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Studies on Mexican Paleontology

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Late Cretaceous ophiuroid from Chihuahua (photograph by Leonora Martín-Medrano).
Bauhcis moranii from the Oligocene of Puebla (photograph by Sergio R. S. Cevallos-Ferriz).

Top cover illustrations:
Tselfatia sp. from Turonian outcrops of Vallecillo, Nuevo León (photograph by Alberto Blanco-Piñón). *Megaxantho zoque* from Maastrichian outcrops of Ocozocoautla, Chiapas (photograph by Francisco Vega).

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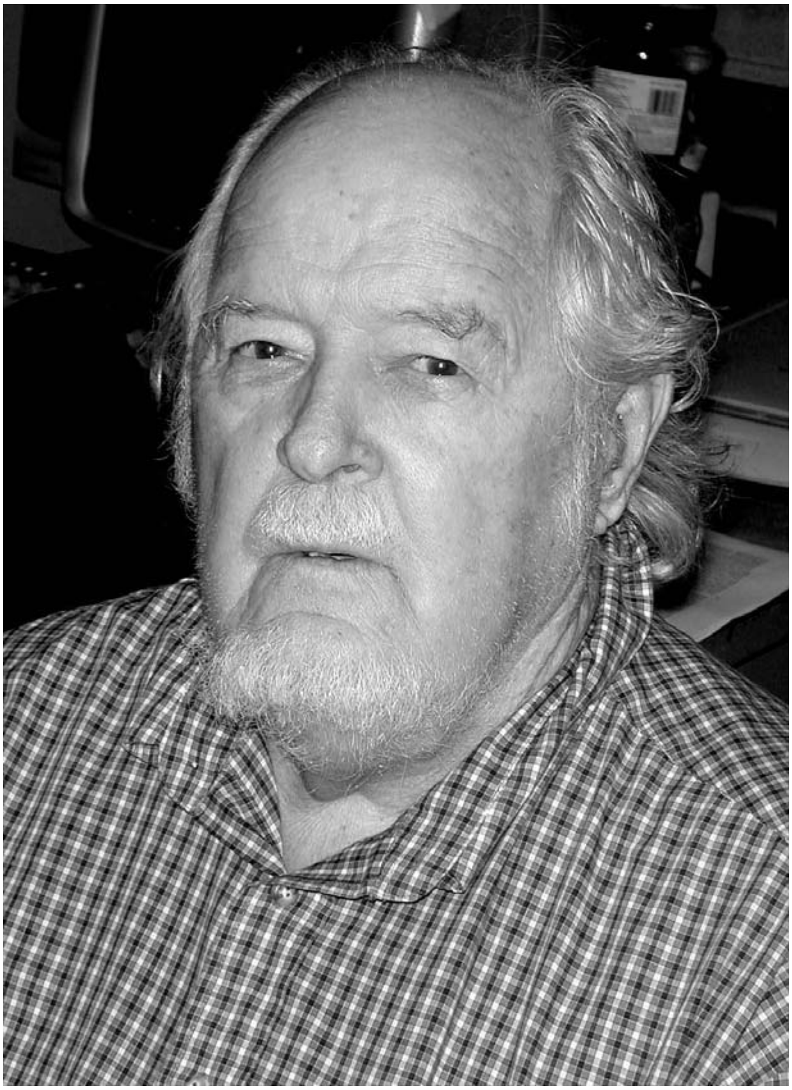
In Memoriam

While this book was in press, our dear and respected colleague Shelton P. Applegate (1928-2005), unexpectedly passed away. For many of us, more than a fellow researcher and a friend, he was an enthusiastic and esteemed teacher. Evidence for this can be found in the chapter by Alvarado-Ortega *et al*., contained in this volume, where “Shelly” is considered the founder of “Mexican Paleoichtyology”. We feel extremely fortunate to have had him share his passion and controversial ideas on Paleontology and Earth Sciences. For all his contributions and genuine love for Mexico, we will sorely miss him. We, editors and authors, would like to dedicate this book to his memory.



Foreword

During the last few years, the number of contributions to the Paleontology of Mexico has increased considerably. Paleontological work in Mexico has been focused on providing important information for petroleum exploration and specific studies dealing with pollen, foraminifera, radiolaria, dinoflagellates, rudists, and ammonites. Often these reports were published only in local or regional journals and therefore not available to the scientific community at large. The purpose of this book is to offer an updated review of the fossil groups from Mexico, providing their significance to the stratigraphy, tectonics, sedimentology, evolution and paleontology of Mexico whose study has proved to be relevant in stratigraphy, tectonics, sedimentology, and evolution. The fossil record of Mexico ranges from Precambrian to Pleistocene. Almost every Mexican State has reported fossil localities with ongoing studies and potential for the discovery of new localities. Even those localities that have been studied since the eighteen-century, such as the early Cretaceous San Juan Raya, have recently reported new fossil groups. Unfortunately, much of the fossil reports from Mexico have been published in Spanish from local journals, which represent a language barrier to the international community. There is little doubt that the paleontological history of Mexico deserves to be known in other countries. By making this book available to the international scientific community we hope that interest in the fossil record of Mexico will grow. Important topics, such as the Cretaceous/Tertiary controversy, were not included in this book because the topic has received a lot of attention and many papers in English have already been published. The main value of this book is the compilation, updated information and critical review of research on the diverse taxonomic groups, which include plants, pollen, corals, rudists, bivalves, crustaceans, echinoids, ophiuroids, brachiopods, fishes, amphibians, reptiles and mammals, as well as a review of one of the most famous localities of Mexico: Tepexi de Rodríguez, Puebla. The first chapters deal with the study of plant macrofossils and pollen, with emphasis on paleoenvironmental interpretations, stratigraphic implications, and paleogeographic considerations. The invertebrate chapters include reviews of taxa, biostratigraphy, and paleobiogeographic implications. The vertebrate chapters emphasize the importance of taxa recently found in different locations of Mexico, including evolutionary implications and correlation with other localities around the world. Chapter authors present this work not in Spanish but in English and we are grateful to all of them for this. There are excellent books on diverse topics, dealing with fossils of Mexico, but this is the first book to be published that represents the most active research groups in the country including interpretative reviews of many taxa. This book will be useful for teaching, reference, research and for the enthusiast to the relicts of the past.

Preface

Mexico, as a world paradigm of diversity and prolonged natural history, could not leave aside a fundamental aspect of her cultural inheritance, namely, the nature and evolution of life, as contained in the fossil register of animals and plants left in rocks of all epochs in the Mexican territory. This book, because of its timeliness and precious content, undoubtly will remain for years to come as a classical work in the scientific literature related to the subject. Throughout its 13 chapters it can be found either treated for the first time, or otherwise aptly reviewed, the results of many decades of research on fundamental fossil groups that tell us about the geologic, paleogeographic, and paleobiologic evolution of the past 350 million years in this part of the planet.

From the revision of the late Paleozoic fossil register of invertebrates (Chapter 8), represented in Mexico in formations that extend from Chiapas in the southeast, to Sonora and Baja California in the northwest, to the analysis of recent advances on the paleontology of the Tlayua Quarry in the State of Puebla (Chapter 13), a fossiliferous locality that is justly considered one of the most important paleontologic discoveries of the past century, this book also has the virtue to show the quality of life forms as a central element for the full understanding of how the Mexican territory was tectonically integrated, and also how these geologic changes of the earthly environment might have influenced the evolution of its inhabitants to the present time (Chapter 1). Particularly welcome is research material that deals with essential aspects of the plant fossil record (Chapter 2), Mammals (Chapter 12), or Dinosaurs (Chapter 11) that inhabited the Mesozoic or Cenozoic continental basins of Mexico, as well as others that bring to the attention of the international community animal groups for which the Mesoamerican and particularly the Mexican region was the theater of rapid changes and radiation, and yet little or nothing had been published before in Mexico (Chapters 5, 7, 9 and 10). Indeed, classical and internationally well known Mexican fossil groups such as Rudists (Chapter 4), Echinoids (Chapter 6), and Corals (Chapter 3), are more timely treated in the book to the benefit of readers interested in major episodes of natural history, as recorded in the Mexican geology and paleontology, and how this history integrated with the ever changing earth of those times.

Considering the various aspects handled by both original research, as well as in revision chapters, one very important added value should be the rather extensive bibliography of almost 1000 references related to the central topic contained in the book, an invaluable information which by itself constitutes a tribute to the memory of pioneer contributions by researchers that have worked in Mexico for the past two centuries.

Finally, as a student of the Mexican physical geology for several decades, and therefore may be as a relative outsider to the main subject of the book, I wish to congratulate sincerely the builders of this great work, and wish for it the best success it undoubtly deserves, and I am sure it will achieve.

Fernando Ortega-Gutiérrez
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Chapter 1

Geological setting and phytodiversity in Mexico

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1. Abstract

The joint discussion of biotic and abiotic factors allows proposal of a hypothesis in which the dynamic nature of the geological processes and of the organisms facilitate the understanding of the biodiversity of Mexico. In this respect, we highlight that since the Cretaceous, Mexico had a configuration similar to that of a peninsula that increased in size through time, but that with the establishment of the Isthmus of Panama approximately 3.5 my ago, it no longer had such a configuration. During this peninsular configuration, the main mountain belts of Mexico formed in different episodes of time attaining variable sizes through dynamic and fluctuant processes until they reached their extant physiognomy. At the same time the retreat of the seas was significant in exposing positive zones of the continent, where life was established. Finally, after occupying their current positions, the Baja California Peninsula and the Yucatan Peninsula started providing cover to the central continental mass of Mexico. The fossil record suggests that while all of this occurred, the newly generated environments were occupied by plants that were formerly part of higher latitude communities of North America. That through the land bridges that connected

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North America with Europe and Asia, plants with different geographical affinities arrived in Mexico. Also with the establishment of the Chortis Block as the northern part of Central America, at least part of the plants already growing on the Chortis Block arrived into the rest of Central America eventually expanding their distribution into South America. The interaction of the biological processes, as suggested by the fossil record with the environment, coupled with the geological setting, promoted the development and establishment of a distinctive biota among which, the endemic plants that characterize today the vegetation of Mexico stand out.

Some of the extant Mexican plants were already present in the Oligocene and possibly since the Eocene. Finally, the current landscape and the elements that conform it began their "modernization" some 3.5 million years ago, but they may have a longer history that started in the Cretaceous.

2. Introduction

The diversity and taxonomic relationships of the extant flora and vegetation of Mexico, compared with that of other geographical regions, has been reported since, at least, the beginning of the XIX century (e.g., Hemsley, 1879-1888; Engler, 1882, 1905; 1914; Standley, 1936; Johnston, 1940; Sharp, 1951, 1953; Matuda, 1953; Miranda, 1958, 1960; Toledo, 1982; Rzedowski, 1965, 1991). Recognizing that diversity and taxonomy support the natural history of the participating lineages, two hypotheses have been proposed to explain the conformation of the extant vegetation of Mexico and Central America. The first idea explains the wealth of vegetation in Mexico as a function of the pressures that the environment and/or the climate exercised upon the plant communities during the establishment of the Isthmus of Panama and through the Ice ages of the Plio-Pleistocene. This idea is possibly the most widespread one. This proposal implies that the biological rearrangement of plants took place only in the last 3.5 million years when the current landscape conformed (Axelrod, 1950; Raven, 1963; Sarukhán, 1968; Graham, 1973, Burnham and Graham, 1999). In contrast, a second hypothesis that has acquired greater importance in recent years suggests that the diversity and the geographical relationships of the vegetation that today develop in Mexico and Central America have a considerably longer history in the region, possibly going back to the Cretaceous (ca. 135 mybp), but at least to the Paleocene (65 mybp), or slightly earlier (Bray, 1898, 1900; Krueger, 1934; Johnston, 1940; Rzedowski, 1991; Wendt, 1998). This second hypothesis also acknowledges the influence of the environment and/or climate as prominent factors that guided the development of populations and communities, but emphasizes the age in which this interaction occurred. Although both hypotheses highlight the importance of physical parameters as dynamic factors influencing the biological track of plants, their discussion from a historic perspective has been reported, in the best of the cases, with little detail.

Communities composed of a particular mixture of organisms that coexist and interact in given areas produce the characteristic biodiversity of a region. The establishment of these communities is linked to a natural assemblage of variable factors such as air, water, soil, temperature, altitude and latitude, that due to their own interactions, offer the biota different settings in which life may develop. Defining these settings and the communities they contain has been an arduous task; to the point that today the topic continues to be the center of important debates (e.g., Hemsley, 1879-1888; Johnston, 1924; Wiggins, 1960; Miranda, 1952; Rzedowski, 1966, 1972; Trejo-Vázquez and González-Medrano, 2001). The form in which these factors had interacted through time in the area occupied today by Mexico and Central America surely favored the establishment of various settings that are not necessarily similar to the extant ones. Understanding how this region was geologically built up and identifying the plants that were able to establish in different settings at the same time, allows the proposal of this new hypothesis to explain the biodiversity that characterizes the region and introduces an historical biogeographic component to the lineages that conform it.

3. Organization of this Chapter

In the following sections, some prominent aspects of the integration of the geological setting of Mexico and the northern portion of Central America during the Upper Cretaceous and Cenozoic will be presented. These scenarios generate a general vision (not widely discussed here) of the orography, hydrography and distribution and extension of the seas during different time periods. These factors, along with others, influenced the distribution of air, marine currents and humidity; together they imposed restrictions to the distribution of the plants according to their ecological capabilities. Immediately following, some aspects of the paleobotanical record of the area will be presented, beginning in the Upper Cretaceous. Finally a mechanism to explain how the vegetation that today develops in the region is proposed.

4. Geological Setting

The geological evolution of Mexico and Central America during the Cretaceous and Cenozoic had significant influence on the processes that controlled the integration of their vegetation (Fig. 1). To better understand the main geological events that took place in Mexico during this time interval, the following general processes can been recognized: i) development of large magmatic provinces (Sierra Madre Occidental, Faja Volcánica Mexicana, Sierra Madre del Sur); ii) fragmentation and displacement of continental segments including the opening of the Gulf of California and the displacement of the Chortis Block; iii) marine regression that outlined the current contour of Mexico; and iv) formation and lifting of the eastern orogenic belt (Sierra Madre Oriental).

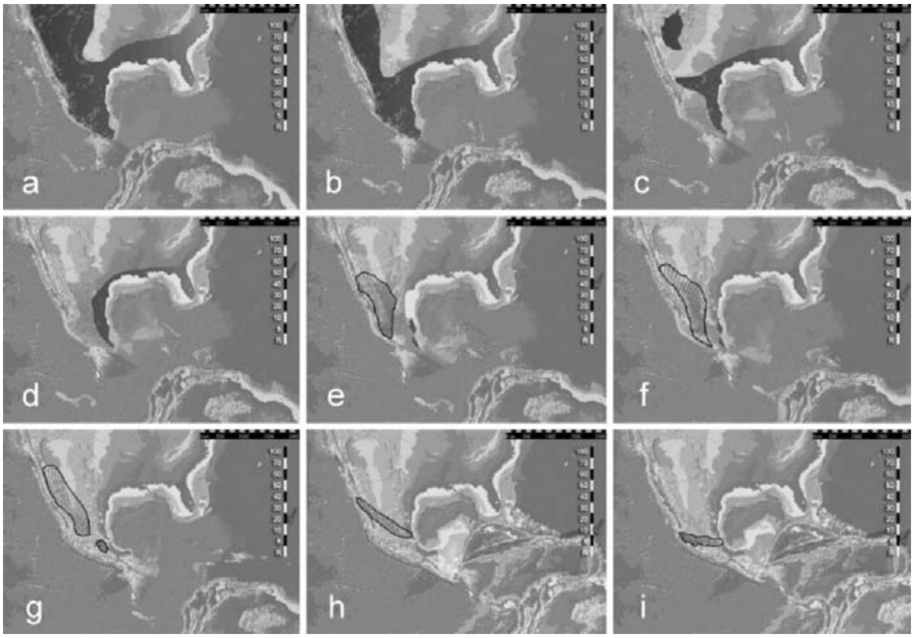


FIGURE 1. Schematic reconstruction of the geological history of Mexico during the last 100 million years, highlighting significant features. Black lines represent the approximate extension of the volcanic arch. a) Albian; generalization of marine transgressions, b) Maastrichtian; lifting of the northwest portion, c) Upper Paleocene; continuation of the marine regressions while the Laramide deformation is in progress, d) Middle Eocene; extensive volcanic activity e) Upper Eocene; displacement of the Chortis Block starts, widening of the Volcanic Arch, f) Lower Oligocene; ignimbritic flare up, g) Early Miocene; extensional pulses and change in orientation (now NW-SE) of the Volcanic Arch, h) Late Miocene; opening of the Gulf of California begins and formation of the Faja Volcánica Mexicana, i) Early Pliocene; emergence of the Yucatan Peninsula, the connection between the Pacific and the Caribbean is interrupted.

i) *Development of large magmatic provinces* (Fig. 1). Development of the Sierra Madre Occidental, which has a general N-S orientation along the Pacific coast, started in the north of the country spanning from Cretaceous to the early Miocene (Figs. 1a-g). During the Eocene volcanic rocks formed a wider Sierra Madre Occidental (Fig 1e, Aguirre-Díaz and McDowell, 1991). At the onset of the Oligocene (ca. 32-28 mybp) the volcanic activity of this province became especially intense, forming the largest ignimbrite deposit on the planet (Fig. 1f, Ortega *et al*. 1992; McDowell and Clabaugh, 1979). It has been calculated that most of these volcanic products, reaching average thickness of 1,000 m, were deposited in the span of 4 million years (Ortega *et al*. 1992; Ferrari *et al*. 2002).

The Faja Volcánica Mexicana is a volcanic arch with an extensive variety of stratovolcanos, monogenetic cones, etc. This volcanic province has been active since the Middle Miocene and it is composed by almost 8,000 volcanic centers in an area of approximately 1,000 km by 20-150 km (Velazco-Tapia and Verma, 2001). It is oriented in an E-W direction and divides Mexico into two regions: a drought and subtropical region towards the north; and a humid and tropical region to the south. The Sierra Madre del Sur is composed of plutonic and volcanic rocks of Paleocene to Middle Miocene age (Morán-Zenteno *et al*. 2000). However, the southern margin of the Mexican Pacific demonstrates that the region was exposed to intense lifting and erosion as there are extensive plutons exposed.

The aforementioned enormous volcanic activity contributed a colossal volume of materials that through time transformed the physiography of Mexico (e.g., morphology and hydrology). As igneous material piled up, new mountain chains with varying altitudes were formed, opening and/or closing basins with a consequent change in the hydrologic conditions. This common process most likely affected the magnitude of the natural barriers and selective forces that influenced the distribution of plants. Furthermore, gas emissions as well as the presence of suspended particles in the atmosphere, suggest the development of special atmospheric conditions in the region. For example, depending on the concentration of free gases in the stratosphere due to volcanic activity, SO and CO2 may have opposite effects and may perform differently at different time scales depending on how long these gases stay in the atmosphere. Thus, a regional warming, based on the greenhouse effect, would be expected due to the presence of SO during a relatively short period of time, but if the time span is bigger (months to ca. 10 years) the large eruptions may cause cooling instead. In contrast, the CO2 emissions may cause a regional warming in the scale from 10 to 10,000 years (Wignall, 2001).

ii) *Fragmentation and displacement of continental segments* (Fig.1). The fragmentation and displacement of continental blocks is a distinctive feature of the Cenozoic geology of Mexico. Two important processes can be recognized, the displacement of the Chortis Block, and the formation of the Baja California Peninsula.

The Chortis Block, a continental fragment that spans from Honduras to Nicaragua (Anderson and Schmidt, 1983), moved along the southwestern margin of the Mexican Pacific Coast in an interval of time during the Cenozoic. The oldest recognized position for this continental block during the Upper Cretaceous was at a maximum latitude similar to that of the region of Zihuatanejo (Fig. 1a-c, Schaaf *et al*. 1995). Its movement southwards began some 40 mybp (Fig. 1d). As the movement of this block proceeded (Fig 1e-i), three main effects that limited the biota distribution in the past could be predicted. First, some continental areas were gradually exposed or protected from the influence of the ocean. Second, in the southern margin of the Mexican Pacific an intense lifting of the continental crust was promoted, allowing the formation of large basins with continental deposits, altering the drainage, and promoting important processes of erosion. And finally, the establishment of a land connection between North and South America, approximately 3.5 mybp, as it contacted the portion that today is South Central America.

The formation of the Baja California Peninsula and the opening of the Gulf of California are also related to the fragmentation and displacement of a continental fragment. Approximately 5 million years ago (Fig. 1h-i), the Oriental Pacific Plate began spreading northwards, entering in the incipient Gulf of California and initiating a marine invasion (Martín-Barajas, 2000). From that moment on, the separation of continental blocks continued, generating extensional tectonic processes that began the formation of the basin and range system in the area. The opening of the Gulf of California is the consequence of a right lateral movement between the Pacific and North America plates.

iii) *Marine regressions* (Fig. 1). The marine regressions that extensively affected eastern Mexico during the Cenozoic contributed to the configuration of the region. They also were a determinant factor for the establishment of the flora and vegetation through the habilitation of positive exposed areas where organism became established.

iv) *Lifting of the oriental orogenic belt* (Fig. 1). The Laramide orogeny, a process linked to the marine regressions, started in the Late Cretaceous and ended in the Middle Eocene (Fig. 1a-d), prompting since then the retreat of the seas and influencing the current configuration of the area. The territory that emerged due to this process increased the surface of the country in ca. 100% (Ortega et al., 1992), offering the continental biota a considerable new space for its establishment and development. The retreat of the seas was a gradual process, with alternation of regressions and transgressions, each one of which had individual characteristics in different regions. As previously pointed out, the formation of diverse sedimentary basins is an important characteristic of the geology of Mexico, and in this respect, the Coastal Plain of the Gulf of Mexico is a prominent example. As seas withdrew and the orogenic system of the Sierra Madre Oriental conformed and lifted, one of the more important mountain systems of the current geography of Mexico became established.

5. Outstanding Aspects of the Fossil Record

The hypotheses that had been previously proposed to explain the origin of the vegetation of Mexico were mainly based on interpretations of the extant flora and vegetation. In a few exceptions, fossil plants collected in Mexico, -but little studied-, were considered (e.g., Rzedowski, 1978). Instead, fossils of higher latitude paleocommunities were frequently extrapolated in order to fill this gap (e.g., United States of North America, Europe; e.g., Graham, 1973, 1976). The limited integration of the flora and vegetation of Mexico and the misuse of other biological principles (e.g., the present is the key to the past) encouraged the extrapolations, to the point that the biological and geological processes that were taking place in the area were, at best, marginally considered.

It is a fact that the fossil record of the flowering plants of Mexico has not been extensively studied and that the majority of the reports are known from the palynological record (whose focus has been mainly biostratigraphic) limiting in that sense the knowledge of the taxonomic affinities of the plants (Cevallos-Ferriz and Ramírez, 1996; Martínez-Hernández and Ramírez-Arriaga, 1996). Nevertheless, the combined work on macro and microfossils of the flowering plants of Mexico, made in recent years, renders more than 200 identified taxa. Although this number of identified plants is still low to firmly support a conclusive explanation for the integration of the vegetation of Mexico, it is sufficient to promote reconsideration of some ideas. For example, *Ilex, Quercus* and *Pinus* grow natively in the tropical regions of Mexico today, but traditionally, their origin is considered to have occurred north of Mexico and they have been used as an example of plants that reached the southern part of North America when the ice sheets spread on the continent during the Plio-Pleistocene. However, *Ilex* and *Pinus* are now known from Eocene sediments of the NE of Mexico and *Pinus* and *Quercus* are important elements of the Mexican taphofloras since the Oligocene (Martínez-Hernández and Ramírez-Arriaga, 1996). Thus, their participation in the integration of the vegetation of Mexico has to be reconsidered. In a similar way, the presence of plants in the tropical forests of Mexico like *Cyrilla, Ticodendron, Alfaroa* and *Oreomuna* has been explained as northern elements that became established in the south when seeking shelter during the glacial maximum of the Plio-Pleistocene. Another example concerning these reinterpretations involves the recognition of fossils of certain groups such as Anacardiaceae and Leguminosae in Mexico (Figs. 8-18). Traditionally, Mexican presence of these plant families has been interpreted as a consequence of the establishment of the Isthmus of Panama, through which they supposedly arrived. However, the known fossil record in the Mexican territory of the former may go back to the Cretaceous and members of the latter have been collected in Eocene sediments in northern Mexico, suggesting once again the need for a reevaluation of our ideas on the integration of vegetation in low latitude North America (e.g., Magallón-Puebla, 1994a; González-Medrano, 1996; Calvillo-Canadell and Cevallos-Ferriz, 2001, 2005; Martínez-Millán, 2000; Martínez-Cabrera, 2002; Ramírez and Cevallos-Ferriz, 2000a, 2002).

Among the taxa that grew in Mexico during the Tertiary there are some that suggest relationships with plants of different regions of the world. For example, *Eucommia* (Fig. 19; Eucommiaceae) was widespread in the Northern Hemisphere during the Eocene-Miocene but today lives only in the humid forests of China (Magallón-Puebla and Cevallos-Ferriz, 1994b). *Cedrelospermum* (Fig. 21; Ulmaceae) is an extinct taxon that coexisted with *Eucommia* in the Miocene (Magallón-Puebla and Cevallos-Ferriz, 1994c). The presence of *Statzia* (Fig. 22; *incertae sedis*) in Mexico is extremely interesting, since aside from this report, it is only known from

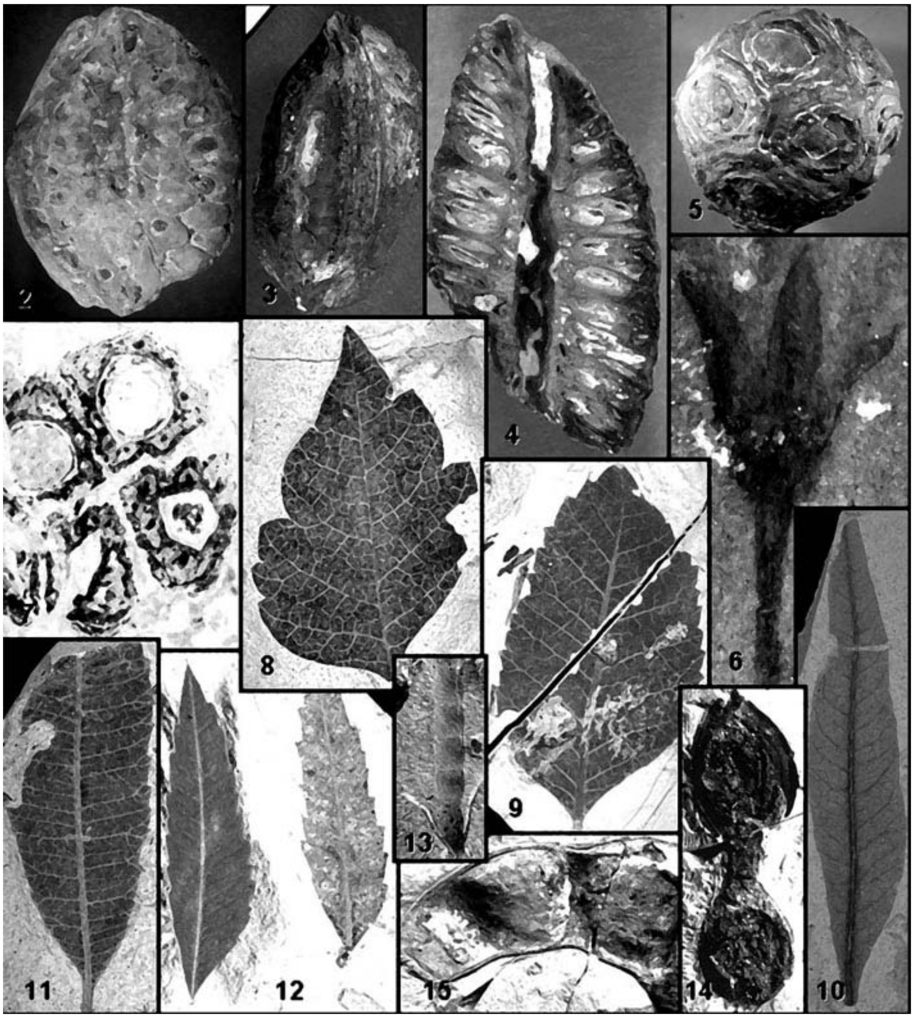
Oligocene sediments of Roth, Germany (Magallón-Puebla and Cevallos-Ferriz, 1994d) suggesting again, relationships with the other regions of the Northern Hemisphere. Some flowers recovered from the amber of Simojovel, Chiapas, are comparable to the *Statzia* impression/compression fossils from Tepexi de Rodríguez, Mexico and Roth, Germany. Other Tertiary plants of Mexico suggest relationships with other regions of the world, *Berberis* and *Mahonia* (Figs. 20, 23, 27; Berberidaceae) may be related to extant plants of Asia and South America (Ramírez and Cevallos-Ferriz, 2000b) while *Copaiferoxylon* (Leguminosae) supports old relationships with Africa or South America (Cevallos-Ferriz and Barajas-Morales, 1994).

Some other fossil plants of the Tertiary of Mexico point to important links with the Caribbean and reinforce those with South America. Certainly, *Hymenaea* (Leguminosae), the plant that produced the amber of the Oligocene-Miocene of Simojovel, Chiapas, Dominican Republic and Puerto Rico leads the list (Calvillo-Canadell, 2000). Not less surprising is the presence of *Haplorhus and Loxopterygium* (Anacardiaceae) among the fossils collected in Mexico. The former is an endemic plant that grows at present in the dry zones of Peru and Chile (Ramírez *et al*., 2000; Ramírez and Cevallos-Ferriz, 2002), while the latter grows naturally from Venezuela to Argentina (Colina-Hernández, pers. com. 2000); however, both of them are found as fossils in the Oligocene of Mexico and Miocene of Ecuador (Burnham and Carranco, 2004). Other plants that suggest old and complex historic floristic links between Mexico and South America are *Inga* and *Pithecellobium* (Figs. 16-17; Leguminosae). Although their current distribution includes the two areas, their diversity is greater in South America, but the oldest known fossil record comes from Eocene and Oligocene sediments in Mexico (Calvillo-Canadell and Cevallos-Ferriz, 2001, 2005).

The fossil record of *Tapirira* (Anacardiaceae) suggests, in a subtle way, a southwards movement of the lineage during the Tertiary; this pattern may also be reinforced by the fossil record of other taxa (Martínez-Cabrera, 2002). The oldest record of this lineage corresponds to wood from the Eocene of Wyoming (Manchester, 1977). More recently, woods of this taxon appear in Oligocene-Miocene sediments of Baja California and Baja California Sur, and its flowers are known from even younger rocks containing the amber of Simojovel (Miranda, 1963; McKeown *et al*. 1991; Martínez-Cabrera, 2002). Finally, today *Tapirira* is found growing naturally in Southern Mexico and Northern South America (Terrazas and Wendt, 1995).

A recent report of *Berberis* (Figs. 20, 23; Berberidaceae) from Oligocene sediments of Central Mexico (Ramírez and Cevallos-Ferriz, 2000a) introduces to the discussion some important aspects as information from both, fossils and extant plants are used in conjunction. Today, this genus grows naturally in North and South America, but not in Mexico. Its fossil record, nevertheless, demonstrates that during the Tertiary it was able to grow in Mexico and that the characters of the fossil leaves collected in this region link them to extant species of South America and Asia (Ramírez and Cevallos-Ferriz, 2000a).

Another important piece of information that can be extracted from the fossil



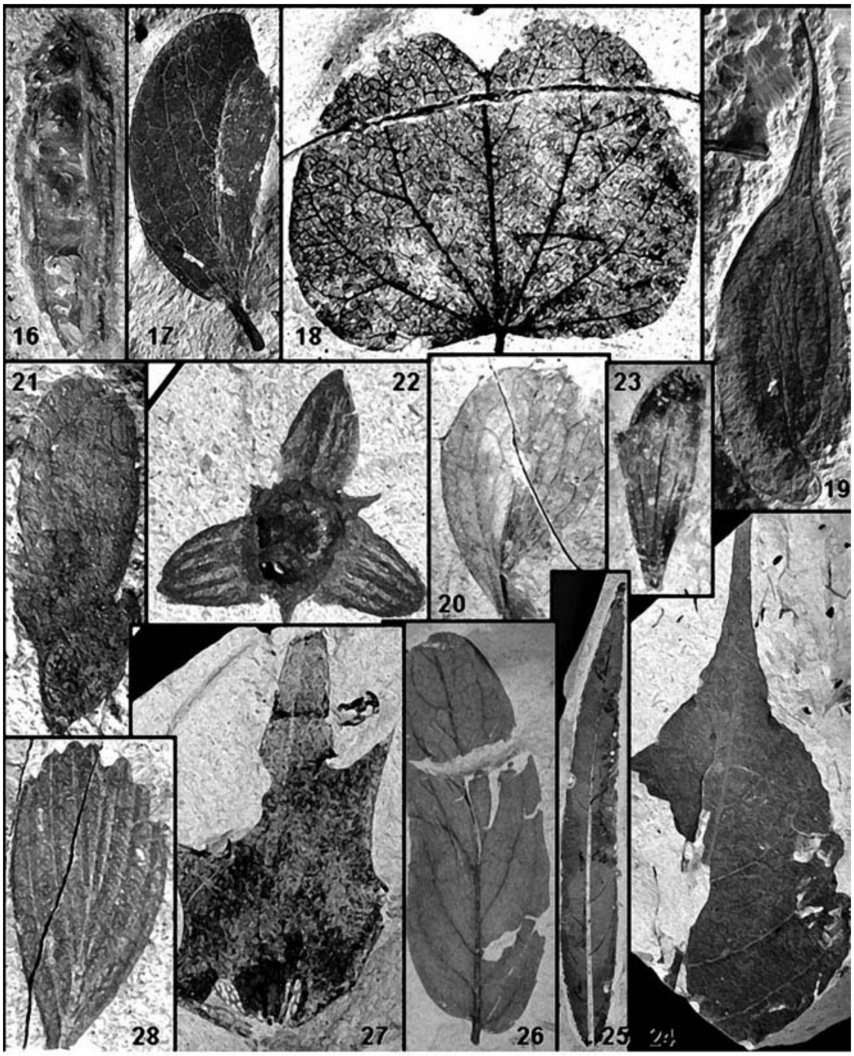
FIGURES 2-15. 2-6. Cretaceous fossils. 7-15. Tertiary fossils. 2.- *Striatornata sanantonensis* (Musaceae). 3.- *Tricostatocarpon silvapinedae* (Strelitziaceae). 4.- Hamamelidaceous fruit. 5.- Fruit of a probable Araceae. 6.- Flower of Rhamnaceae. 7.- *Tarahumara sophieae* (Haloragaceae). 8-12. Anacardiaceae. 8.- *Rhus toxicodendroides*. 9.- *Pseudosmodingium terrazasiae*. 10.- *Pistacia marquezii*. 11.- *Comocladia intermedia.* 12.- *Pseudomodingium mirandae* (right) and extant specimen (left), for comparison. 13-15. Leguminosae. 13.- *Reinweberia ornithopoides.* 14.- *Sophora sousae*. 15.- *Lysiloma mixtecana* .

record of Mexico is the recognition of the minimum age in which the precursors of endemic genera or species, such characteristic of the current vegetation of the country, first appeared. For example, in Oligocene sediments of the surroundings of Tepexi of Rodríguez, Puebla, which are assumed an age of 32 my, fossil fruits and leaves suggest that lineages that currently give the vegetation of the region a unique character were already present by that time. Among them are *Pseudosmodingium* (Figs. 9, 12, Anacardiaceae), *Comocladia* (Fig. 11, Anacardiaceae), *Mimosa* (Leguminosae), *Sophora* (Fig. 14, Leguminosae), *Lysiloma* (Fig. 15, Leguminosae), *Reinweberia* (Fig. 13; Leguminosae), and *Populus* (Fig. 24; Salicaceae) (Magallón-Puebla and Cevallos-Ferriz 1994a; Martínez-Millán, 2000; Ramírez *et al*. 2000; Ramírez and Cevallos-Ferriz, 2000b, 2002).

Detailed comparison between fossil and extant plants based on leaf architecture of Oligocene leaves collected in the Los Ahuehuetes locality within the surroundings of Tepexi of Rodríguez, Puebla, makes it evident that although the identified genera can be similar to those of the current vegetation of the area, at the specific level, there are important differences (Ramírez and Cevallos-Ferriz, 2000a, 2000b, 2002; Velasco de León *et al*. 1998; Velasco de León and Cevallos-Ferriz, 2000). Furthermore, similar studies with some fossil plants of the Miocene-Pliocene of Hidalgo and of the Plio-Pleistocene of Morelos suggest that the development of the extant species took place in relatively recent times. It is also extremely interesting that the assemblage of fossil plants in the outcrops so far studied show a combination of elements that are characteristic of different types of extant vegetation. This suggests that the types of vegetation now recognized have also changed, and therefore, it is necessary to understand how the patterns of plant association varied through time (Velasco de León, 1999; Ramírez-Garduño, 1999).

6. Integration of the Biodiversity

During the assemblage of Mexico as part of the North American Plate, the accretion of blocks has always been an important process, especially during the Paleozoic and Mesozoic; but it is during the Cenozoic that this process along with the displacement of lands, culminated in the current configuration of the region. A discussion of the vegetation of Mexico and the integration of the plants from an historical point of view is presented next. This discussion starts in the Upper Cretaceous, where the oldest plant macrofossils have been reported, since the majority of the continental land was formerly covered by sea. However, it is necessary to mention some enigmatic Lower Cretaceous pollen grain records; *Afropollis* (Winteraceae) and *Retimonocolpites* (Laurales) are found in Aptian/Albian sediments of Michoacán and Colima and, *Tricolpites* (Hamamelidaceae) and cf. *Spathiphyllum* (Araceae) in Durango (Martínez-Hernández and Ramírez-Arriaga, 1996). These records suggest the presence of exposed areas in the central part of Mexico, representing perhaps islands in which the angiosperms were able to become established (Martínez-Hernández and Ramírez-Arriaga, 1996). Stems or wood of *Palmoxylon and Mimoxylon* from Cretaceous sediments of Oaxaca had been reported (Müller-Stoll and Mädel, 1967; Cevallos-Ferriz and Ricalde-Moreno, 1994; Cevallos-Ferriz and Barajas-Morales, 1994), but unfortunately the locality where the material was collected has not been found again,



FIGURES 16-28. Tertiary fossils. 16.- Fruit similar to *Inga*. 17.- Leaflet similar to *Pithecellobium*. 18.- *Bauhcis moranii.* 19.- *Eucommia constans* (Eucommiaceae). 20.- *Berberis tepexiana* (Berberidaceae). 21.- *Cedrelospermum manchesteri* (Ulmaceae). 22.- *Statzia (Insertae sedis)*. 23.- *Berberis lozanofolia* (Berberidaceae). 24.- *Populus dentiacuminata* (Salicaceae). 25.- *Salix alencasterae* (Salicaceae). 26.- *Salix balsana* (Salicaceae). 27.- *Mahonia martinezii* (Berberidaceae). 28.- *Cercocarpus mixteca* (Rosaceae).

so the presence and age of these plants cannot be confirmed.

The most extensive and best known positive continental area of the southern portion of the North American Plate where life could have established in the Upper

Cretaceous corresponds to portions of the northern states of Mexico, in the so called Paleopeninsula of Coahuila (Fig. 1b). This paleopeninsula extended from the north-center portion of Tamaulipas to the southern region of Coahuila and then to the NE tip of Baja California. There is indication that some islands existed toward the south, but little is known about the life established on them. However, some fragments of wood collected in the surroundings of Huetamo, Michoacán, have been identified as *Araucarioxylon*. Some other conifers had been reported from the paleopeninsula of Coahuila, especially from its coal deposits, and in Sonora and Baja California (Rueda-Gaxiola, 1967; Martínez-Hernández *et al.* 1980; Weber, 1972).

Nevertheless, the angiosperms are more common in all these sediments. The macrofossils collected so far around Rincón Colorado in Coahuila, represent plants of the families Arecaceae, Musaceae (Fig. 2), Strelitziaceae (Fig. 3), Ranunculaceae, Menispermaceae, Hamamelideae (Fig 4), Phytolaccaceae, Rhamnaceae (Fig. 6) and probably Araceae (Fig. 5) (Rodríguez de la Rosa and Cevallos-Ferriz, 1994; Rodríguez de la Rosa *et al.* 1998; Pérez-Hernández *et al.* 1997). From Sonora, members of Arecaceae and Haloragaceae (Fig. 7) have been reported (Cevallos-Ferriz, 1983; Hernández-Castillo and Cevallos-Ferriz, 1999); and in both sites *Paraphyllanthoxylon*, a wood type that may represent Lauraceae, Anacardiaceae or Burseraceae, among other families, has been described.

These plants show that in the Upper Cretaceous, the biota of the positive continental parts of Mexico was represented by groups that today are more common either in the Northern (e.g., Ranunculaceae, Menispermaceae) or in the Southern Hemisphere (e.g., Musaceae, Strelitziaceae, Anacardiaceae) (Raven and Axelrod, 1974; Taylor, 1990). Furthermore, the fossil record of some of the families that are currently more diverse in the Southern Hemisphere, suggests that during the Cretaceous, and possibly the Tertiary, they were more diverse in the Northern Hemisphere. This observation highlights the need of a cautious interpretation of the biogeographic patterns of the past, especially if they are used as a reference to explain the current distribution of plants.

Unfortunately, macrofossils from the Paleocene have not been collected in Mexico. Nevertheless, the pollen record of the Burgos Basin, Coahuila, suggests that a community comparable to those reported from the Mississippi Embayment in United States was capable of establishing itself within Northwestern Mexico during this time (Martínez-Hernández and Ramírez-Arriaga, 1996). By the end of the Cretaceous, plants related to those from the Mississippi Basin followed the retreat of the Epicontinental Sea establishing themselves in the south; in a similar way during the Tertiary, they followed the transgression-regression cycles of Eastern Mexico. At the same time, the Sierra Madre Occidental was developing southwards promoting the exposition of central Mexico. In general terms, the region at this point, was in the shape of a great peninsula (Figs. 1a-1c).

By the Eocene, part of the elements reported in the Burgos Basin flora, (e.g., *Ilex,* Sapotaceae, Juglandaceae, Betulaceae) had expanded southwards, reaching some areas of Chiapas (Martínez-Hernández and Ramírez-Arriaga, 1996). Also, by the Eocene, Leguminosae (Fig. 16) is recognized through well preserved fruits and seeds in La Popa Basin, Nuevo León (Calvillo-Canadell and Cevallos-Ferriz, 2001). The Leguminosae, a major component of the extant vegetation of Mexico, seems to have expanded its distribution during the Eocene and Oligocene, since it is well represented in Oligocene and Miocene sediments of Baja California Sur, Puebla, Tlaxcala, Oaxaca and Chiapas (Figs. 13-17; e.g., Miranda, 1963; Magallón-Puebla and Cevallos-Ferriz, 1994a; Cevallos-Ferriz and Barajas-Morales, 1994; Müller-Stoll and Mädel, 1967; Calvillo-Canadell and Cevallos-Ferriz, 2001, 2005; Castañeda-Posadas pers. com. 2002). These examples further support the idea that by this time, the vegetation of Mexico represented an extension of the Northern Hemisphere Tertiary flora (e.g. Rzedowski, 1991; Wendt, 1998). However, it also suggests that by this time, representatives of Mexican endemic lineages were already present in the region, giving to the southern Tertiary vegetation of North America a distinctive character. It is during the Oligocene too that the rose family (Rosaceae) also appears in the fossil record of the region (Fig. 28).

The Oligocene was an important moment for plant life in Mexico (Fig. 1f). For ca. 4 million years (32–28 mybp) ignimbrites flare up in the Sierra Madre Occidental building the largest structure of this kind in the world. This volcanic arch subsequently (from the Middle Miocene on) evolved and changed its orientation to conform to the Faja Volcánica Mexicana (Fig. 1g; Ferrari *et al.* 1999). During this time also, the Yucatan Peninsula was still covered by sea and what today is the Baja California Peninsula was part of the continent. Most likely, their subsequent geological evolution generated important and variable physiographic and climatic conditions that influenced biological selection, radiation and evolution (Fig. 1h-i). The southwards movement of the Chortis Block is particularly important to generate an idea of the geological setting where the plants were establishing themselves (Fig. 1h-i). Mexico had the configuration of a peninsula, but along its southern western coast, the displacement of the Chortis Block generated some degree of continentality, modifying the environmental conditions under which plants were able to establish, grow, radiate, etc.

The diversity of some groups of plants attained during the Oligocene contrasts with today's plant flora. For example, the presence of six genera of Anacardiaceae and eleven species of Salicaceae in the Los Ahuehuetes locality in Puebla does not have counterparts amongst the current vegetation (Figs. 8-12, 24-26; Ramírez Garduño, 1999; Ramírez and Cevallos-Ferriz, 2002). Although the diversity found in the fossil record is contradictory with respect to the current communities, most likely, these differences reflect the existence in the past of different paths that the plant communities followed, paths determined by the variable dynamics of the geological setting and the biological response of the plants to the changing environment. Definitely, these dynamic biological-geological interactions significantly contributed to the relatively sudden appearance of endemic plants in Mexico. That through the evolution of the stage (geology) and the actors (plants) during the Neogene, the megadiversity of plants and environments that are currently observed in the landscape of the region generated and established.

The fossil plant record, in increasingly younger sediments, continues documenting types of vegetation composed of elements that currently would be associated with different communities. Some researchers have suggested that this mixture of plants in the fossiliferous outcrops is due to the occurrence of alochthonous and indigenous elements (e.g., Martínez-Hernández and Ramírez-Arriaga, 1996; Graham, 1976). They predict the presence of mountains close to the fossil localities and assume an altitudinal gradient in which it would be possible to locate different communities (Martínez-Hernández and Ramírez-Arriaga, 1996; Graham, 1976). While this scenario cannot be discarded, one would expect that these strong physiographic alterations would be reflected in the geological record, especially in post-Miocene times.

To fully understand the complexity of the integration of the biota and communities of Mexico, it is important to discuss the geological process along with the plants inhabiting the different settings, and the way these were associated. An integral view would be incomplete if some climatic parameters that had a predominant role in this history were not mentioned. For example, the climatic belts that are recognized today did not always have the same extension; they expanded or contracted according to the position of the continents, the presence/absence of ice on the poles and the circulation of air and marine currents as well as their temperature, among other factors. With regard to the integration of the vegetation of Mexico during the last 70 million years, the bridge connecting North and South America, the Isthmus of Panama had only existed for the last 3.5 million years. Before that time, Mexico had the shape of a peninsula and most likely all the factors discussed above performed differently if compared with their extant behavior. Before the Isthmus of Panama formed, the double climatic cell that today characterizes both hemispheres was not well established. Shortly before Mexico became fully connected to South America, the shape of the country changed from a prominent peninsula to its current configuration by the addition of the Yucatan Peninsula to its southeastern region and the Baja California Peninsula to its northwestern region. Most likely, the addition of these peninsulas altered the physical factors of the environment to some extent, generating in the main continental mass new conditions for the establishment of plants. Furthermore, to this new conformation of Mexico we must add an important factor for the integration of its vegetation; the ice sheets that progressed upon the continents during the Plio-Pleistocene. Certainly, in the latest 3.5 million years the diversity of the flora and vegetation of Mexico that had established and developed in the region through the Upper Cretaceous and Tertiary became "modernized" and started resembling more and more the present day vegetation.

Finally, it is important to highlight that this long historical process explains how some southern and northern lineages were able to arrive into Mexico during the Cretaceous and Tertiary while it still explains how other lineages could have arrived