozamia, Microcycas* and *Zamia,* the fossil record and geological evidence suggest, as probable, the segregation of the ancestors of modern genera in North America during the late Mesozoic. *Dion* and *Ceratozamia* are distributed in Mexico and northern central America, and their southern limit coincides with the southern limit of North America (including the Central American Peninsula) during the Cretaceous. *Zamia,* as suggested by the fossil record, achieved its modern pan-neotropical distribution at beginning of Cenozoic. *Zamia* was probably isolated in the West Indies by the migration

eastwards of the Cretaceous chain of volcanic islands, which could have harbored faunas and floras. The Cretaceous arc could have also provided « stepping stones » for dispersal of *Zamia* between the two continents during the Middle and Late Cretaceous. *Microcycas* was probably isolated in Cuba by the same events that isolated *Zamia* in the West Indies.

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SUMMARY

The distribution and the ecology of the New World cycads are presented. *Dion* is distributed in Mexico and Honduras. *Ceratozamia* is distributed in Mexico, Guatemala and Belize. *Microcycas* is endemic to Cuba. *Zamia* is distributed in Georgia and Florida (U.S.A.), the Greater Antilles, the Bahamas, Mexico, Central America, Colombia, Venezuela, Ecuador, Peru, Brazil and Bolivia.

The present distribution, the close relationships among *Ceratozamia*, *Microcycas* and *Zamia*, and the fossil record, and, the geological history of America, suggest that the ancestors of the modern genera were segregated in North America during the Late Mesozoic. *Zamia* was probably isolated in the West Indies by the migration eastwards of the chain of volcanic islands, in existence during the Cretaceous time between North and South America. The Cretaceous arc could have also provided stepping stones for dispersal of *Zamia* in South America during Middle and Late Cretaceous time. *Microcycas* was probably isolated in Cuba by the same events that isolated *Zamia* in the West Indies.

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