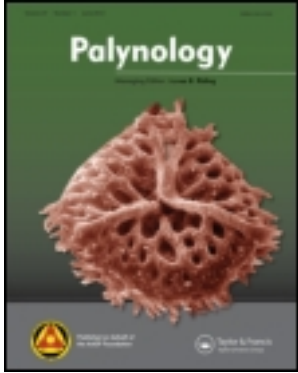


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Palynological evidence for Middle Miocene vegetation in the Tehuacán Formation of Puebla, Mexico

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Palynological assemblages from the Tehuacán Formation (TF), geochronologically dated as Middle Miocene (15.6 ± 0.4 Ma), provide evidence of a highly diverse flora that, at the generic level, is similar to the extant flora in the Tehuacán Valley. We propose that, during Miocene times, plant communities may have been formed of similar botanical elements to those seen today in the region, with some taxa adapted to semiarid conditions. While major temperate floristic elements of *Pinus*, *Quercus*, *Juniperus*, cloud forest and mexical vegetation can be recognized, components of tropical deciduous forests, such as Burseraceae, Leguminosae and Cactaceae, are also present, indicating semiarid conditions. Semiarid local conditions are also inferred from the geological record, consisting of lacustrine and alluvial fan deposits, which contain abundant evaporites beds. This lithology was formed under high evaporation and moderate precipitation conditions, as usually occurs in small basins fed by a seasonal input of water in semiarid environments. Important differences in the vegetation from the TF palynoflora as compared to older associations from south-central Mexico can be inferred, such as an increase in the diversity of semiarid taxa, belonging to Leguminosae and Burseraceae, and the oldest abundant occurrence of the Cactaceae.

Keywords: Tehuacán Formation; Miocene; palynostratigraphy; Neogene plant paleocommunities; Mexico

1. Introduction

The Tehuacán Valley (TV) (Figure 1) is the most meridional arid to semiarid zone in North America, characterised by a distinctive biotic megadiversity with a high degree of endemism for different taxonomic groups such as the Cactaceae (Tribe Pachycereae), Leguminosae, Burseraceae, Agavaceae, Fagaceae, etc. (Smith 1965; Dávila et al. 2002). This exceptional biodiversity constitutes a highly diverse mosaic of 29 vegetation types, with shrublands and tropical deciduous forests at lower elevations, dominated by columnar cacti, Leguminosae, Burseraceae, Agavaceae, Compositae, gallery forests and *Juniperus* forests, chaparral-like vegetation termed mexical, as well as oak, pine-oak, cloud and pine forests at higher elevations (Valiente-Banuet et al. 1998, 2000, 2009).

For decades, a central question has been how to explain the presence of this high biodiversity in such a relatively small area of 10,000 km² when contrasted with other larger counterpart areas of North America with similar diversities. Although traditionally the study of species richness patterns has been focused on

environmental correlations and processes occurring at local scales (Donoghue 2008), large-scale patterns of species richness respond primarily to historical effects (Wiens & Graham 2005; Wiens & Donoghue, 2004; Donoghue 2008). Knowing the biogeographical histories of extant taxa, and how their distributions have varied over time, is important in proposing an explanation for species richness patterns at a regional scale. Biogeographical and palaeontological evidence indicates that extant species in specific areas originated during different geological intervals and places, and therefore the assessment of the historical presence of taxa is central in biogeography and ecology. In particular, the Paleogene/Neogene is exceptionally important for the evolution and mixing of different taxa in Mexico (Rzedowski 1978; Becerra 2005; Valiente-Banuet et al. 2006). Consequently, the history of the floral diversity which occurs today in the TV can be understood by means of geological and palynological studies of Paleogene/Neogene lithostratigraphical units, which allow us to infer climate changes and the morphotectonic setting where the actual vegetation evolved.

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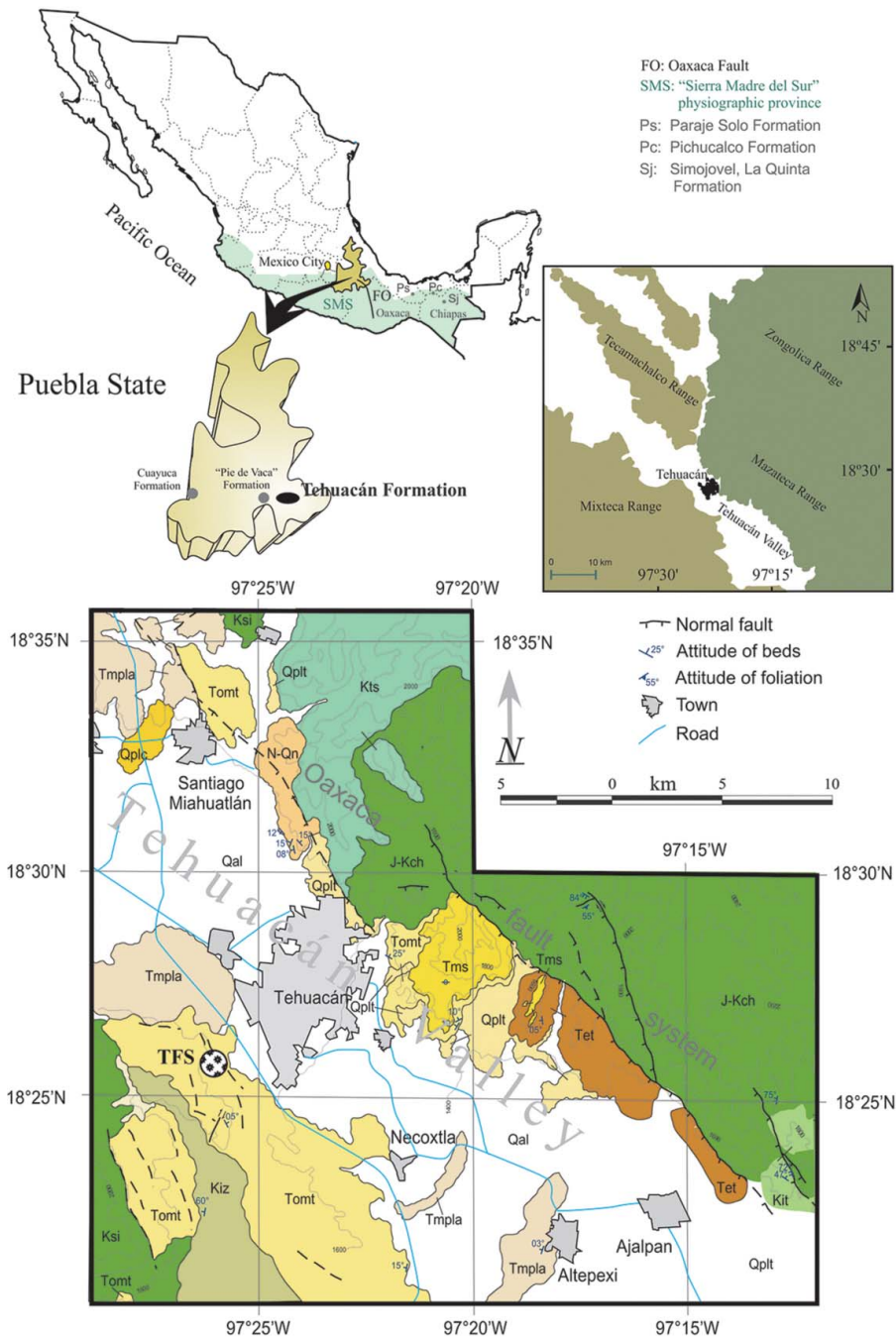


Figure 1. Location of the sections studied of the Tehuacán Formation (TFS) and geological map, modified from Dávalos-Álvarez et al. (2007). Labels on lithostratigraphical units are the same as those used in the lithostratigraphical column of Figure 2.

The TV belongs to the ‘Sierra Madre del Sur’ physiographic province (Figure 1), in which the Oaxaca Fault is an important regional structure that was active during the Cenozoic (Centeno-García 1988; Dávalos-Álvarez 2006; Dávalos-Álvarez et al. 2007), forming many continental basins. The Tehuacán Formation (TF) (Figures 1, 2) is the principal Cenozoic fill of the TV, and was deposited in an endorheic basin generated by movement on the Oaxaca Fault System (Avellaneda

et al. 1987). The age of the TF has been estimated by isotopic dates, which provide an interval of deposition from the Late Oligocene to the Middle Miocene (Dávalos-Álvarez 2006; Dávalos-Álvarez et al. 2007).

Although, there have been some palaeopalynological studies of Cenozoic sediments in Mexico, most of them have been focused on Paleogene basins. Nearly all the published Miocene palynofloras are from basins in southeastern Mexico. Oligo–Miocene

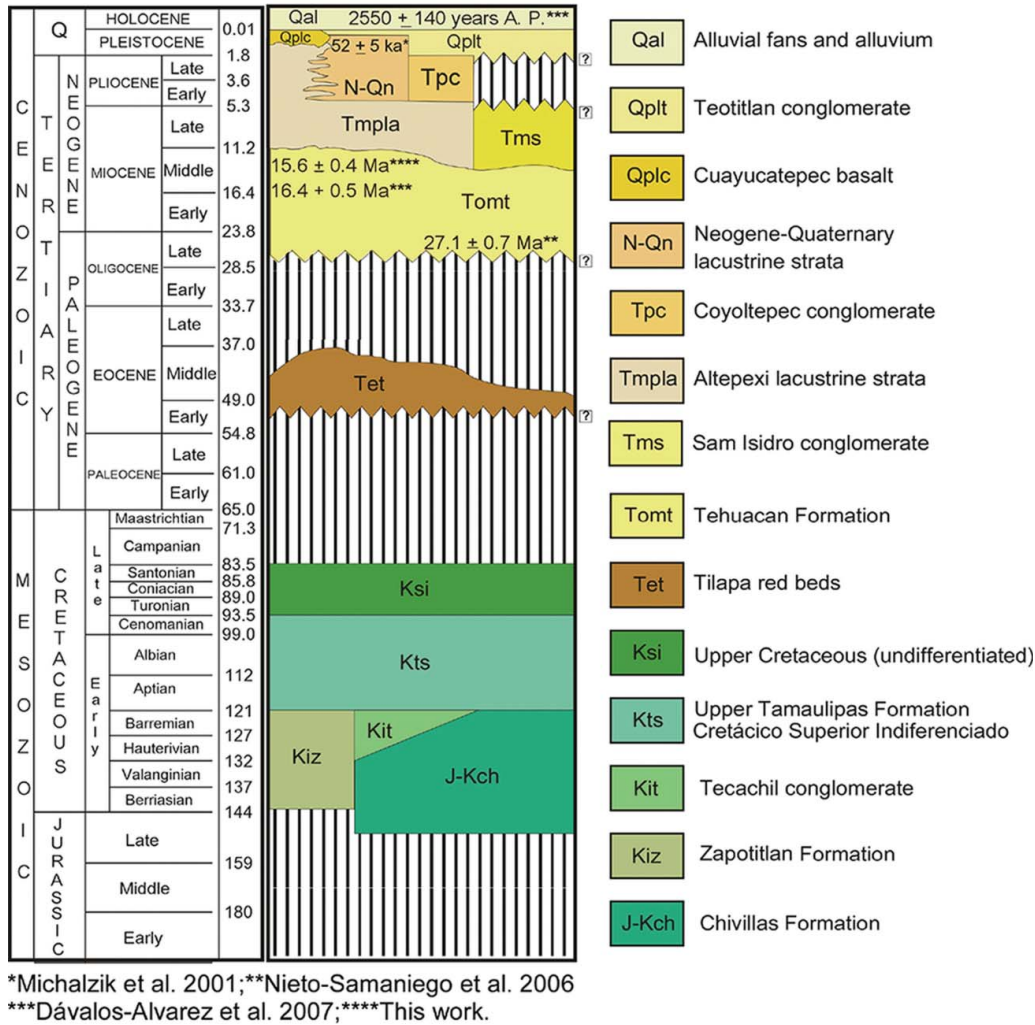


Figure 2. Lithostratigraphical column for the geological map, modified from Dávalos-Álvarez et al. (2007).

sedimentary rocks from Simojovel (Chiapas State) were studied by Langenheim et al. (1967) and Tomasini-Ortiz & Martínez-Hernández (1984). Biaggi (1978) analysed palaeoenvironmental conditions and plant communities from the La Quinta Formation in the same area that was subsequently studied by Graham (1999). Also, Palacios & Rzedowski (1993) reported fossil palynofloras from Lower–Middle Miocene sediments from Pichucalco (Chiapas State) (Figure 1). In general, these studies reported tropical rain forest, lowland vegetation and mangrove, as well as temperate communities such as *Pinus* and cloud forest.

Previous palynostratigraphical research from the Balsas Group (Cuayuca and Pie de Vaca formations), in basins adjacent to the TV, has allowed the reconstruction of local and regional plant communities, as well as the climatic conditions prevailing during Late Eocene to Early Oligocene. These studies indicate that, during the Paleogene, pollen assemblages showed diverse plant palaeocommunities corresponding to

climate regimes ranging from temperate moist to semi-arid, distributed throughout an altitudinal gradient (Martínez-Hernández & Ramírez-Arriaga 1999, 2006; Ramírez-Arriaga 2005; Ramírez-Arriaga et al. 2006). However, there is a remarkable lack of studies on Miocene floras in the TV (Ramírez-Arriaga et al. 2010).

This report is the first palynological study of the TF. Its purpose is to elucidate the origin of the current plant diversity by providing data about palaeovegetation and palaeoclimate during the late Middle Miocene climatic optimum.

2. Area studied

2.1 Geological setting

Cenozoic structures in southern Mexico are mainly strike-slip and normal faults, which formed pull-apart and graben basins, filled with continental alluvial and lacustrine deposits (Nieto-Samaniego et al. 1995, 2006; Schaaf et al. 1995; Morán-Zenteno et al. 1996; Tolson

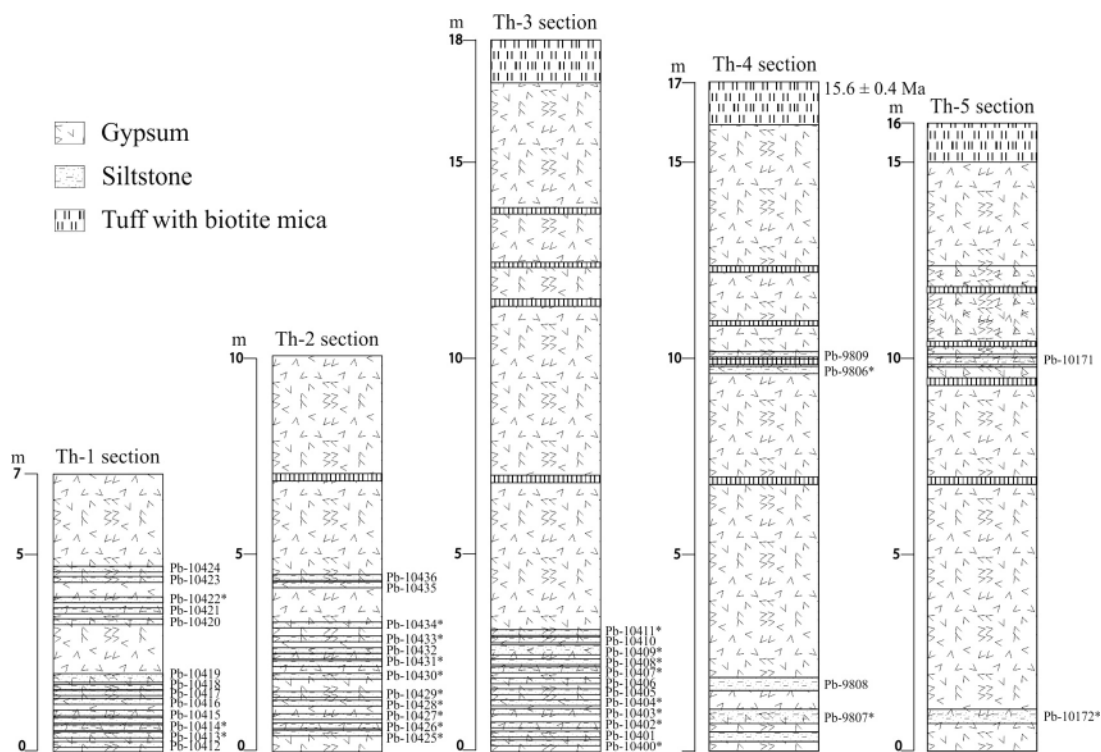


Figure 3. Lithological sections of the Tehuacán Formation, showing the levels sampled and the tuff horizon with biotite. Productive samples are indicated with (*). The geochemically dated sample was obtained from the top of section Th-4.

1998; Alaniz-Álvarez et al. 2002; Cerca et al. 2004). The TV is located within a half-graben formed by the Oaxaca Fault System (Figure 1). Sedimentation within the TV has been active since the Early Eocene (Figures 1, 2). Three main sedimentary episodes can be identified in the stratigraphical record. The older unit is the ‘Tilapa red beds’ that overlie the Mesozoic marine strata with an angular unconformity. The ‘Tilapa red beds’ consist of sandstone, limestone and conglomerate, with beds 20 to 30 cm thick. Thin beds of evaporites occur mainly towards the top of the deposit. The ‘Tilapa red beds’ are tilted, forming an angular unconformity with the overlying TF. The second sedimentary episode is recorded by the TF, which is the principal deposit in the TV (Barrientos-Reyna 1985). The first geological study of the TF was made by Aguilera (1906), who described a sequence of limestones and siltstones, with some intercalations of volcanic rocks. In general, this unit is heterolithic and varies from conglomerates to siltstones as well as evaporites (Dávalos-Álvarez 2006). In the lower part of the TF, limestone, sandstone, mudstone and siltstone lithofacies predominate, contrasting with the upper part that has a dominance of limestone, evaporites (mainly gypsum) and volcanic tuffs (Dávalos-Álvarez 2006; Dávalos-Álvarez et al. 2007). Evaporites appear commonly as thin veins and isolated small bodies. The

sampling zone for this study comprised thick beds of evaporites interbedded with thin siltstone beds, located in the upper part of the TF.

For the TF, a minimum thickness of 400 m is documented from outcrop studies. However, according to the geological sections proposed by Dávalos-Álvarez et al. (2007), the total thickness of the formation could reach 700–800 m. The age has been determined from stratigraphical relationships, correlation with other geological units, and potassium (K)-argon (Ar) dating. The deposit spans the Late Oligocene–Middle Miocene interval (Figure 2). A disconformity is interpreted as being above the TF, underlying the ‘Altepeixi lacustrine strata’ at the western edge of the valley and the ‘San Isidro conglomerate’ in the eastern part (Figures 2, 3). The disconformity indicates that deposition of the ‘Altepeixi lacustrine strata’, ‘San Isidro conglomerate’, ‘Coyotepec conglomerate’, ‘Neogene–Quaternary lacustrine strata’ and ‘Teotitlán conglomerate’ represents the third sedimentary episode, which occurred in the Middle Miocene–Pleistocene interval (Dávalos-Álvarez 2006) (Figures 1, 2).

2.2 Present environmental setting

The TV corresponds to the southern arid and semiarid province (Rzedowski 1978). The climate is determined



Figure 4. Detailed pollen diagrams from sections Th-1 and Th-2 of the Tehuacán Formation. For the scale in metres for each section, see Figure 3.

by trade winds or easterly winds in the summer, with monsoon rains. In winter, westerly winds and occasionally polar or northerly winds occur with rain in the mountains (Valiente-Banuet et al. 2000, 2009). Dryness in this region is due to a rain shadow created by the Zongolica Range (Figure 1). Climatic types vary with altitude and local conditions; however, the most common climatic regime in Tehuacán is arid and semi-arid (Bs and Bw). The mean annual temperature is 17.9 °C, with 443.7 mm of annual precipitation (García 2004).

Twenty-nine vegetation types have been reported today, most of them (24 plant communities) growing under arid and semiarid conditions, such as columnar cacti forests, scrubland, and tropical dry forest (for a detailed description see Valiente-Banuet et al. 2000, 2009).

3. Methodology

Samples for palynological studies were collected from five outcropping sections of evaporites (Th-1 to Th-5) in the upper part of the TF, located southwest of Tehuacán City (Th-1: 18°26'115" N, 97°26'9.7" W; Th-2: 18°26'16.8" N, 97°26'9.5" W; Th-3: 18°26'16" N, 97°26'9" W; Th-4: 18°26'17" N, 97°26'10" W; Th-5:

18°26'17" N, 97°26'13" W) (Figures 1, 3). These sections (7, 10, 18, 17, and 16 m thick, respectively) were sampled at the base and middle part (Figure 3). Only thin siltstones interbedded within the thick evaporites were sampled. A total of 43 siltstone samples were processed using standard techniques (Traverse 2007), but only 23 of them were productive.

Identifications and palynomorph counts were made using a ZEISS Axiolab microscope. An AxioCam digital camera and Axiovision image capturing software were used for palynomorph photography. Pollen and spore identifications were made by comparison using specialised literature. One to three slides per sample were scanned in order to count all the taxa present. Slides are deposited in the Palynology Laboratory collection of the Institute of Geology, Universidad Nacional Autónoma de México (UNAM).

3.1 Diversity and evenness indexes

The diversity index for each sample was calculated according to the following equation:

$$H' = - \sum_i^n pi \ln \cdot pi. \tag{1}$$

where H' is the diversity index (measured for pollen-spore diversity), p_i is the proportion of each palynomorph type (i) encountered in the sample and \ln is the natural logarithm (Shannon & Weaver 1949).

The evenness index (Pielou 1977) of each sample is calculated following Pielou's equation:

$$J' = \frac{H'}{H'_{\max}} \quad (2)$$

where J' is evenness, H' is the Shannon-Weaver Diversity Index, and H'_{\max} is the natural logarithm of the total number of pollen-spore taxa found in the sample. This index indicates when heterogeneous (values approach zero) or homogeneous (values approach one) pollen-spores are present in the samples analysed.

3.2 Parsimony analysis of endemism (PAE)

The palynomorph diversity of the TF is compared with five other Cenozoic basins (Tables 3 and 4) to determine floristic relationships via parsimony analysis of endemism (PAE) (Rosen 1988; Morrone & Crisci 1995; Morrone 2004; Ramírez-Arriaga et al. 2008). These are the Pie de Vaca Formation (Late Eocene–Early Oligocene: Martínez-Hernández & Ramírez-Arriaga 1999), the Cuayuca Formation (Late Eocene–Early Oligocene: Ramírez-Arriaga et al. 2008), the La Quinta Formation (Oligocene–Miocene: Biaggi 1978), the Pichualco Formation (Miocene: Palacios & Rzedowski 1993), and the Paraje Solo Formation (Pliocene: Graham 1975).

The PAE analysis was conducted using a WINCLADA data matrix (Nixon 2002), where rows correspond to formations and columns correspond to palynomorphs that are present (1) or absent (0) in each formation. In order to promote a hierarchical grouping, areas are grouped by the presence of taxa (instead of absence). NONA computer program ver2.0 was used to carry out the parsimony analysis (Goloboff 1993). The parsimony analysis was performed using a heuristic search with tree bisection and reconnection (TBR) branch swapping with 500 replications, holding 10 trees per replication, and further expanding the memory to hold up to 10,000 trees. The three statistics (Length = L, Consistency Index = CI and Retention Index = RI), which reflect the degree of conflict amongst the data, were calculated with Winclada. Methodologically, the clades for the most parsimonious solutions can be supported by species that are only present in the grouped formations, and also by species that are present in independently grouped formations, or by the absence of species. In this study, only clades supported by the presence of palynomorphs were obtained, and unique occurrences are emphasised.

3.3 Dating method

A tuff with biotite was collected at the top of section Th-4 (Figure 3, Table 2). Biotite was separated in the Geochemistry Department of the Institute of Geology, UNAM, and analysed by the K-Ar dating method in the Geochronology and Isotopic Geochemistry Laboratory of Activation Laboratories Ltd. (ACTLABS), Ontario, Canada.

4. Results

4.1 General features of the Tehuacán Formation palynoflora

The productive samples from the TF yielded well-preserved palynomorphs, including pollen, spores and algae. The total palynomorph count ranged from 117 to 310 in nine samples, 406–965 in six samples, 1002 to 6581 in five samples and only three samples contained < 100 pollen, spores and algae. A high diversity ($n = 94$) of palynomorphs was recovered from the TF, which is summarised in Table 1. Considering the diversity of the pollen and spores (Table 1), angiosperm pollen dominate the associations, with a higher quantity of Dicotyledoneae than Monocotyledonae. A lower diversity of gymnosperm pollen and spores are present.

4.2 Palaeopalynology

4.2.1 Th-1 section

Thirty-eight taxa were recovered from the three productive samples from section Th-1; within them the richness varies from five to 37 taxa, the diversity index of pollen-spores ranged from 1.3 to 2.6 and the evenness index varied from 0.7 to 0.9 (Table 1). Abundant taxa that reach values $\geq 10\%$ were *Alnus* (11.4%), Compositae (17.1%), *Momipites* (10.9%), Sterculiaceae (14.3–18.2%), *Cupressus-Juniperus-Taxodium* (22.9–54.5%) and *Pinus* (33.8%). Other common taxa are Amaranthaceae-Chenopodiaceae (4.2–5.7%), *Betula* (9.1–8.6%), *Corsiniipollenites* (1%), Leguminosae (5.5%) (Plate 4, figures 11, 15), *Liquidambar* (2.9%), Melastomataceae (1.9%), *Psilatricolpites* (3.2–9.1%), *Quercus* (8.6%) and *Sparganiaceaeipollenites* (8.4%). Some minor elements are *Acacia*, Anacardiaceae, Cactaceae (Plate 3, figures 4, 5), Gramineae, *Liliacidites*, *Malpighia*, *Mutisiapollis*, Palmae, *Perisyncolporites*, *Ulmus*, and Vitaceae. A detailed pollen diagram of palynomorphs recovered from the Th-1 section is given as Figure 4.

4.2.2 Th-2 section

In the Th-2 section, 56 taxa are recognised from nine samples. The richness per sample varies from 14 to 36

Table 1. List of the palynomorphs identified in this study: total counts, diversity index and evenness of pollen-spores are included at the end.

	Th-1			Th-2			Th-3			Th-4		Th-5
Trilete spores												
<i>Canarozonosporites</i> Pant ex Potonié 1956											2	Pb-10172
<i>Cicatricosporites</i> Potonié & Gelletich 1933											3	Pb-9806
Cyathaceae	8	4	5	32	4	2	5	1	2	1	64	Pb-9807
<i>Lusatisporis</i> aff. <i>detmannae</i> (Drugg) Srivastava 1972											25	Pb-10411
<i>Osmundacidites</i> Couper 1953											4	Pb-10409
<i>Riccia</i> L.											4	Pb-10408
<i>Selaginella</i> P. Beauv.			5				2			1	2	Pb-10407
<i>Stereosporites</i> Pflug in Thomson & Pflug 1953											2	Pb-10404
Monolete spores												
<i>Polypodium</i> L.	6	2	2	5	1	6	2	3	2	2	3	Pb-10403
<i>Polypodiaceoisporites</i> Potonié 1956			1			1				1		Pb-10402
Gymnosperms												
<i>Cupressus</i> L. - <i>Juniperus</i> L. - <i>Taxodium</i> L.	8	6	2	26	1	6	2	3	4	1	2	Pb-10400
<i>Ephedra</i> L.			1									Pb-10434
<i>Pinus</i> L.	2	1	105	102	17	59	15	11	2	2	3	Pb-10433
<i>Podocarpus</i> L'Hér. Ex Pers.												Pb-10431
Monocotyledonae												Pb-10430
Agavaceae												Pb-10429
<i>Arecipites</i> Woodehouse 1933 emend. Nichols et al. 1973												Pb-10428
Gramineae			2	17	6	6	1	1	1	2	1	Pb-10427
<i>Liatridites</i> Couper 1953			2	8	10	3	4	3	1	4	1	Pb-10426
<i>Monocolpites</i> Biswas 1962												Pb-10425
Palmae			1	2	2	55	1	2	4	9	1	Pb-10422
<i>Sparganiaceaeapollenites</i> Thiery 1937	26	75	9	9	55	20	3	3	4	9	30	Pb-10414
<i>Sriramonocolpites</i> Mathur & Mathur 1969												Pb-10413
<i>Verrumonocolpites</i> Pierce 1961												
Dicotyledonae												
<i>Acacia</i> Mill.	2				1				2		1	
<i>Alnus</i> Mill.	4				3				1		1	
Amaranthaceae - Chenopodiaceae	2	13	37	1	18	4	23	1	2	2	9	

Table 1. (Continued)

	Th-1			Th-2			Th-3						Th-4		Th-5									
	PB-10413	PB-10414	PB-10422	PB-10425	PB-10426	PB-10427	PB-10428	PB-10429	PB-10430	PB-10431	PB-10433	PB-10434	PB-10400	PB-10402	PB-10403	PB-10404	PB-10407	PB-10408	PB-10409	PB-10411	PB-9807	PB-9806	PB-10172	
Anacardiaceae			1	6	2	3	1	2	6	3	4	1	8	2	2	4	1	1	3		1			1
<i>Anacolosidites</i> Cookson & Pike 1954																								
<i>Betula</i> L.	3	1	1	2				1														2	4	
Bignoniaceae																						1		
<i>Bursera</i> Jacq. ex L.	1	15	1	1	6	1	1	8	3	1	1		3	3	9	2	2	1	1	2	25		5	
Cactaceae – pericarpate	18	1	1	1	2	2		6	1	2			1	1	3	2	5	1	1	3	9		1	
Cactaceae – peripotate	1							1					1	1										
Cactaceae – tricolpate	1												1	1				1			6		3	
<i>Caesalpinia</i> spp.													1	1							13			
<i>Calliandra</i> Benth.													1	1							2			
Campanulaceae (<i>Adenophora</i> Fisch.)													1	1							1			
<i>Carya</i> Nutt.																								1
Combretaceae													1								6			
Compositae	6	13	2	14	18	2	2	8	11	2	1	2	6	23	5	2	5	2	2	2	17	42	14	
Convolvulaceae													1											
<i>Corsiniipollenites</i> Nakoman, 1965	3			1	2	2		1											1	1	13		4	
<i>Cricotriporites</i> Leideimeyer 1966	2																							
<i>Croton</i> L.													1											
<i>Cupuliferoidaepollenites</i> Potonié, Thomson & Thiergart 1950 ex Potonié 1960																					10			
Euphorbiaceae													8	9	9	2	3		1	1	1			3
<i>Foveotricolpites</i> Pierce 1961				12		5	4	1	5										1	1	2			3
<i>Foveotricolporites</i> Pierce 1961																					2			
<i>Fraxinus</i> Tourn. ex L.					2	4		1					1	1	1						2			1
<i>Gematricolpites</i> Pierce 1961 (Linaceae)																					2			
<i>Juglans</i> L.																					2			
Leguminosae				17	9	1	22	4	2	1	1	1	3	10	14	1	4				9	13	1	
<i>Liquidambar</i> L.	1												1								8	6	2	
<i>Malpighia</i> Plum. ex L.																								
Malpighiaceae													1								4			2
Malvaceae													1								4			1

(continued)

Table 1. (Continued)

	Th-1			Th-2					Th-3					Th-4		Th-5								
	PB-10413	PB-10414	PB-10422	PB-10425	PB-10426	PB-10427	PB-10428	PB-10429	PB-10430	PB-10431	PB-10433	PB-10434	PB-10400	PB-10402	PB-10403	PB-10404	PB-10407	PB-10408	PB-10409	PB-10411	PB-9807	PB-9806	PB-10172	
<i>Malvaipollis</i> Harris 1965				1	1	1																		
Melastomataceae			6										1		1						1			
<i>Mimosa</i> L.				1																				
<i>Momipites</i> group			34	48	4	110	16	22	61	6	9	4	15	62	66	28	19	9	6	11	76	1		68
Moraceae/Urticaceae			12	3	3	1	1	1	4	1	2	2	1	1	5						1	2		
<i>Mutisiapollis</i> Macphail & Hill 1994	1					1															2			
<i>Myrtacoidites</i> Cookson et Pike ex Potonié 1960						1				1												1		1
Nyctaginaceae																								
Onagraceae													2	2	5					3		2		
<i>Perisyncolporites</i> Germeraad, Hopping & Muller 1969			1																					
<i>Platanus</i> L.																								
Polemoniaceae				1		1																		2
<i>Polyadopollenites</i> Pflug & Thomson in Thomson & Pflug 1953				1																				
Polygonaceae					1																			
<i>Psilatricolpites</i> Van der Hammen ex Van der Hammen & Wynstra 1964	1	10	1	3	1	2	5	17	2	2	2	3	10	13	2	1	2	2	2	15	5			19
<i>Psilatricolporites</i> Mathur 1963						8	1	1	3	1	1		3	1	2	2	2				1			
<i>Psilatricolporites</i> (Van der Hammen) Mathur 1966																								
<i>Quercus</i> L.	3	1	9	1	18	2	21	14	2	2	2	1	4	6	2	2	2	2	2	3	8	5	6	
<i>Retitricolpites</i> (Van der Hammen) Pierce 1961		11	9	1	47	1	4	6	2	2			4	4	1	1	1	2		9	1	3		
<i>Retitricolporites</i> (Van der Hammen)			3	9	3	2		6					23	2	3	5	1	1	1	13	2			
<i>Retitricolporites</i> Van der Hammen ex Ramanujam 1966													1		1	1								
Rosaceae		2	11	2	3	7	25		2	2		1	4	2	13	16	5	19	14	7	14	7	42	
Rubiaceae																					4			
Sapindaceae						1															2	1		
<i>Stephanocolpites</i> . <i>Combretum</i> / <i>Terminalia</i>																								

(continued)

Table 1. (Continued)

	Th-1			Th-2			Th-3			Th-4		Th-5								
Sterculiaceae	5	2	8	6	1	2	1	6	2	1	2	2	Pb-10172	Th-5						
<i>Striatopollis</i> Krutzsch 1959b							1						Pb-9806	Th-4						
<i>Striatricolporites</i> Leidekmeyer 1966							1						Pb-9807	Th-4						
<i>Thomsonipollis magnificus</i> (Th. & Pfl.) Krutz.													Pb-10411	Th-3						
<i>Thomsonipollis sabinetownensis</i> Elsik 1974													Pb-10409	Th-3						
Tiliaceae													Pb-10408	Th-3						
<i>Tricolpites</i> Cookson 1947													Pb-10407	Th-3						
<i>Tricolporopollenites</i> Pflug & Thomson in Thomson & Pflug 1953													Pb-10404	Th-3						
<i>Tricolporopollenites baculiferus</i> , Elsik (Euphorbiaceae Sapitum)													Pb-10403	Th-3						
<i>Ulmus</i> L.													Pb-10402	Th-3						
Vitaceae													Pb-10400	Th-3						
Algae													Pb-10434	Th-2						
<i>Leiosphaeridia</i> sp.													Pb-10433	Th-2						
<i>Tetraporina</i> Naumova ex Bolkhovitina 1953													Pb-10431	Th-2						
Total count	35	11	310	6581	275	2256	488	406	3099	80	564	137	117	117	166	173	166	1002	140	490
Pollen and spore Diversity Index (H')	2.0	1.3	2.6	2.8	2.6	2.1	2.6	2.6	2.8	2.5	2.3	2.3	2.5	2.7	2.7	2.4	2.7	2.6	2.6	2.4
Eveiness (J')	0.9	0.8	0.7	0.8	0.8	0.6	0.9	0.8	0.8	1	0.7	0.9	0.9	0.7	0.8	0.8	0.9	0.6	0.8	0.7

Table 2. Age determination for the tuff interbedded in the upper part of the Tehuacán Formation.

Sample	Rock type	Mineral	Coordinates	K %	⁴⁰ Ar Radiogenic nI/gr	⁴⁰ Ar Atmospheric %	Age (Ma)
Th-4	Tuff	Biotite	18°26'17" N 97°26'10" W	7.88	4.712	13.6	15.6 ± 0.4

Mineral separation in the Instituto de Geología, Universidad Nacional Autónoma de México.
Analysis performed by Activation Laboratories Ltd.

K, potassium; Ar, argon.

taxa, the diversity index of pollen-spores ranged from 2.1 to 2.8 and the evenness ranged from 0.6 to 1 (Table 1). Abundant taxa that reach percentages $\geq 10\%$ are Compositae (15.6%), *Cupressus-Juniperus-Taxodium* (10.8%), *Momipites* (10.3–22.8%), *Pinus* (10.9–41.4%), *Quercus* (20.8%) (Plate 4, figure 10), and *Sparganiaceae-pollenites* (10.3–16.1%). Pollen grains and spores which are frequently found, but not in abundance, are *Acacia* (2.3%), *Alnus* (4%), *Amaranthaceae-Chenopodiaceae* (1–8%), *Anacardiaceae* (1.3–8%) (Plate 2, figures 7, 10), *Ephedra* (1.1–2%) (Plate 1, Figure 13), *Leguminosae* (1–4.6%), *Moraceae* (1–3.3%) (Plate 4, figure 16), *Cyathaceae* (1–6.6%) and *Polypodium* (1–5.4%). Other minor components are *Arecipites*, *Bursera* (Plate 4, figures 1, 2), *Cactaceae*, *Caesalpinia*, *Calliandra* (Plate 4, figure 13), *Combretaceae* (Plate 4, figure 9), *Corsiniipollenites*, *Euphorbiaceae*, *Foveotricolporites* (Plate 4, figure 8), *Fraxinus*, *Gramineae*, *Liliacidites* (Plate 4, figures 5–7), *Malpighia* (Plate 4, figure 17), *Malvacipollis*, *Mimosa*, *Mutisiapollis*, *Myrtaceidites*, *Palmae* (Plate 4, figure 12), *Polemoniaceae*, *Polygonaceae*, *Psilatricolporites* (Plate 4, figure 14) *Rosaceae*, *Sapindaceae*, *Sterculiaceae*, *Tiliaceae* and *Ulmus*. A detailed diagram of palynomorphs recovered from the section Th-2 is given as Figure 4.

4.2.3 Th-3 section

The total taxa recognised in the two samples from the Th-3 section are 55; the within sample richness varies

from 17 to 38, the diversity index of pollen-spores ranged from 2.4 to 2.7 and the evenness varied from 0.7 to 0.9 (Table 1). The most abundant taxa that achieve values $\geq 10\%$ are Compositae (12.4%), *Leguminosae* (14%), *Momipites* (11.3–16.9%), *Pinus* (10.1–27.7%), *Rosaceae* (16.2%), *Sparganiaceae-pollenites* (10.5–11.3), and spores of *Cyathaceae* (10.8%) and *Selaginella* (12.4%). Elements which are frequent are *Alnus* (1.1–4.3%), *Amaranthaceae-Chenopodiaceae* (1.3–3.4%), *Anacardiaceae* (1.3–3.3%), *Cactaceae* (5.1%), *Euphorbiaceae* (2–2.3%), *Ephedra* (1.7–6.5%) and *Liliacidites* (2.1–3.3%). Other taxa which are present in minor percentages are *Acacia*, *Agavaceae*, *Arecipites*, *Bursera*, *Caesalpinia*, *Convolvulaceae*, *Corsiniipollenites*, *Croton*, *Fraxinus*, *Gramineae*, *Liquidambar*, *Malpighiaceae*, *Malvaceae*, *Melastomataceae*, *Moraceae*, *Mutisiapollis*, *Palmae*, *Polygonaceae*, *Sterculiaceae*, *Ulmus* and *Lusatisporis*. A detailed diagram of palynomorphs recovered from section Th-3 is given as Figure 5.

4.2.4 Th-4 section

Sixty-six taxa were identified in two samples from this section; the within-sample richness varies from 25 to 60 taxa, the diversity index of pollen-spores was 2.6 and the evenness varied from 0.6 to 0.8 (Table 1). The most abundant taxa recognised with percentages $\geq 10\%$ are Compositae (30.9%) and *Pinus* (46.9%) (Plate 1,

Table 3. Cenozoic studies considered for the parsimony analysis of endemicity (PAE) analysis herein.

	AUTHOR(S)	FORMATIONS AND LOCALITIES	ENVIRONMENT
PLIOCENE	Graham (1975)	Paraje Solo Formation: Coatzacoalcos, Veracruz	Lagoon-nearshore
MIOCENE	Palacios & Rzedowski (1993)	Pichucalco Formation: Chiapas	Mangrove-nearshore
MIDDLE MIOCENE	This study	Tehuacán Formation: Puebla	Continental
OLIGOCENE–MIOCENE	Biaggi (1978)	La Quinta Formation: Chiapas	Lagoon-nearshore
EOCENE–OLIGOCENE	Ramírez-Arriaga et al. (2008)	Cuayuca Formation: Puebla	Continental
	Martínez-Hernández & Ramírez-Arriaga (1999)	Pie de Vaca Formation: Tepexi, Puebla	Continental

Table 4. Pollen and spores present in Mexican Cenozoic formations with identification numbers (Id) that correspond to the cladogram (Figure 6) obtained from the parsimony analysis of endemicity (PAE) analysis. The taxa were reported by Martínez-Hernández & Ramírez-Arriaga (1999: Pie de Vaca Formation), Ramírez-Arriaga et al. (2008: Cuayuca Formation), Biaggi (1978: La Quina Formation), Palacios & Rzedowski (1993: Pichucalco Formation), Graham (1975: Paraje Solo Formation) and Tehuacán Formation (this study). Puebla (Pue), Chiapas (Chis), and Veracruz (Ver) States.

PAE Id	TAXA	Pue Cuayuca Formation	Chis La Quinta Formation	Ver Paraje Solo Formation	Chis Pichucalco Formation	Pue Pie de Vaca Formation	Pue Tehuacán Formation
0	<i>Abies</i>	0	0	1	1	1	0
1	<i>Acacia</i>	1	1	0	1	1	1
2	<i>Acer</i>	0	1	0	1	0	0
3	<i>Aesculidites</i>	0	0	0	1	0	0
4	Agavaceae	0	0	0	1	1	1
5	<i>Aglaoeidia</i>	1	0	0	0	1	0
6	<i>Alchornea</i>	1	1	1	1	0	0
7	<i>Alnus</i>	1	1	1	1	0	1
8	<i>Alsophila</i>	0	1	1	1	0	0
9	Anacardiaceae	1	0	0	0	1	1
10	<i>Annona</i>	1	0	0	1	0	0
11	<i>Anthoceros</i>	1	0	0	0	1	0
12	<i>Arecipites</i>	1	1	0	0	0	1
13	<i>Armeria</i>	1	0	0	0	1	0
14	<i>Asplenium</i>	0	1	0	1	0	0
15	<i>Ayenia</i>	0	0	0	1	0	0
16	<i>Betula</i>	0	0	0	0	1	1
17	Bignoniaceae	0	0	0	0	1	1
18	Bombacaceae	1	0	0	0	1	1
19	<i>Bombax</i>	0	1	0	1	0	0
20	Bromeliaceae	0	0	0	1	0	0
21	<i>Bursera</i>	1	0	1	1	1	1
144	Cactaceae	0	0	0	0	0	1
22	<i>Caesalpinia</i>	1	0	0	0	1	1
145	<i>Calliandra</i>	0	0	0	0	0	1
23	<i>Camazonosporties</i>	1	0	0	0	0	0
146	Campanulaceae	0	0	0	0	0	1
24	<i>Carya</i>	1	0	0	1	1	0
25	Caryophyllaceae	0	1	0	0	1	0
26	<i>Cassia</i>	0	0	0	1	0	0
27	<i>Castanea</i>	0	0	0	1	0	0
28	<i>Casuarinidites</i>	1	1	0	0	0	0
29	<i>Catopsis</i>	0	0	0	1	0	0
30	<i>Cedrela</i>	0	0	1	1	0	0
31	<i>Cedrus</i>	0	1	0	1	0	0
32	<i>Celtis</i>	1	1	1	1	0	0
51	Chenopodiaceae- Amaranthaceae	1	1	1	1	1	1
34	<i>Cicatricosisporites</i>	0	1	0	0	0	1
35	<i>Clethra</i>	0	1	0	1	0	0
36	Clethraceae	0	0	0	0	1	0
37	<i>Coccoloba</i>	0	0	1	1	0	0
147	Combretaceae	0	0	0	0	0	1
38	<i>Combretum</i>	0	1	1	1	0	0
39	Commelinaceae	1	0	0	0	0	0

(continued)

Table 4. (Continued)

PAE Id	TAXA	Pue	Chis	Ver	Chis	Pue	Pue
		Cuayuca Formation	La Quinta Formation	Paraje Solo Formation	Pichucalco Formation	Pie de Vaca Formation	Tehuacan Formation
40	Compositae	1	0	1	1	1	1
148	Convolvulaceae	0	0	0	0	0	1
41	<i>Corsiniipollenites</i>	1	0	0	0	1	1
42	<i>Corylus</i>	0	1	0	1	1	0
149	<i>Cricotriporites</i>	0	0	0	0	0	1
150	<i>Croton</i>	0	0	0	0	0	1
43	<i>Cupania</i>	0	1	1	0	0	0
44	<i>Cuphea</i>	0	0	1	1	0	0
45	<i>Cupressus-Juniperus-Taxodium</i>	1	0	0	1	1	1
46	<i>Cupuliferoipollenites</i>	0	1	0	0	0	1
47	<i>Cyathea</i>	0	1	1	0	0	0
48	Cyatheaceae	1	0	0	1	1	1
49	<i>Cycadopodites</i>	0	0	0	1	0	0
50	Cyperaceae	1	0	1	0	1	0
52	<i>Engelhardtia</i>	0	1	1	1	0	0
53	<i>Ephedra claricristata</i>	1	0	0	0	1	0
54	<i>Ephedripites</i>	1	0	0	1	1	1
55	<i>Equisetum</i>	0	1	0	1	0	0
56	<i>Eucommia</i>	1	0	0	0	1	0
57	<i>Eugenia</i>	0	1	1	1	0	0
58	Euphorbiaceae	1	0	0	0	0	1
59	<i>Fagus</i>	0	1	0	1	0	0
60	<i>Faramia</i>	0	0	1	1	0	0
61	<i>Ficus</i>	1	1	0	0	0	0
151	<i>Foveotricolpites</i>	0	0	0	0	0	1
152	<i>Foveotricolporites</i>	0	0	0	0	0	1
62	<i>Fraxinus</i>	0	1	0	1	0	1
153	<i>Gematricolpites</i>	0	0	0	0	0	1
63	Gesneriaceae	1	0	0	0	1	0
64	Gramineae	1	1	1	1	1	1
65	<i>Guarea</i>	0	0	1	1	0	0
66	<i>Hedyosmum</i>	0	0	1	1	0	0
67	<i>Heliocarpus</i>	0	0	0	0	1	0
68	<i>Hemitelia</i>	0	0	1	0	0	0
69	<i>Ilex</i>	0	1	1	1	1	0
70	<i>Jamesonia</i>	0	1	0	1	0	0
71	<i>Juglans</i>	1	1	1	1	1	1
72	Labiatae	1	1	0	0	1	0
73	<i>Laevigatosporites</i>	1	0	0	1	1	0
74	Leguminosae	1	0	0	0	1	1
75	<i>Leiosphaeridae</i>	1	0	0	0	0	1
76	<i>Leiotriletes</i>	1	0	0	1	0	0
77	<i>Leptolepidites</i>	1	0	0	0	0	0
78	<i>Liliacidites</i>	1	1	0	1	1	1
79	<i>Liquidambar</i>	1	1	1	1	1	1
80	<i>Lycopodium</i>	1	1	1	1	1	0
81	<i>Lygodium</i>	0	1	0	1	0	0
33	<i>Malpighia</i>	0	0	1	1	0	1
82	Malpighiaceae	0	0	0	1	1	1
83	<i>Malvacipollis</i>	1	0	0	0	1	1

(continued)

Table 4. (Continued)

PAE Id	TAXA	Pue	Chis	Ver	Chis	Pue	Pue
		Cuayuca Formation	La Quinta Formation	Paraje Solo Formation	Pichucalco Formation	Pie de Vaca Formation	Tehuacan Formation
84	Melastomataceae	0	0	0	1	0	1
85	Meliaceae	1	0	0	1	1	0
86	<i>Meliosma</i>	0	0	1	1	0	0
87	<i>Mimosa</i>	1	0	1	1	0	1
88	<i>Momipites</i>	0	1	0	0	0	1
89	<i>Momipites coryloides</i>	1	0	0	0	1	1
90	<i>Momipites microcoryphaceous</i>	1	0	0	0	1	1
91	<i>Momipites triorbicularis</i>	0	0	0	0	1	0
92	<i>Momipites triradiatus</i>	1	0	0	0	1	0
93	<i>Monocolpopollenites</i>	0	1	0	0	0	0
94	Moraceae	1	0	0	0	1	1
154	<i>Mutisiapollis</i>	1	0	0	0	0	1
95	<i>Myrica</i>	0	0	1	1	0	0
96	Myrtaceae	1	1	0	0	1	1
155	Nyctaginaceae	0	0	0	0	0	1
97	<i>Nypa</i>	0	1	0	1	0	0
98	<i>Nyssa</i>	0	1	0	1	0	0
99	Onagraceae	1	1	0	0	0	1
100	Palmae	0	0	0	0	1	1
101	<i>Passiflora</i>	0	0	1	1	0	0
102	<i>Pelliciera</i>	0	1	0	1	0	0
156	<i>Perisyncolporites</i>	0	0	0	0	0	1
103	<i>Picea</i>	1	0	1	1	1	0
104	<i>Pinus</i>	1	1	1	1	1	1
105	Piperaceae	0	0	0	1	0	0
106	<i>Platanus</i>	1	0	0	1	1	1
107	<i>Platycarya</i>	1	0	0	1	0	0
108	<i>Podocarpus</i>	0	0	1	1	1	1
157	Polemoniaceae	0	0	0	0	0	1
158	<i>Polyadopollenites</i>	1	0	0	0	0	1
109	<i>Polygala</i>	0	1	0	1	0	0
110	Polygalaceae	1	0	0	0	1	0
111	Polygonaceae	1	0	0	0	1	1
112	Polypodiaceae	0	1	0	0	1	1
113	<i>Polypodiisporites</i>	1	0	0	0	0	0
114	Pontederaceae	0	0	0	0	1	0
115	<i>Populus</i>	0	0	1	1	0	0
159	<i>Psilatricolpites</i>	0	0	0	0	0	1
160	<i>Psilatricolporites</i>	1	0	0	0	0	1
161	<i>Psilatirporites</i>	0	0	0	0	0	1
116	Pteridophyta	1	0	0	0	0	1
117	<i>Pteris</i>	0	1	1	1	0	0
118	<i>Pterocarya</i>	1	1	0	0	1	0
119	<i>Quercus</i>	1	1	1	1	1	1
120	<i>Reevesia</i>	0	0	0	0	1	0
162	<i>Retitricolpites</i>	0	0	0	0	0	1
163	<i>Retitricolporites</i>	0	0	0	0	0	1
164	<i>Retitriporites</i>	0	0	0	0	0	1
121	<i>Rhamnus</i>	1	0	0	1	0	0
122	<i>Rhizophora</i>	0	1	1	1	0	0

(continued)

Table 4. (Continued)

PAE Id	TAXA	Pue Cuayuca Formation	Chis La Quinta Formation	Ver Paraje Solo Formation	Chis Pichucalco Formation	Pue Pie de Vaca Formation	Pue Tehuacan Formation
123	Rosaceae	1	0	0	0	1	1
165	Rubiaceae	0	0	0	0	0	1
124	<i>Salix</i>	1	1	0	1	0	0
125	Sapindaceae	1	0	0	0	1	1
126	<i>Selaginella</i>	1	1	1	1	1	1
127	<i>Serjania</i>	0	0	1	1	0	0
128	<i>Smilax</i>	0	0	1	1	0	0
129	Solanaceae	0	0	0	0	1	1
130	<i>Sphaeropteris</i>	1	1	0	0	0	0
131	<i>Sphagnum</i>	0	0	0	1	1	0
166	<i>Stephanocolpites</i>	0	0	0	0	0	1
132	Sterculiaceae	1	1	0	0	0	1
133	<i>Stereisporites</i>	1	0	0	0	0	1
167	Striatopollis	0	0	0	0	0	1
168	<i>Striatricolporites</i>	0	0	0	0	0	1
134	<i>Struthanthus</i>	0	0	1	1	0	0
135	<i>Thomsonipollis</i>	1	0	0	1	0	1
136	<i>Tilia</i>	0	1	0	1	0	0
137	Tiliaceae	1	0	0	0	1	1
138	<i>Tillandsia</i>	0	0	0	1	0	0
139	<i>Tournefortia</i>	0	1	1	1	0	0
169	<i>Tricolpites</i>	0	0	0	0	0	1
170	<i>Tricolporopollenites</i>	0	0	0	0	0	1
140	<i>Typha</i>	1	0	0	0	1	0
141	<i>Ulmus</i>	1	1	1	1	1	1
142	Urticaceae	1	1	0	1	1	0
143	<i>Verrucatosporites</i>	0	0	0	1	0	0
171	Vitaceae	0	0	0	0	0	1

figure 14). Also, common were *Alnus* (5.1%) (Plate 1, figure 15), *Cupressus-Juniperus-Taxodium* (6.6%) (Plate 3, figure 1), Cyathaceae (6.5%) (Plate 1, figure 5), Gramineae (6.6%), Leguminosae (9.6%) (Plate 2, figure 5), *Liliacidites* (6.6%), *Momipites* (7.8%) (Plate 3, figure 12), Rosaceae (5.1%) and *Sparganiaceapollenites* (5.8%) (Plate 2, figure 2). Minor components are *Acacia* spp. (Plate 2, figures 1, 8), Amaranthaceae-Chenopodiaceae (Plate 2, figure 9), *Betula* (Plate 2, figure 6), *Bursera* (Plate 1, figure 10; Plate 4, figure 3), Cactaceae (Plate 3, figures 3, 6), *Cicatricosisporites* (Plate 1, figure 2), *Caesalpinia* (Plate 2, figure 12), Combretaceae, Compositae (Plate 2, figure 13; Plate 3, figures 8–10), *Corsiniipollenites* (Plate 2, figure 17; Plate 3, figure 13), *Ephedra* (Plate 1, figures 9), Anacardiaceae (Plate 2, figure 16), Bignoniaceae, *Leiosphaeridia* (Plate 1, figure 4), *Liquidambar* (Plate 1, figure 7), Malpighiaceae (Plate 2, figure 14),

Malvaceae (Plate 3, figure 14), *Mutisiapollis* (Plate 3, figure 7), *Myrtacidites*, *Polypodium* sp. (Plate 1, figure 1), *Quercus* (Plate 3, figure 2), *Selaginella* (Plate 1, figures 3, 6), *Stephanocolpites*, *Tetraporina* (Plate 1, figure 8), *Thouinia* (Plate 1, figure 11) and *Ulmus* (Plate 2, figure 15). Figure 5 is a detailed diagram of palynomorphs recovered from section Th-4.

4.2.5 Th-5 section

Thirty-eight taxa were recovered from the single productive sample from this section, the diversity index of pollen-spores is 2.4 and the evenness is 0.7 (Table 1). The most abundant taxa are *Momipites* (16.8%), Rosaceae (10.4%) and *Pinus* (35.8%), followed by frequent elements such as Compositae (3.5%), *Quercus* (1.5%) and *Sparganiaceapollenites* (6.7%). The less abundant

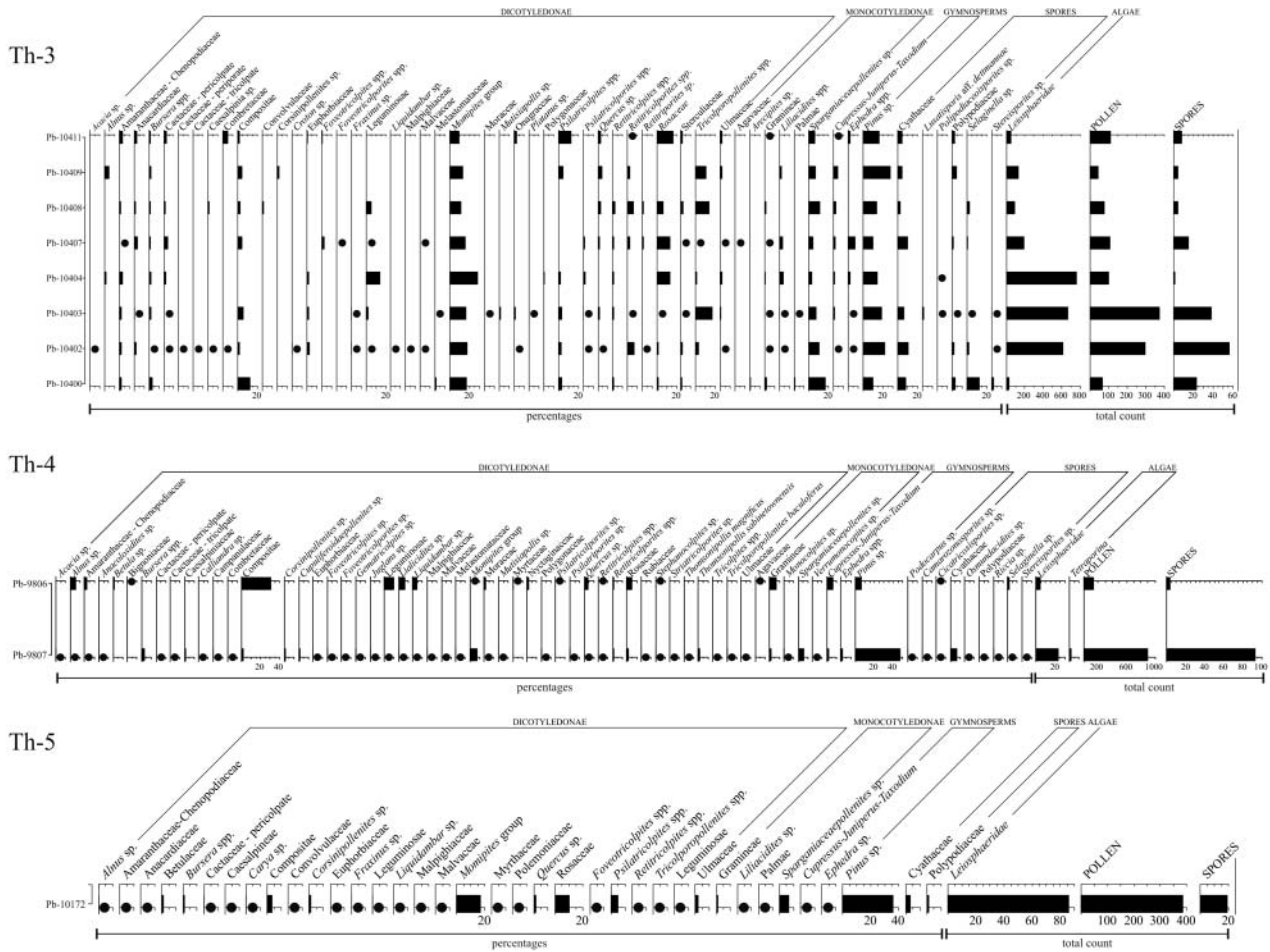


Figure 5. Detailed pollen diagrams from sections Th-3, Th-4 and Th-5 of the Tehuacán Formation. For the scale in metres for each section see Figure 3.

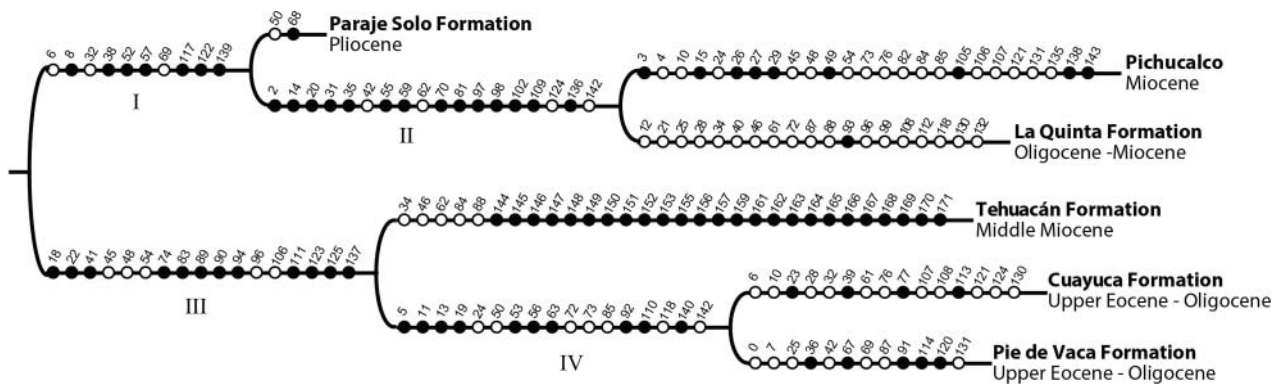


Figure 6. Cladogram (Length = 260, Consistency Index = 0.66, and Retention Index = 0.47) resulting from parsimony analysis of endemcity (PAE) comparisons of Cenozoic basins (see Table 3). Solid circles indicate the unique presence of palynomorphs (numbers as in Table 4); the empty circles indicate no unique presence of palynomorphs; I, II, III, and IV indicate the clades discussed in the text.

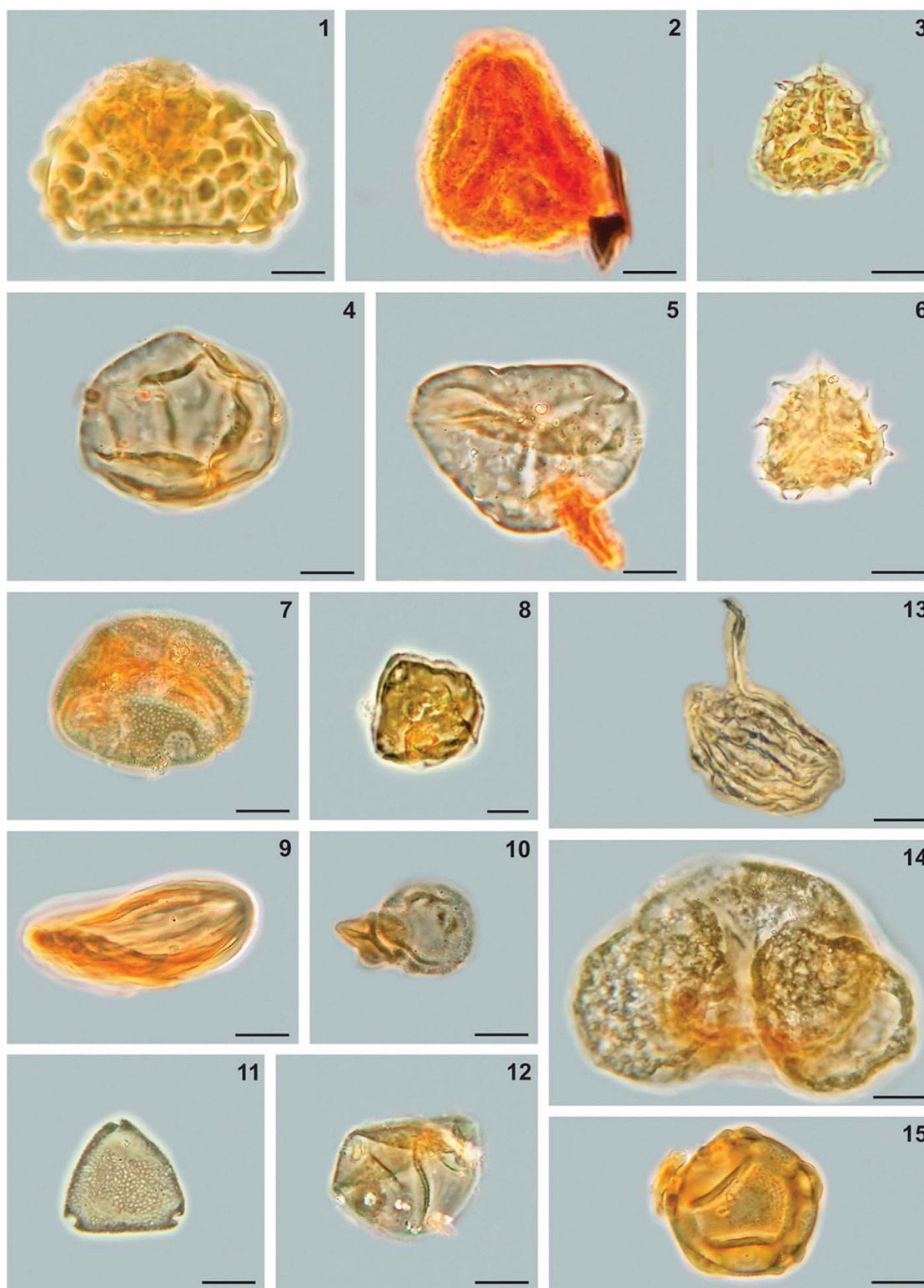


Plate 1. Spores, algae, and pollen grains recovered from the Tehuacán Formation. The scale bars represent 10 μ m. Figure 1. *Polypodium* sp. (slide Pb-9807-1, EF: H37/2). Figure 2. *Cicatricosisporites* sp. (slide Pb-9807-1: 103.7/15.7). Figures 3, 6. *Selaginella* sp. (slide Pb-9807-2: 98.7/21.3). Figure 4. *Leiosphaeridia* sp. (slide Pb-9807-1, EF: D35/2). Figure 5. Cyathaceae (slide Pb-9807-1, EF: C36/4). Figure 7. *Liquidambar* sp. (slide Pb-9806-3: 108/9.7). Figure 8. *Tetraporina* sp. (slide Pb-9807-3, EF: R35/2). Figure 9. *Ephedra* sp.1 (slide Pb-9807-1, EF: F27/3). Figure 10. *Bursera* sp. (slide Pb-9807-1, EF: D38/2). Figure 11. *Thouinia* sp. (slide Pb-9807-1, EF: H43/2). Figure 12. Gramineae (slide Pb-9806-3: 103.5/12.6). Figure 13. *Ephedra* sp.2 (slide Pb-10429-3, EF: L43/2). Figure 14. *Pinus* sp. (slide Pb-9807-1: 108/22.7). Figure 15. *Alnus* sp. (slide Pb-9807-1, EF: L32/3).

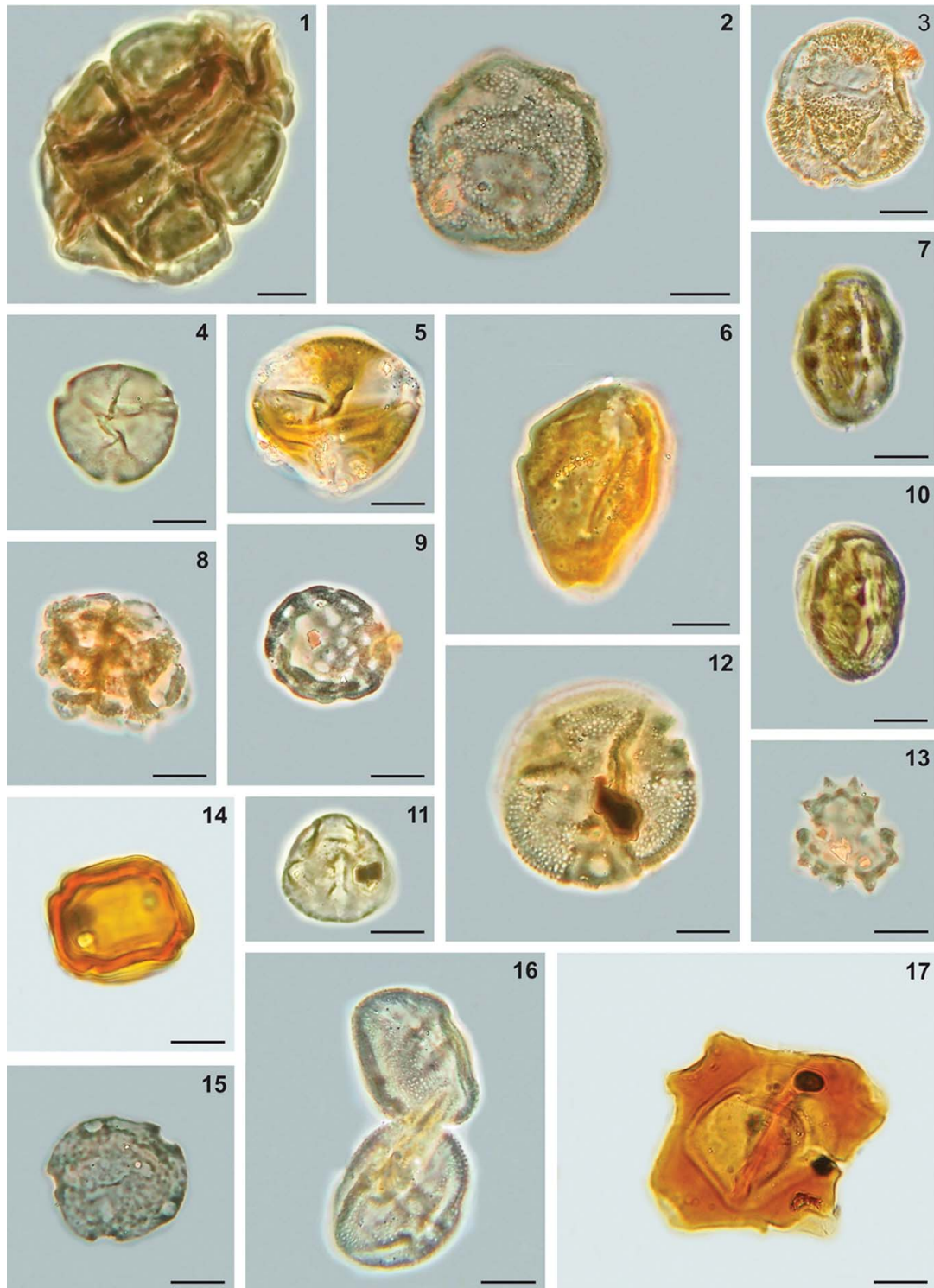


Plate 2. Pollen grains from the Tehuacán Formation. The scale bars represent 10 μm . Figure 1. *Acacia* sp. (slide Pb-9807-3, EF: P33/2). Figure 2. *Sparganiaceapollenites* sp. (slide Pb-9807-1, EF: D38/1). Figure 3. Euphorbiaceae (slide Pb-9807-2: 98.3/23). Figure 4. *Momipites microcoryphaeus* Potonié 1931 (slide Pb-9807-1, EF: F43/1). Figure 5. Leguminosae (slide Pb-9806-5: 102/2.6). Figure 6. *Betula* sp. (slide Pb-9806-3: 114.5/12.6). Figures 7, 10 Anacardiaceae (slide Pb-10425-1: 110.4/16.8). Figure 8. *Acacia* sp. (slide Pb-9807-1, EF: S43/4). Figure 9. Amaranthaceae-Chenopodiaceae (slide Pb-9807-1, EF: G42/4). Figure 11. Leguminosae (slide Pb-9807-3). Figure 12. *Caesalpinia* sp. (slide Pb-9807-1, EF: R33/4). Figure 13. Compositae type 1 (slide Pb-9807-1: 105.1/19.9). Figure 14. Malpighiaceae (slide Pb-9807-1: 100.1/16.3). Figure 15. *Ulmus* sp. (slide Pb-9807-1, EF: G29/2). Figure 16. Anacardiaceae (slide Pb-9807-1: 121.6/9.3). Figure 17. *Corsiniipollenites* sp. 2 (slide Pb-9807-1: 119.8/16.3).

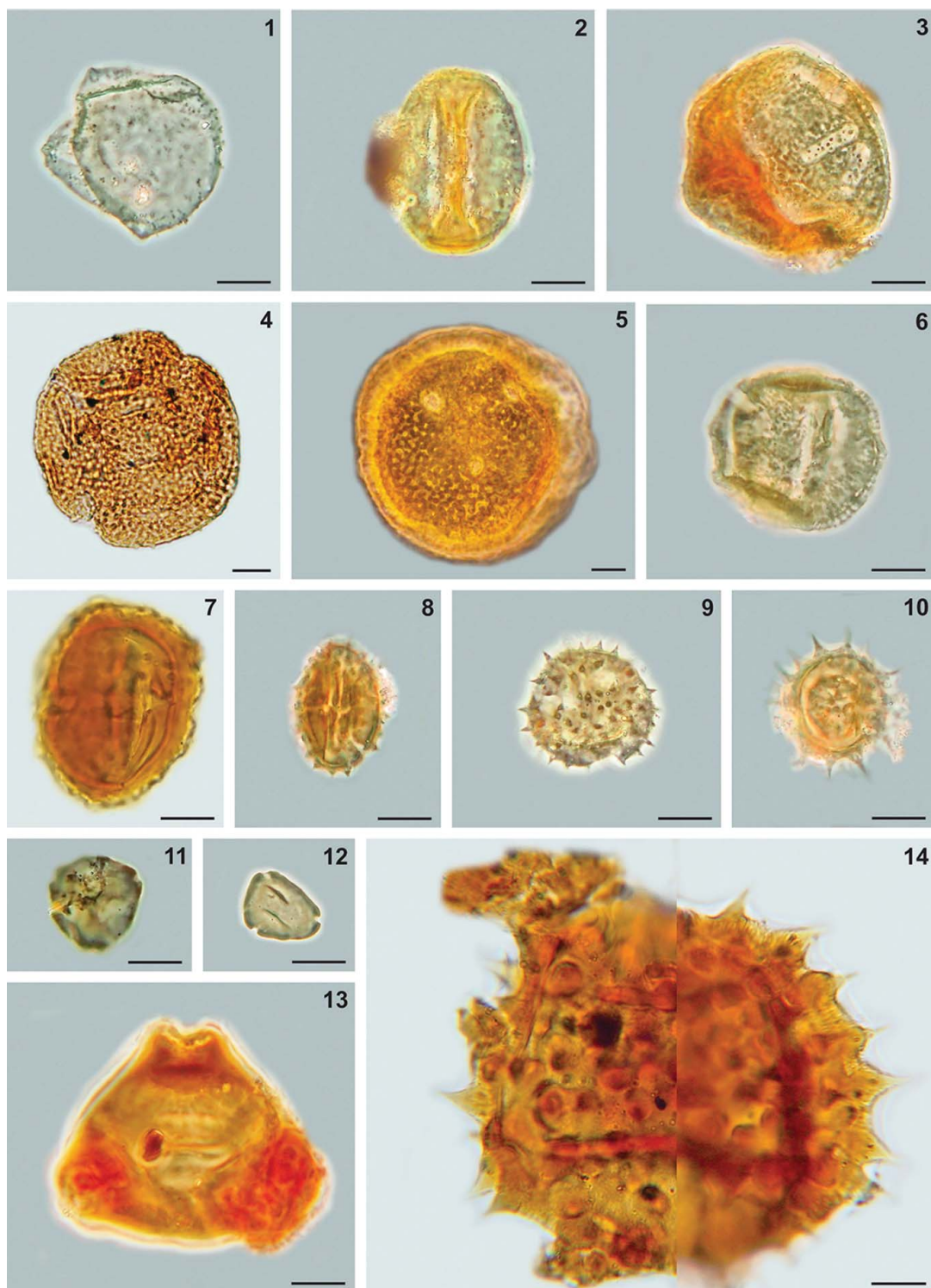


Plate 3. Pollen grains from the Tehuacán Formation. The scale bars represent 10 μ m. Figure 1. *Cupressus/Juniperus/Taxodium* Type (slide Pb-9807-1, EF: K38/2). Figure 2. *Quercus* sp. (slide Pb-9806-3: 112.8/8.7). Figure 3. Cactaceae pericolpate (slide Pb-9807-1, EF: H39/3). Figure 4. Cactaceae pericolpate (slide Pb-10422-1G: 88.1/16.9). Figure 5. Cactaceae periporate (slide Pb-10422-1G: EF: F38/1). Figure 6. Cactaceae tricolpate (slide Pb-9807-1, EF: D42/3). Figure 7 *Mutisiapollis* sp. (slide Pb-9807-1, EF: D27/2). Figure 8. Compositae type 2 (slide Pb-9806-3: 110/10). Figure 9. Compositae type 3 (slide Pb-9807-1, EF: C27/2). Figure 10. Compositae type 4 (slide Pb-9806-5, EF: N30/4). Figure 11. *Momipites triorbicularis* Leffingwell 1971 (slide Pb-9807-1: 122/10). Figure 12. *Momipites coryloides* Woodehouse 1933 (slide Pb-9807-1, EF: J41/1). Figure 13. *Corsinipollenites* sp. (slide Pb-9807-1, EF: D27/2). Figure 14. Malvaceae (slide Pb-9807-1, EF: Q25/1).



Plate 4. Pollen grains from the Tehuacán Formation. The scale bars represent 10 μm . Figure 1. *Bursera striate* (slide Pb-10425-1, EF: F50/2). Figures. 2. *Bursera striate-reticulate* (slide Pb-10425-1, EF: F43/3). Figure 3. *Bursera microreticulate* (slide Pb-9807-1). Figure 4. *Fraxinus* sp. (slide Pb-10172-1, EF: E34/3). Figure 5. *Liliacidites* sp. 1 (slide Pb-10425-1, EF: U48/1). Figure 6. *Liliacidites* sp. 2 (slide Pb-10425-1: 108.2/8.8). Figure 7. *Liliacidites* sp. 3 (Pb-10427-3, EF: H37/2). Figure 8. *Foveotricolporites* sp. (slide Pb-10428-3, EF: Q32/4). Figure 9. Combretaceae (slide Pb-10425-1: 102/7.1). Figure 10. *Quercus* sp. (slide Pb-10425-1: 111.2/17.7). Figure 11. Leguminosae (slide Pb-10422-1G: 96/5). Figure 12. Palmae (slide Pb-10428-3, EF: V33/4). Figure 13. *Calliandra* sp. (slide Pb-10433-3, EF: L46/4). Figure 14. *Psilatricolpites* sp. (slide Pb-10433-3, EF: S36/1). Figure 15. Leguminosae (slide Pb-10422-1G: 95.5/5.6). Figure 16. Moraceae (slide Pb-10434.3, EF: T40/2). Figure 17. *Malpighia* sp. (slide Pb-10425-1, EF: S33/2). Figure 18. Polemoniaceae (slide Pb-10172-2, EF: G36/3).

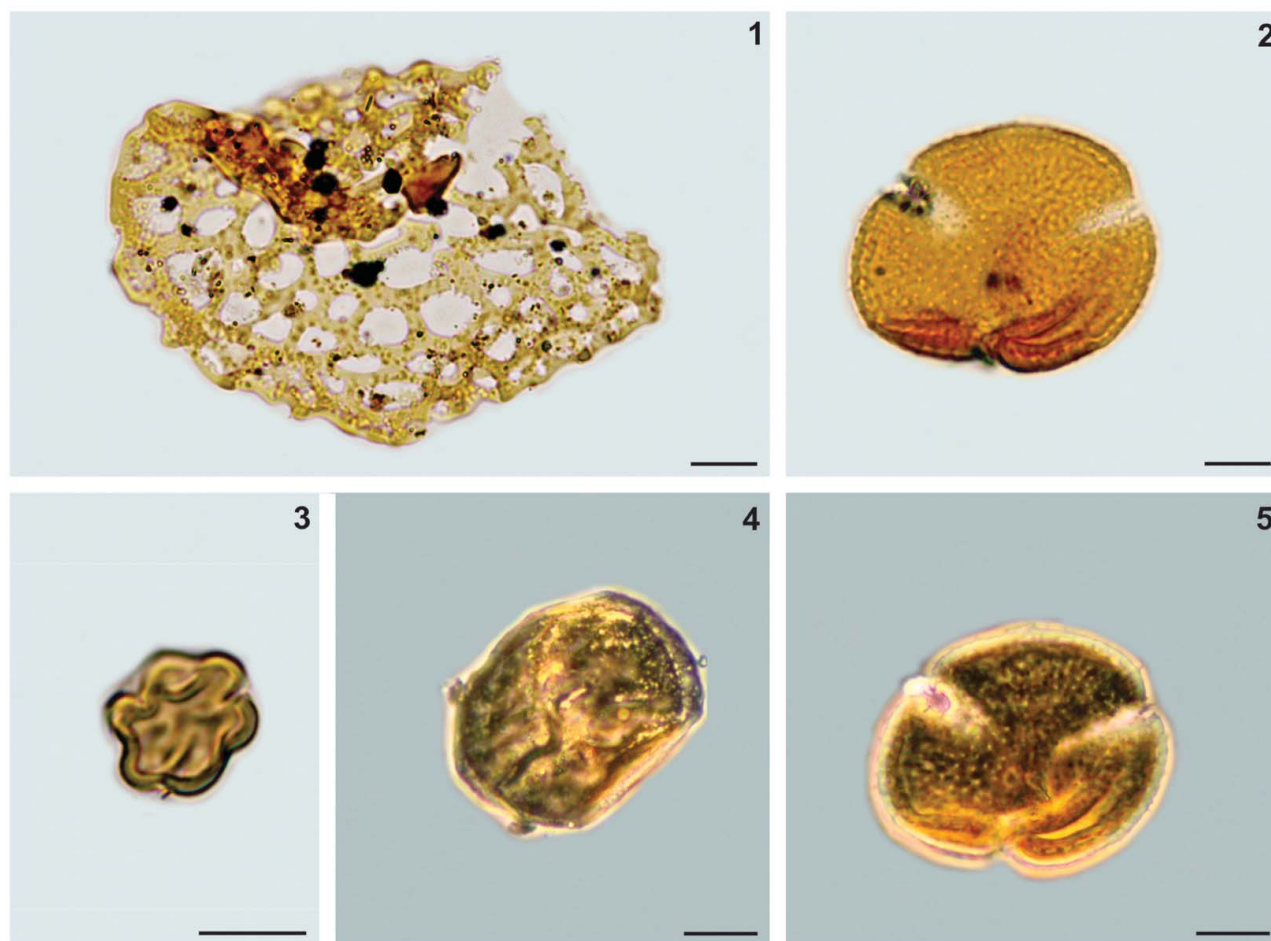


Plate 5. Figure 1. Agavaceae Pb-10407-3, EF: N35/2; Figures 2, 5. *Neobuxbaumia* type Pb-10422-6, EF: V44/2. Figure 3. Melastomataceae Pb-10422-1: 106.9/16.5. Figure 4. *Lusatisporis* aff. *dettmannae* Pb-10403-1, EF: Q36/2.

taxa are *Alnus*, Amaranthaceae-Chenopodiaceae, Anacardiaceae, Betulaceae, *Bursera*, Cactaceae, *Caesalpinia*, *Carya*, Convolvulaceae, *Corsiniipollenites*, *Cupressus-Juniperus-Taxodium*, Euphorbiaceae, *Ephedra*, *Fraxinus* (Plate 4, figure 4), Gramineae, Leguminosae, *Liliacidites*, *Liquidambar*, Malpighiaceae, Malvaceae, *Myrtacidites*, Palmae, Polemoniaceae (Plate 4, figure 18), *Ulmus* sp., and the spores of Cyathaceae and *Polypodium*. Figure 5 is a detailed diagram showing the relative abundance of palynomorphs recovered from section Th-5.

4.3 Descriptions of Agavaceae, Burseraceae and Cactaceae

The descriptive terminology is based on Punt et al. (2007).

Agavaceae (Plate 5, figure 1)

Monads, oblate, heteropolar, bilateral symmetry, monosulcate. Exine subectate, columellate, reticulate,

heterobrochate, lumina from 4 to 14 μm , simplicolumellate and duplicolumellate muri, 2 μm width. Exine < 1 μm thick, columella heterogeneously distributed under the muri. Polar axis = 52 μm , equatorial axis = 76 μm .

Botanical affinity: *Agave* cf. *asperrima* Jacobi (López 2010).

Burseraceae

Bursera microreticulate (Plate 4, figure 3)

Monads, oblate spheroidal, isopolar, radial symmetry, triporate. Aspidate elliptical pores with discontinuous convergent thickness. Exine subectate, columellate, microreticulate. Exine < 1 μm thick, sexine/nexine relationship 1:1, lumen and muri < 1 μm . Polar axis = 15 μm , equatorial axis = 15 μm .

Botanical affinity: *Bursera* aff. *aptera* Ramírez (Palacios 1984).

Bursera striate-reticulate (Plate 4, figure 2)

Monads, subprolate, isopolar, radial symmetry, triporate. Aspidate elliptical pores with discontinuous convergent thickness of 2–3 μm . Exine subtectate, reticulate-striate, columellate. Exine 1 μm thick. Polar axis = 25 μm , equatorial axis = 26 μm .

Botanical affinity: *Bursera* aff. *fagaroides* (Kunth) Engl. (Palacios 1984).

Bursera striate (Plate 4, figure 1)

Monads, subprolate, isopolar, radial symmetry, triporate. Aspidate elliptical pores with discontinuous convergent thickness of 1 μm . Exine subtectate, striate, columellate. Exine < 1 μm thick, sexine/nexine relationship 1:1, polar axis = 27 μm , equatorial axis = 21 μm .

Botanical affinity: *Bursera* aff. *aloexylum* (Schiede ex Schltdl.) Engl. (Palacios 1984).

Cactaceae

Cactaceae tricolpate (Plate 5, figures 2, 5)

Monads, subprolate, isopolar, radial symmetry, tricolpate. Exine tectate, columellate, perforate, supramicroequinate, columellate diameter of 1 μm . Exine 2–3 μm thick, sexine/nexine relationship 2:1. Polar axis = 39 μm , equatorial axis = 32 μm .

Botanical affinity: *Neobuxbaumia* Backeb. (Leuenberger 1976).

Cactaceae pericarpate (Plate 3, figures 3, 4)

Monads, spheroidal, apolar, radial symmetry, pericarpate, colpi 11–12 μm length. Exine tectate, columellate, foveolate, supramicroequinate. Exine 3 μm thick, columella diameter \leq 1 μm , sexine/nexine relationship 2:1. Diameter = 48–53 μm .

Botanical affinity: *Astrophytum* F. Ritter (Leuenberger 1976).

Cactaceae periporate (Plate 3, figure 5)

Monads, spheroidal, apolar, radial symmetry, periporate, pore diameter of 6–9 μm . Exine tectate, columellate, foveolate, supramicroequinate. Exine 4–5 μm thick, columella diameter of 1–2 μm , sexine/nexine relationship 3:1. Foveolae of 2–3 μm . Diameter = 67–75 μm .

Botanical affinity: *Cylindropuntia* (Engelm.) F.M. Knuth (Leuenberger 1976).

4.4 Environment of deposition and climate

All the stratigraphical sections studied are in the upper part of the TF and consist predominantly of impure yellowish evaporites with intercalated thin siltstones. The presence of algae such as *Tetraporina* and *Leiosphaeridia* provide evidence of a lacustrine environment of continental origin. The presence of taxa such as Agavaceae, Burseraceae, Cactaceae,

Compositae, Leguminosae, *Ephedra* and *Quercus*, among others (Table 1), indicates semiarid local plant communities. In general, semiarid local conditions during the Middle Miocene are well documented not only by the palynomorph content, but also sedimentologically by the occurrence of thick beds of evaporites that were formed as a result of high evaporation and moderate precipitation. Evaporite beds with siltstone intercalations are evidence of a changing water column in the Neogene lakes due to flood or drought conditions.

4.5 Age of the Tehuacán Formation

The age of the TF has been considered previously as Cretaceous (Aguilera 1906), Eocene–Oligocene (Calderón-García 1956) and Pliocene–Quaternary (Hernández-Estévez 1980). However, most recent reports give an age of 16.4 ± 0.5 Ma (K-Ar of biotite) for the upper part of the TF (Dávalos-Álvarez 2006; Dávalos-Álvarez et al. 2007).

Three of the five outcrop sections of evaporites (Th-3 to Th-5) are capped by a whitish tuff with biotite mica. A sample of this tuff from the top of section Th-4 (Figure 4) yielded a K-Ar isotopic date on biotite of 15.6 ± 0.4 Ma (Table 2). This age is considered the minimum age of this stratigraphical unit and is in close agreement with the previous age reported for the upper part of the TF by Dávalos-Álvarez (2006). Nieto-Samaniego et al. (2006) reported an age of 27.1 ± 0.7 Ma (K-Ar in muscovite) for the base of the TF. In summary, according to the most recent age reports, the TF represents an interval of deposition from the Late Oligocene to Middle Miocene.

5. Discussion

The main finding of this study is that the Middle Miocene palynological assemblages recovered from the TF show a high taxonomic diversity, and are similar to the extant flora. This high similarity suggests that the TF has maintained a high percentage of the Paleogene–Neogene floristic components which may account for its present megadiversity.

Palynological assemblages are characterised by the presence of *Pinus* and *Quercus*, which at present constitute forests above 2000 m above sea level, and *Taxodium* which is the most dominant element of gallery forests growing near rivers (Valiente-Banuet et al. 2000). Moreover, the presence of genera such as *Liquidambar*, *Betula*, *Podocarpus*, *Alnus*, *Selaginella* and ferns (*Camarozonosporites*, *Cicatricosisporites* and Cyathaceae), as well as *Momipites* (*Alfaroa-Engelhardtia-Oreomunnea*) is indicative of cloud forests (Luna et al. 1999; 2000; Alcántara et al. 2002;

González-Espinosa et al. 2011). Modern cloud forests, situated between elevations of 600 and 3000 m, exhibit high biotic diversity and a fragmented distributional pattern (Luna et al. 1999, 2000, 2001; Alcántara et al. 2002). Arboreal taxa such as *Alfaroa*, *Alnus*, *Oreomunnea* and *Quercus* have been cited as quantitatively important (Rzedowski 1996). This forest type has been recorded in temperate humid conditions, and has been considered transitional between tropical and temperate vegetation since the Paleogene–Neogene (Alcántara et al. 2002), showing floristic affinity with the deciduous forests of North America (Miranda & Sharp 1950) and eastern Asia (Sharp 1966). A cloud forest with a dominance of *Engelhardtia* has been reported in the Chinantla region of Oaxaca (Figure 1) (Rzedowski & Palacios 1977), growing under humid temperate conditions.

Palaeocommunities of *Pinus–Quercus* forests and cloud forest have been reported in the Late Eocene to Early Oligocene Cuayuca and Pie de Vaca formations in two basins located in the state of Puebla (Figure 1) (Martínez-Hernández & Ramírez-Arriaga 1999; Ramírez-Arriaga et al. 2006, 2008). Currently, the *Pinus–Quercus* forest grows at an altitude of 2500 m in the mountains of Tehuacán (Valiente-Banuet et al. 2000).

Other elements recovered from the TF, such as *Rhus*, Rosaceae, *Quercus* and *Fraxinus*, are at present major components of the mexican shrubland consisting of low-stature shrubs and trees (1–3 m high) and broad-leaved sclerophyllous species with 40–100% coverage of woody vegetation (Valiente-Banuet et al. 1998). The presence of these floristic elements supports the long-standing claim that a significant number of genera in this vegetation are represented in Paleogene–Neogene palaeofloras and in many cases the living species are very similar to the fossil species (Axelrod 1958, 1975, 1989). This vegetation originated from alliances in older laurophyllous forests that adapted to a spreading dry climate, occupying much of the southwestern United States and adjacent Mexico by the end of the Oligocene, and expanding their range during the Miocene (Axelrod 1977).

Taxa recovered from the TF belonging to Leguminosae (*Acacia*, *Caesalpinia*, *Calliandra*), Cactaceae, Burseraceae, Euphorbiaceae, Compositae, Malvaceae and Acanthaceae are at present major components of tropical deciduous forests and shrublands in the TV (Table 1). The tropical deciduous forest is one of the most widespread types of vegetation, extensively distributed from sub-humid to semiarid climates in Mexico (Vázquez 1999; Becerra 2005). This plant community is characterised by trees about 7–10 m high, growing on slopes (Valiente-Banuet et al. 2000) and is dominated by legumes and Burseraceae (Becerra 2005). The presence of this vegetation type in

the palynoflora is in accordance with the distribution of the tropical deciduous forest during the Paleogene/Neogene proposed by Becerra (2005). Previous studies suggested that the tropical deciduous forests could have been very extensive since the Paleogene, as they have been well documented in other continental deposits such as in the Upper Eocene to the Lower Oligocene of the Pie de Vaca and Cuayuca formations (Ramírez-Arriaga 2005; Martínez-Hernández and Ramírez-Arriaga 2006; Ramírez-Arriaga et al. 2006; 2008). During that time, the abundance of Burseraceae was recognised, although at this time the family did not have a high diversity.

Climatic changes during the Miocene also drove the diversification of Leguminosae lineages; some examples are well documented in the TF pollen assemblages, with a high diversity of *Caesalpinia* and Fabaceae. Also, an abundance of different species of *Bursera* occurred in the palynoflora (2.4–3.2% in the Th-2, 2–3.4% in Th-3 and 2.5% in Th-4). These were elements of the tropical deciduous forest and contributed to a peculiar community of ‘cuajiotales’ dominated by different species of *Bursera* which are deciduous trees adapted to warm and semiarid conditions. *Bursera* comprises today about 100 species with the major diversity, about 84 taxa, reported from Mexico, most of them ($n = 80$) endemic (Miranda 1947; Rzedowski 1978; Becerra 2005). According to time-calibrated phylogeny, between 20 and 5 Ma (during the Miocene), 60 new *Bursera* lineages diverged with a peak rate of diversification at 13.5 Ma (Becerra 2005). The presence of three species of *Bursera* recovered from the TF palynomorph assemblages strongly supports that diversification of this taxon occurred prior to the Middle Miocene. Similarly, the Cactaceae are well represented in the palynological assemblages from the TF for the first time, a finding that is in accordance with the idea that the cactus lineage diverged from its closest relatives ≈ 35 Ma ago, with major diversification events during the Late Miocene ≈ 10 –5 Ma (Arakaki et al. 2011), and contemporaneous with the diversification of the North American agaves (Good-Avila et al. 2006). However, the presence of Agavaceae and Cactaceae, including some *Neobuxbaumia*-type pollen, in the TF indicates that the tropical deciduous forest was the ancestral environment for these groups of plants, but that diversification probably started earlier than the diversification peak for both taxonomic groups in the Late Miocene (Good-Avila et al. 2006; Arakaki et al. 2011).

5.1 Parsimony analysis of endemism (PAE) between Cenozoic Mexican basins

The PAE included the presence/absence of 171 palynomorphs (Table 4), and resulted in one cladogram with

L = 260, CI = 0.66 and RI = 0.47 (Figure 6). The cladogram shows two principal clades (I and III). Clade I includes the Paraje Solo, Pichualco and La Quinta formations grouped by the presence of *Also-phila* (8), *Combretum* (38), *Engelhardtia* (52), *Eugenia* (57), *Pteris* (117), *Rhizophora* (122) and *Tournefortia* (139). Also, the Pichualco (Miocene) and La Quinta formations (Oligocene–Miocene) were grouped (II) by the occurrence of *Acer* (2), *Asplenium* (14), Bromeliaceae (20), *Cedrus* (31), *Clethra* (35), *Equisetum* (55), *Fagus* (62), *Jamesonia* (70), *Lygodium* (81), *Nypa* (97), *Nyssa* (98), *Pelliceria* (102), *Polygala* (109) and *Tilia* (136).

The Clade III group includes the Tehuacán, Cuayuca and Pie de Vaca formations defined by the presence of Bombacaceae (18), *Caesalpinia* (22), *Corsini-pollenites* (41), Leguminosae (74), *Malpighia* (33), *Momipites coryloides* (89), *Momipites microcorypha-ceous* (90), Moraceae (94), Polygonaceae (111), Rosa-ceae (123), Sapindaceae (125) and Tiliaceae (137).

The Pie de Vaca and Cuayuca formations (IV), both Upper Eocene–Oligocene, are grouped by the presence of *Aglao-reidia* (5), *Anthoceros* (11), *Armeria* (13), *Bombax* (19), *Ephedra claricristata* (53), *Eucom-mia* (56), Gesneriaceae (63), *Momipites triradiatus* (92), Polygalaceae (110) and *Typha* (140).

Finally, Cactaceae (144), *Calliandra* (145), Campa-nulaceae (146), Combretaceae (147), Convolvulaceae (148), *Cricotriporites* (149), *Croton* (150), *Foveotri-colpites* (151), *Foveotricolporites* (152), *Gematricolpites* (153), Nyctaginaceae (155), *Perisyncolporites* (156), Polemoniaceae (157), *Psilatricolpites* (159), *Psilatripor-ites* (161), *Retitricolpites* (162), *Retitricolporites* (163), *Retitriporites* (164), Rubiaceae (165), *Stephanocolpites* (166), *Striatopollis* (167), *Striatricolporites* (168), *Tricolpites* (169), *Tricolporopollenites* (170) and Vitaceae (171) are exclusively found in the TF.

In summary, Clade I includes three basins from tropical areas (the Paraje Solo, Pichualco and La Quinta formations); in contrast, Clade III group includes basins from semiarid regions (the Tehuacán, Cuayuca and Pie de Vaca formations). The Cuayuca and Pie de Vaca formations are closely related in the PAE analysis.

5.2 Palaeoclimatic interpretations

Recent progress in the study of deep-sea sediment stable isotopes gives valuable information on Cenozoic climate evolution. According to $\delta^{18}\text{O}$ records, from the Middle Paleocene to the Early Eocene, the most pronounced warming trend occurred, with a peak in the Early Eocene Climate Optimum (EECO, 52–50 Ma). Cooler conditions occurred from the Early–Middle Eocene to Early Oligocene, triggering a rapid

expansion of Antarctic ice-sheets that persisted until the Late Oligocene, when the subsequent warming trend reduced the Antarctic ice sheet until the Middle Miocene. Warmer conditions then peaked with the late Middle Miocene climatic optimum (17 to 15 Ma). Afterwards, gradual cooling conditions until the Early Pliocene allowed the major expansion of Antarctic ice sheets (Zachos et al. 2001).

The late Middle Miocene (17 to 15 Ma) is considered the climax of Neogene warmth. It was one of the last warm episodes in a general cooling trend (Fower & Kennett 1994). The sections analysed of the TF recorded a palynoflora from this late Middle Miocene climatic optimum. Palynomorph assemblages indicate temperate, semiarid climatic conditions in the TV during the Middle Miocene. A diverse local semiarid flora, including Agavaceae, Burseraceae, Cactaceae, Compositae, *Ephedra*, Leguminosae and Gramineae amongst others, was developed in response to a sub-humid climate with strong seasonality. This palaeoclimatic condition was appropriate for the expansion of these taxa and the tropical deciduous forest.

Lithological evidence gives additional information of semiarid conditions. Evaporites are formed under arid climatic conditions where net evaporation exceeds net inflow of solute-bearing waters. That is the reason for using them as indicators of ancient arid climates (Hardie 1991). Sediments of the TF show an increasing trend in clastic components with depth. The clastic nature of sediments in the lower part of the TF indicates a high sedimentation rate, with high rainfall, severe floods or even permanent rivers. In contrast, the upper part of the TF contains thick beds of evaporites, implying a drastic change in the environment, that is to say: very low sedimentation rates, drastically diminished rainfalls, and a high evaporation rate. These changes in basin fill indicate an important climatic change in the area, from relatively more humid to a semi-arid climate. This kind of sedimentary record has been documented and interpreted similarly in other basins (e.g. Hardie 1991; Rahimpour-Bonab & Abdi 2012).

In summary, both the palynoflora recovered from the TF and the thick evaporite beds clearly indicate that warm and semiarid climate conditions were already present in central Mexico at low altitudes during the Middle Miocene. Previous palynological studies have demonstrated that some semiarid plants already existed in southern Mexican basins by Late Eocene–Early Oligocene times (Ramírez-Arriaga 2005; Martínez-Hernández & Ramírez-Arriaga 2006; Ramírez-Arriaga et al. 2006, 2008). Nevertheless, important differences in the vegetation could be inferred from the TF palynoflora compared to older fossil associations from Mexico. The TF palynoflora

contains a high diversity of semiarid taxa, for instance Leguminosae and Burseraceae, along with the first documented abundance of Cactaceae in a fossil palynological association.

Overall, our findings imply that large-scale historical processes, diversification and maintenance of floristic elements through geological time account for the present day Tehuacán Valley megadiversity. Therefore, the historical ecological processes that have allowed taxa to survive in the TV are central questions that must be answered in order to get a complete picture of its biodiversity.

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