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Climatic reconstruction of two Pliocene floras from Mexico

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Abstract The role that climate plays in influencing the physiognomy of modern and fossil plant communities is widely acknowledged and forms the basis for several palaeoclimate proxies. In this work, both univariate Leaf Margin Analysis and multivariate Climate/Leaf Analysis Multivariate Program (CLAMP) were used for the climatic reconstruction of two fossil localities of the Atotonilco El Grande Formation. Using the predominantly North American and Asian calibration data set PHYSG3BRC, supplemented with new African material, results from two sites, Los Baños (present position 20°18′18″N, 98°42′44.4″W) and Sanctorum (20°18′18.5″N and 98°46′52.2″W), indicate that during the Pliocene a mesothermal climate existed with mean annual temperatures between 12 and 22°C, with the most likely being approximately 15°C, and a mean annual temperature range of 21°C. A distinct seasonal variation in rainfall is evident with a mean annual relative humidity of 60–70%. Differences between the sites can be explained by differences in depositional regime and spatial heterogeneity in the predominantly *Quercus*-dominated woodland. The continuous subsequent uplift of the Sierra Madre Oriental, the resulting development of a rain shadow, and the eventual disappearance of a palaeolake appear to have caused a transition to the modern xerophytic shrub vegetation.

Keywords Climatic reconstruction · Foliar physiognomy · CLAMP · Atotonilco El Grande formation · Pliocene · Mexico

Introduction

Today, Mexico hosts many of the main global vegetation types and possesses an extraordinary biodiversity of more than 30,000 plant species encompassing boreal to low latitude elements, together with a great number of endemics. To date, extensive discussions concerning the origin of these elements and apparent endemism in some taxa have been supported by comparatively little direct evidence. How this diversity arose and the relationship, if any, to Pleistocene cooling and southerly migrations of northern lineages remain unresolved issues.

The studies of Graham (1999) and Graham and Palacios Chávez (1996), demonstrate the existence of a few boreal elements in Mexico during the Middle Miocene, followed by an increase in their abundance during the Pliocene as a function of climatic cooling. Other authors, however, comment that plants derived from high latitudes of North America (e.g., *Platanus, Populus, Salix, Pterocarya*) in the central and southern regions of Mexico had to have arrived before the uplift of the Trans-Mexican volcanic belt, since this functions as a biogeographic barrier of major importance (Ramírez and Cevallos-Ferriz 2000a, b). This isola-

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tion is then supposed to have been accompanied by a period of speciation and community restructuring in central Mexico driven by climate change (Martínez-Hernández and Ramírez 1996; Velasco-de León 1999; Ramírez and Cevallos-Ferriz 2002).

In this paper, we add to an emerging body of data on this critical time in the evolution of the Mexican flora by examining two floras from the Pliocene Atotonilco El Grande Formation in an attempt to characterize both the vegetation and the associated climate.

Plant physiognomy

Global climate constantly changes. This variation is a function of influences such as topography, land/sea distributions, orbital variations, and volcanism (Cavalier et al. 1981; Sear and Kelley 1980). The general appearance of vegetation (e.g., its physiognomy) tends to be characteristic of the particular climatic regime in which it grows because, being spatially fixed post germination, plant physiognomy represents specific architectural adaptations to particular environments. Physiognomic environmental adaptation occurs within the capabilities imparted by the genome honed by long-term natural selection. Non-adapted physiognomies fail to survive and, over time, successful physiognomies emerge largely independent of taxonomy (Spicer 2000, 2007, 2008). Adaptive success is not determined by any single architectural feature (Lande and Arnold 1983), and no single feature can be expected to correlate with a single climatic variable. Fitness is influenced instead by numerous interacting traits (Ackerly et al. 2000) spanning the architectures of conducting tissues in roots, stems, and leaves, overall canopy architecture (Hellicker and Richter 2008), and foliar physiognomy. However, before the advent of multivariate techniques for analyzing such complexity, the only option was to examine single features in relation to single climate variables.

For example, Bailey and Sinnott (1915, 1916), in their study with the flora of North Carolina, documented the correlation between leaf margin morphology (toothed vs smooth) with mean annual temperature (MAT). These papers marked the beginning of a series of investigations correlating foliar architectural characters with temperature, precipitation, and humidity (e.g., Wilf 1997; Wilf et al. 1998; Wolfe 1979). Webb (1959) noted a direct relationship between leaf size and precipitation, while Givnish (1984) pointed out leaves from tropical lowlands tend to be narrow as an adaptation that limits overheating. Dolph and Dilcher (1980) recognized that the size of leaves varies with temperature, particularly that large leaves occur in warm conditions provided water is available. In an attempt to quantify leaf size in relation to precipitation, Wilf et al. (1998) found a close relationship (r^2=0.7600) between average leaf area and the log of the annual average precipitation.

Although Wolfe (1979) examined the relationship between climate and the morphology of leaves from humid forests of south-east Asia, and used these data to expand and confirm Bailey and Sinnott's (1915, 1916) work in North America, he subsequently employed a multivariate statistical technique to explore whether other palaeoclimate variables could be deduced from foliar physiognomy. Wolfe named this method CLAMP (Climate-Leaf Analysis Multivariate Program) (Wolfe 1993). Underpinning the current version of CLAMP is Canonical Correspondence Analysis (CCA) (ter Braak 1986), a multivariate statistical technique that is used to arrange samples of leaves from modern vegetation growing under known climatic conditions in multidimensional space. A minimum of 20 species of woody dicot leaves are scored for 31 character states in each modern calibration site and the overall score for each site positions it with respect to other sites in what is termed "physiognomic space". The power of CLAMP lies in its multivariate nature and the quality of these reference or training data (Herman and Spicer 1996; Gregory 1996; Kennedy et al. 2002; Spicer et al. 2005). In Wolfe's original version of CLAMP, physiognomic space as defined by the reference or training sites was calibrated using meteorological data derived directly from recording stations in, or near, the training sites. A more recent development (Spicer et al. 2009) is the use of globally gridded observations that potentially allow any naturalized vegetation site to be used irrespective of the proximity of a meteorological recording station. Fossil leaf assemblages are scored similarly to those leaves found in the training sites, and, from their position in calibrated physiognomic space, the ancient climate can be determined.

Several studies have considered how specific leaf characters might be represented in a fossil assemblage. Burnham et al. (2001) studied the relationship between leaf margin form and climate as found in different habitats of the same forest. They concluded that the frequency of toothed and entire margins may vary drastically resulting in a potential underestimation of temperature between 2.5–5°C for riparian trees. For this reason, the sedimentological context of the fossil assemblage is required to assess taphonomic factors. Others have focused on the loss of fidelity in leaf margin data as a function of taphonomic processes. For example, Spicer et al. (2005), after a study in the Crimea Peninsula using data derived from present-day vegetation, concluded that the loss of the characters of the margin significantly affects the ability to reconstruct climatic variables related to temperature. However, what was also evident from this study was that, because leaf characters are multifunctional and correlate with more than one environmental variable, there is a high level of information redundancy in the CLAMP scoring methodology. Loss of some physiognomic data has minimal impact on the overall outcome provided the loss is not compounded by the loss of other characters. In the case of leaf margins, loss sufficient to compromise CLAMP analyses would also result in leaves being so incomplete that they could not be scored at all.

Area of study

In Mexico, there are few studies to date that utilize foliar physiognomy (Velasco-de León 1999) because in order to use CLAMP the leaves of at least 20 morphotypes are required. In Fig. 1, we show 21 locations in Mexico yielding different angiosperm organs (wood, pollen, fruits, and leaves). This information complements Table 1. Of those locations with leaves, only two of them yield more than 20 taxa. The first of them is the Oligocene Ahuehuetes site in the south of the State of Puebla, on the edge of the Trans-Mexican Volcanic Belt where, in 1999, Velasco de León (1999) recovered 30 leaf morphotypes. The assemblage indicated a temperate climate with summer rains (mesothermal vegetation with a mean annual temperature of 13–20°C); most leaves were in the mesophyll size range and some were sclerophyllous (Velasco-de León 1999).

The region of Santa Maria Amajac in the State of Hidalgo (Fig. 2) is the second leaf-yielding area within the Pliocene Atotonilco el Grande Formation and is the subject of this report.

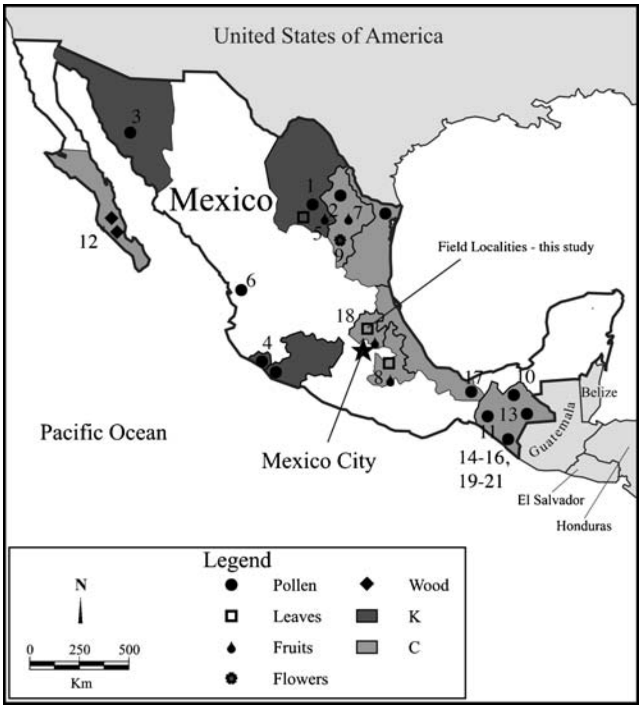


Fig. 1 Map of México showing fossiliferous localities with a record of angiosperms. *K* Cretaceous, *C* Cenozoic. *Numbers* relate to references given in Table 1 (below)

The localities reported in this paper occur in the geomorphologic province of the Trans-Mexican Volcanic Belt (TVB). Volcanism began in the Oligocene and continued through the Pliocene. Today, the TVB has an elevation between 2,000 and 3,000 m (Lugo-Hubp 1990). In south central Mexico (Fig. 2), the TVB is dissected in a NW–SE direction. In the northeast sector, mountains of folded marine sedimentary rocks occur, and in Santa María Amajac, clastic rocks comprising horizontal strata form low-relief hills cut by numerous streams. Cenozoic sediments are represented by the conglomerate rocks of the Pachuca Group and by clastic rocks of the Atotonilco el Grande Formation (Blancan). These underlie pyroclastic and basaltic rocks with ages between 2.5 and 2.3 Mya (Cantagrel and Robin 1979), forming a morphologically well-preserved plateau overlain by recent deposits (Arellano et al. 2005).

In Pliocene times, temporary damming of The Rio Amajac resulted in the formation of a freshwater lake, the Amajac palaeolake, that occupied an area of approximately 85 km^2 at its maximum extent. Lacustrine sedimentation began with the deposition of conglomerates, sand, mud-clay, and clays, the coarser material representing the final fluvial activity before damming occurred. More than 160 m of sediments accumulated together with pyroclastics of different grain sizes. The finer grained sediments, more widespread than the coarse, preserve abundant fossil flora and fauna typical of freshwater environments.

Plant fossils belonging to the families Salicaceae, Platanaceae, Fagaceae, Rosaceae, and Equisetaceae (Arellano et al. 2005) occur at two localities in this area. Taxonomic analysis (Ortiz and Velasco-de León 2006) and (Velasco-de León 2006) indicates that considerable diversity within the genera *Quercus*, *Cercocarpus*, and *Salix* existed in Pliocene times. Numerous gastropods, ostracods, small fishes, vertebrate remains, and some insects, e.g., *Epicauta sanctuorensis* (Zaragoza-Caballero and Velasco-de León 2004), together with diatoms of the genera *Tertiarius, Aulacoseira*, etc., (Caballero et al. 2009; López et al. 2004) also occur in the lake sediments. Throughout this succession, equid fossils have been collected whose teeth are dated as 4.2+0.3 and 4.57+0.002 Mya using K-Ar methods (Kowallis et al. 1998).

Based on the stratigraphic and paleontological record, the Atotonilco el Grande Formation is considered of Blancan (4.75−1.806 Mya) or Zanclean (5.332−3.6 Mya) age (Gradstein et al. 2005).

Methods

The Atotonilco El Grande formation has a thickness of 165 m, estimated by the amalgamation of three measured sections (El paso de Amajac, Los Baños, and Sanctorum)

Table 1 Angiosperm plant fossil localities from Mexico with formations, ages, and authors

	Locality	Formation	Age	Fossil	Author
1	Coahuilla SE	Cerro del Pueblo	K-Campanian	Fruits	Rodríguez de la Rosa and Cevallos-Ferriz 1994
2	Coahuilla	Olmos	Upper K	Pollen, leaves	In Ramírez and Cevallos-Ferriz 2000a
3	Sonora, Huepac	Tarahumara	Upper K	Pollen	Hernández-Castillo and Cevallos-Ferriz 1999
4	Michoacán, Colima	Tepalcatepec	K albian	Pollen	Martínez-Hernández 1992
5	Puebla	Tlayua	K	Pollen	Martínez-Hernández 1992
6	Durango	Gran Tesoro	K lower	Pollen	Martínez-Hernández 1992
7	Coah, Nvo Leon Tamp	Gpo Claiborne-Jackson	Early Eocene	Pollen	In Ramírez and Cevallos-Ferriz 2000a; Magallon-Puebla and Cevallos-Ferriz 1994
8	Puebla, Ahuehuetes	Coatzingo	Eocene–Oligocene	Fruits, leaves	Velasco- de León and Cevallos-Ferriz 1998
9	Nuevo León	La Carroza	Eocene	Flower/fruit	Calvillo-Canadel and Cevallos-Ferriz 2005
10	Chiapas	Rancho Berlin	Lower Oligocene	Pollen	Martínez-Hernández 1992
11	Chiapas, Simojovel	La Quinta	Lower Miocene	Pollen	Graham 1976; Graham and Palacios Chávez 1996
12	Baja California	El Cien	Lower Miocene	Wood	Cevallos-Ferriz and Barajas-Morales 1994
13	Chiapas	Méndez	Lower–Middle Miocene	Pollen	Palacios Chávez and Rzedoswki 1993
14	Chiapas	Ixtapa	Middle–Upper Miocene	Pollen	Martínez-Hernández 1992
15	Chiapas	Presa Mal Paso	Miocene	Pollen	In Ramírez and Cevallos-Ferriz 2000a
16	Chiapas	Tehuantepec	Miocene	Pollen, leaves	Miranda 1963
17	Chiapas	Paraje Solo	Pliocene–Pleistocene	Pollen	Graham 1976
18	Hidalgo	Atotonilco el Grande	Pliocene–	Fruits, leaves	Arellano et al. 2005
19	Chiapas	Concepción Inferior	Pliocene	Pollen	Martínez-Hernández and Ramírez 1996
20	Chiapas	Concepción Superior	Pliocene	Pollen	Martínez-Hernández and Ramírez 1996
21	Chiapas	Agueguexquite	Pliocene	Pollen	Martínez-Hernández and Ramírez 1996

and exhibits a highly variable lithology. It is capped by basaltic flows and volcanic ashes. The fossil material was sampled in two localities. At Los Baños (LB) (20°18′18″N, 98°42′44.4″W) (Fig. 3), the measured thickness was 96.9 m. Fossils were collected from mudstones and sandy strata between 8 and 20 m from the base of the section. In the second locality, Sanctorum (ST) (20°18′18.5″N, 98°46′52.5″W) (Fig. 4), a sediment thickness of about 70 m was measured and sampling was carried out in the lower and central part of the section in mudstones and fine-grained sands. Venation as well as morphology was used to differentiate the morphotypes, and where possible identifications were made by comparisons with herbarium material at MEXU (Herbario Nacional de México) and FETZA (Herbario de la Facultad de Estudios Superiores Zaragoza). Leaves that could not be identified were categorized as morphotypes.

The number of specimens per unit volume of sediment, including fragments, were recorded (Fig. 5). Leaves were divided into complete and incomplete (if any part of the apex, the base or 50% of the lamina was missing) in order to assess their likely transport history and energy conditions during deposition. For the analyses of climate, only complete specimens were considered.

Morphological observations on more than 2,000 fossil leaves were made using an Olympus SHZ microscope.

Leaf Margin Analysis (LMA) to obtain the MAT used the regression of Wolfe (1979) and sampling error equation:

$$\delta[MAT] = c\sqrt{(p(1-p))/r} \tag{1}$$

of Wilf (1997) where c=30.6 and is the slope of the MAT versus leaf margin regression, r is the total species number, and p ($0<p<1$) is the fraction of r species that have entire margins.

Scoring of the 31 character states used in CLAMP followed the protocols of Wolfe (1993), and the scoresheets are available as Online Resource 1 (Los Baños) and 2 (Sanctorum). The physiognomic training data set used was PHYSG3BRC and is also available from the CLAMP website: www.open.ac.uk/earth-research/spicer/CLAMP/Clampset1.html.

Two sets of climate data were used in the calibration. The first, MET3BR, consists of meteorological data obtained from climate stations in or near the modern vegetation sites used for calibration. Inevitably, this calibration represents climate influenced by the vegetation used for the calibration. The second, GRID-

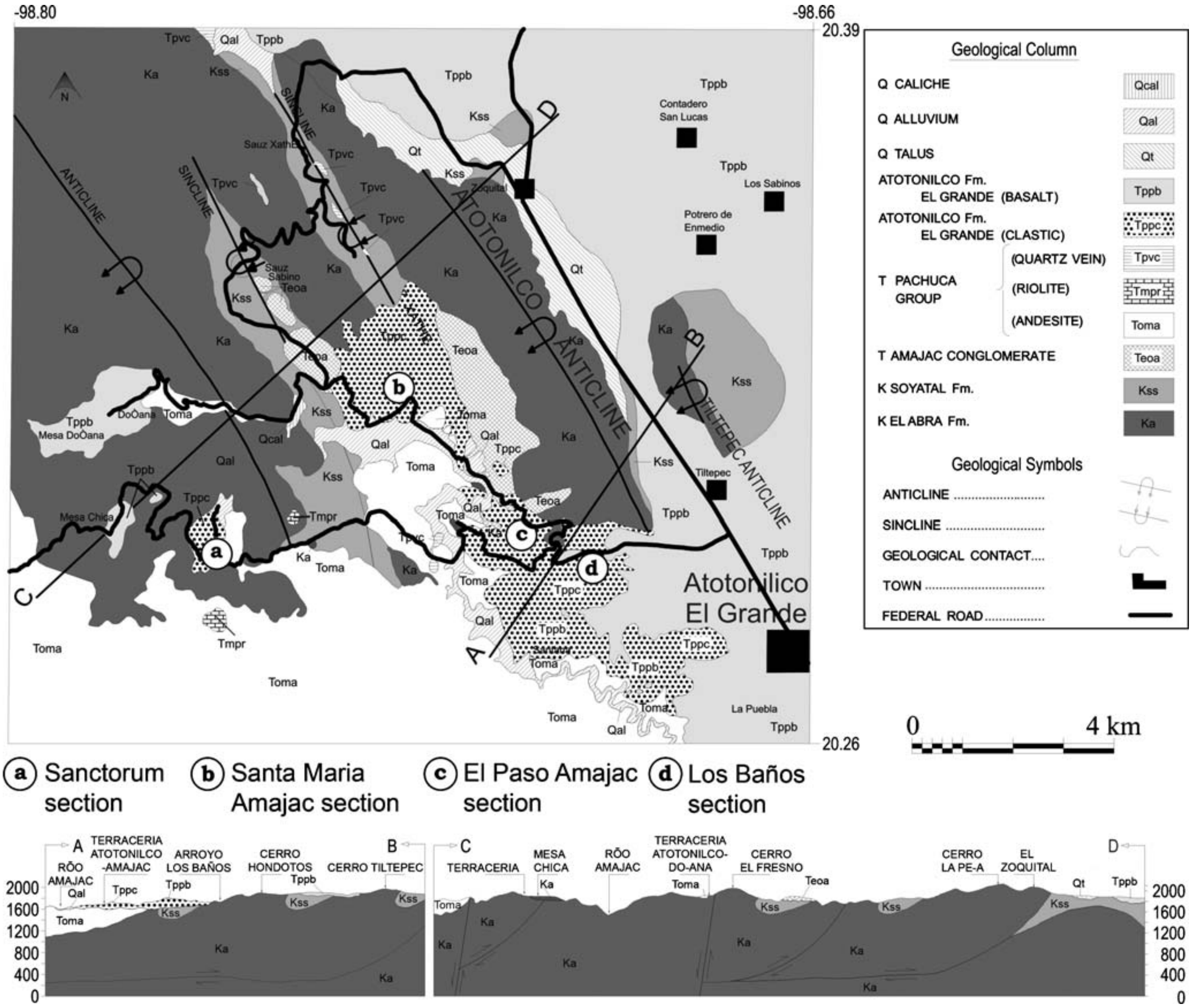
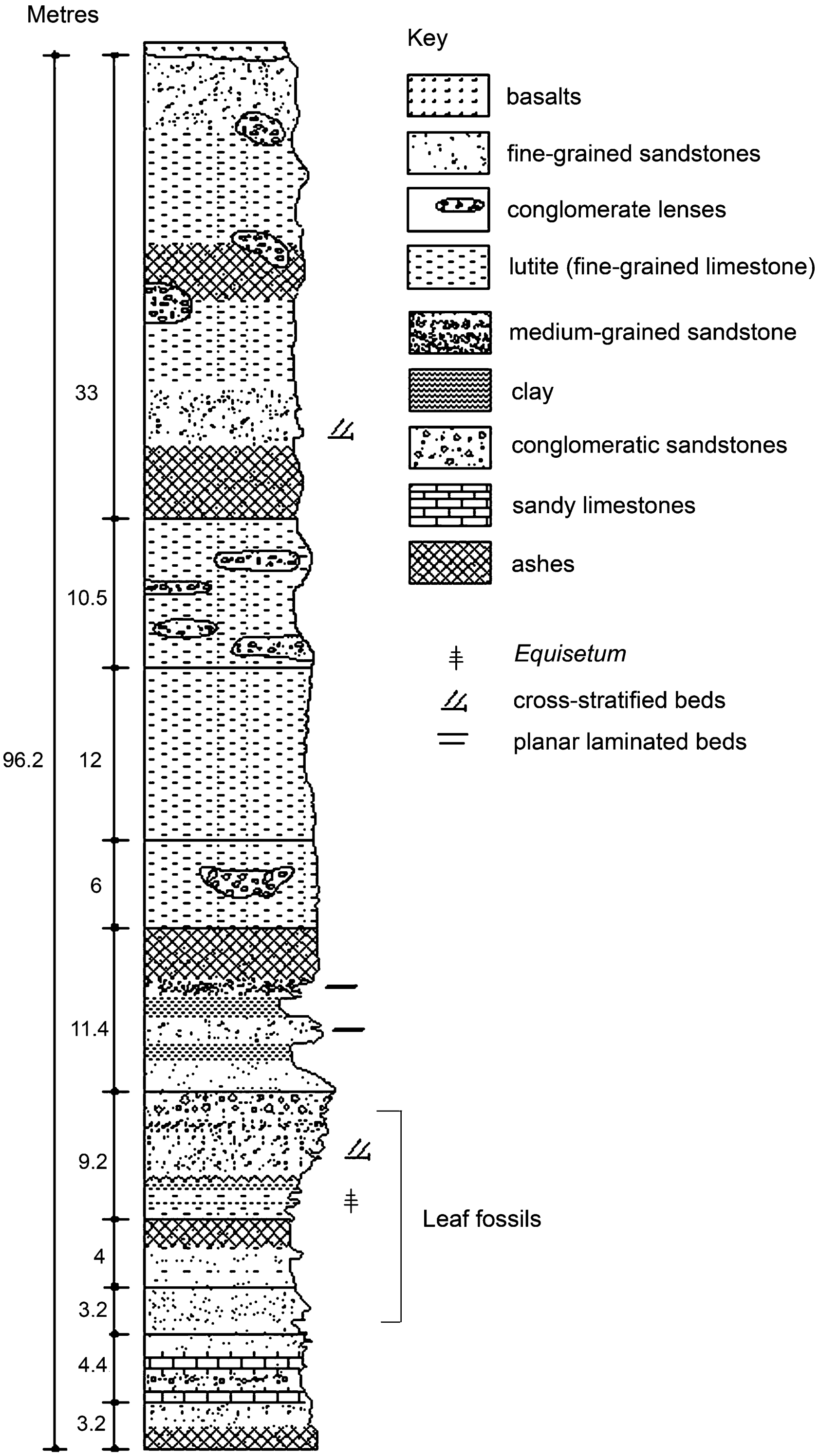


Fig. 2 Geological map of the Santa Maria Amajac Region. Latitudes and longitudes are given in decimal degrees

MET3BR, consists of meteorological data derived from the 0.5 x 0.5° global gridded data of New et al. (1999) corrected for the effect of local altitude using a geographically variable lapse rate. This was obtained using the 3-D climatology of temperature from the European Centre for Medium-Range Weather Forecasts (ECMWF) re-analysis project (Uppala et al. 2005). The specific and relative humidities were also recalculated in the light of the lapse rates. When the lapse rate corrected temperature was much colder than the original, the relative humidity had the potential to exceed 100%. If this was the case, adjustments were made until the relative humidity was equal to 100%. From this, the commonly returned CLAMP climate variables were calculated: mean annual temperature (MAT), warm month mean temperature (WMMT), cold month mean temperature (CMMT), length of the growing season (LGS), mean growing season precipitation (GSP), mean monthly growing season precipitation (MMGSP), precipitation during the three wettest months (3-WET), precipitation during the three driest months (3-DRY), specific humidity (SH), relative humidity (RH), and enthalpy. A more comprehensive account of the methodology and its relationship to the original ungridded calibration is given in Spicer et al. (2009).

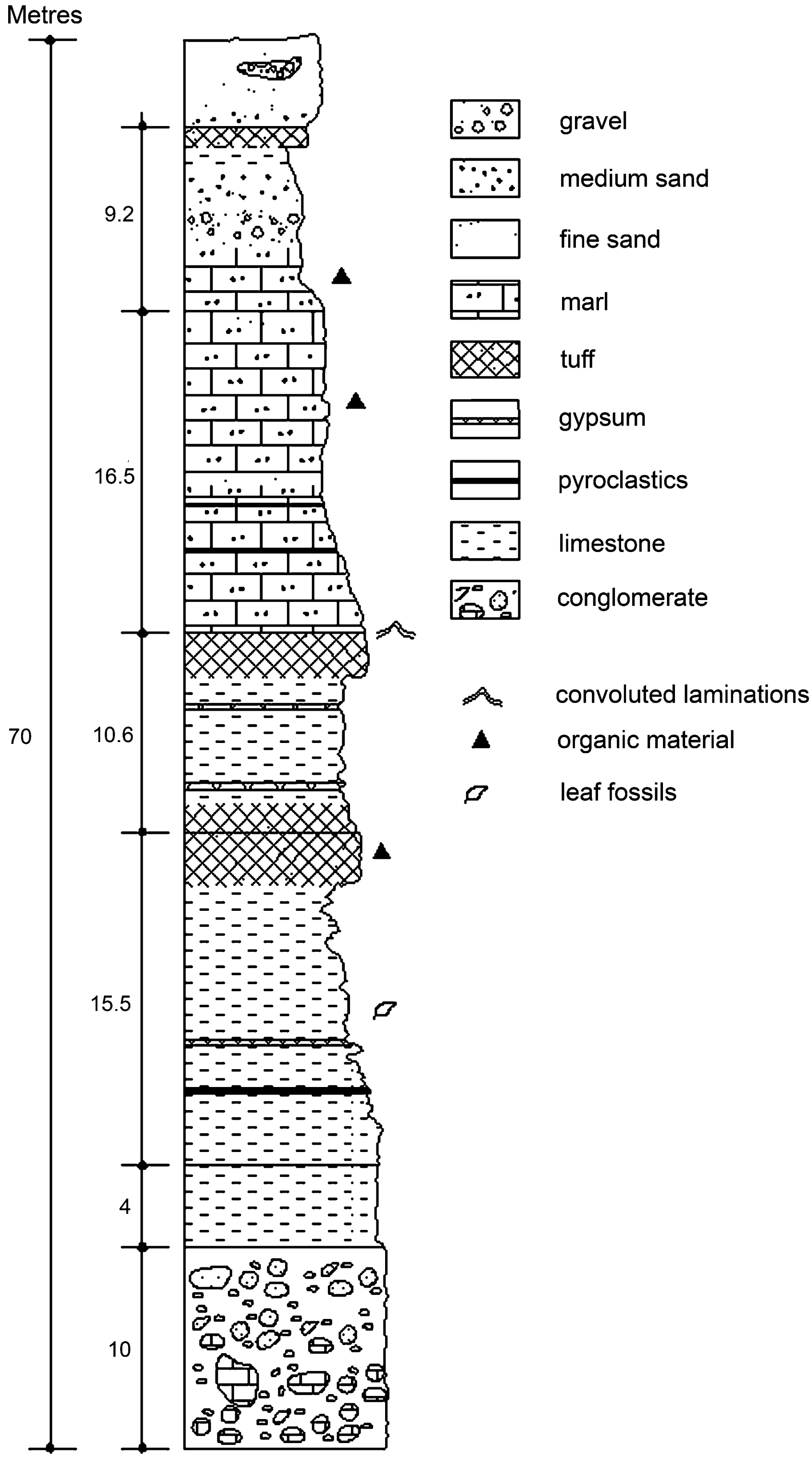
In a novel development to these analyses, the sites from Mexico were examined in the context of newly collected (but as yet unpublished) modern data from physiognomically similar, but taxonomically distinct, vegetation in South Africa. This was done because the Sanctorum site was found to plot at the margins of physiognomic space as defined by the PHYSG3BRC calibration set, which raised the potential for the climate predictions to have higher than

Fig. 3 Sedimentary log of the Los Baños locality



usual uncertainties for a CLAMP analysis. However, the African sites, when plotted as passive samples (i.e. without their meteorological data included in the GRIDMET3BR file and therefore without influencing the PHYSG3BRC calibration), were found to envelop the Sanctorum site. The only climate information available for the African sites was that derived from the gridded data. Instead of undertaking a complete recalibration of CLAMP using the African data (work in progress), an analysis using the PHYSG3BRC and GRIDMET3BR datasets was used to define (passively) the positions of both the fossil Mexican sites and the sites representing modern African vegetation. The nearest

Fig. 4 Sedimentary log of the Sanctorum locality



neighbor approach of Stranks and England (1997) was then applied as follows. The Euclidean distance function:

$$E_{jk} = \sqrt{\sum_{h=1}^{D} \left(X_{hj} - X_{hk}\right)^2} \tag{2}$$

where E_{jk} is the Euclidean distance between sites j and k, $X_{hj} - X_{hk}$ is the distance between sites j and k along dimension h, and D is the number of dimensions (in this case 4), was used to identify the 20 closest sites to the Mexican samples in axes 1–4 space. Because the gridded meteorological data are known for all the modern sites,

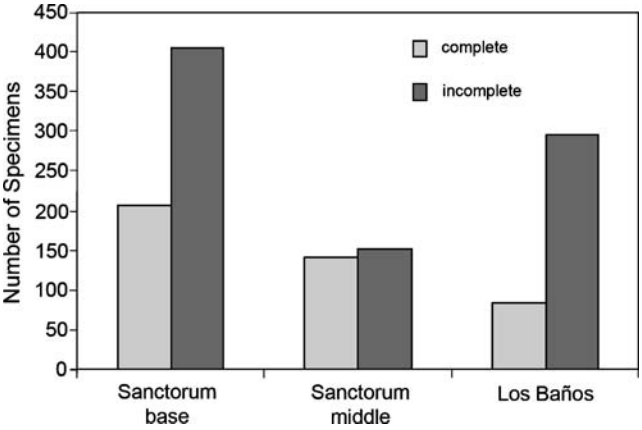


Fig. 5 State of fragmentation of leaves in the localities Sanctorum and Los Baños

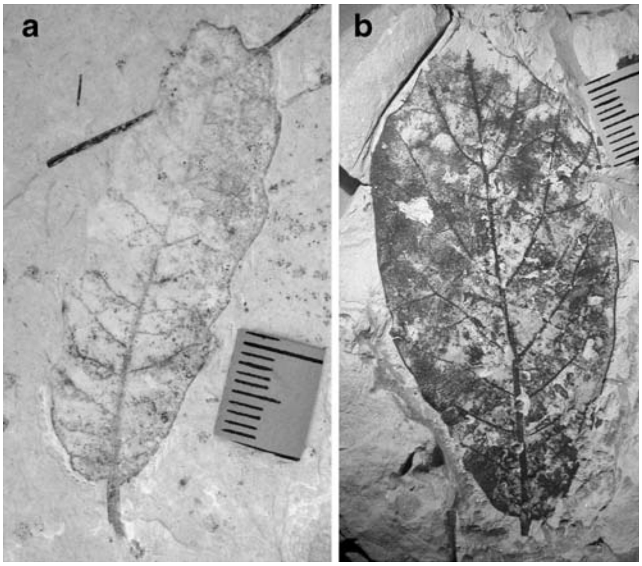


Fig. 6 Morphotypes of *Quercus* showing **a** undulate and toothed margin (Sanctorum), **b** acute apex and distantly spaced teeth (Los Baños). *Scales* in mm

these were used to determine climate/vector score regression equations for the 20 sites. These "local" regressions were then used to determine the palaeoclimate variables for the fossil sites.

Results

Fragmentation

Figure 5 shows the extent of leaf fragmentation at both Sanctorum and Los Baños. At Los Baños, the fossilized material is most abundant in fine sands, though the quality of the impressions is not notable except in those strata where haematite is present, since it favors the fossilization process. The Los Baños locality is interpreted to represent floodplain deposition, and the number of incomplete leaf fragments is three times that of complete leaves, suggesting water energy was high. This is also reflected in flow orientation of the leaves and in cross-stratification that decreases up section. Twenty-five species of leaves were identified, with specimens of *Quercus* (Fig. 6) being the most abundant.

At the Sanctorum locality, the number of incomplete leaves in the basal part of the column was roughly the same as the number of complete leaves, and this balance continued up into the middle part of the measured section. The most abundant genus was *Platanus* (Fig. 7) followed by *Populus* (Fig. 8). *Quercus* was proportionality less abundant than at Los Baños. No fossils were found in the upper part of the section (Fig. 3). A total of 33 leaf species and morphotypes were identified.

Leaf margin analysis

The Los Baños leaf assemblage exhibited 48% entire margins while at Sanctorum 66.7% were entire. These equate to MATs of 14.4±4.2°C for Los Baños and 20.0±4.3°C for Sanctorum.

CLAMP analysis

CLAMP results are shown in Table 2. Uncertainties are expressed as 1 standard deviation (sigma) of the residuals about the 2nd order polynomial regression plot of the observed climate against the relevant vector score. Results using the MET3BR calibration (Table 2a) yield MATs warmer than those obtained using the GRIDMET3BR data (Table 2b) but both fall within the uncertainty ranges of the LMA values. The warmer MET3BR MATs are reflected in higher WMMT and CMMT values and there is no evidence of freezing in any result. Although there are large uncertainties in the precipitation results, Los Baños appears to have been the drier of the two samples with the MET3BR calibration indicating a distinct wet/dry seasonality, the wet season having roughly double the precipitation of the dry season. This difference is not apparent using the GRIDMET3BR calibration and overall the GRIDMET3BR calibration gives drier results. This is because in the gridding process spatially heterogeneous precipitation, such as is generated by convective rainfall (typically late afternoon rainstorms), is averaged over the grid cell that is larger than the area affected by the precipitation event. In contrast, meteorological stations in or near the sites of the calibration vegetation (the basis of the MET3BR dataset) capture such events as they affect the physiognomy of the calibration sites. The GRIDMET3BR results are, however, more comparable to climate data used for climate model evaluation and generated by such models. Both

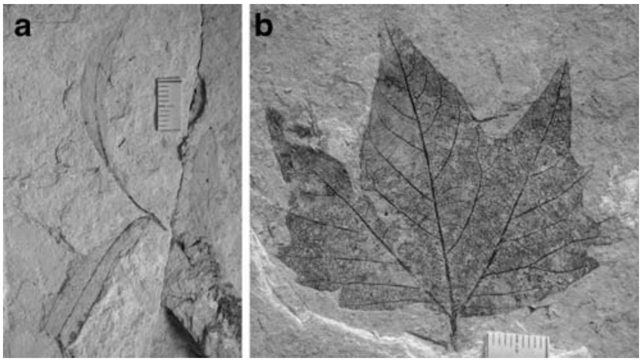


Fig. 7 Examples of leaves of the genera: **a** Salix, **b** *Platanus*. *Scales* in mm. Both are from the Sanctorum section

datasets suggest a similar (within uncertainty) average annual relative humidity of around 66%, and all enthalpy values are within an uncertainty of ±2 sigma.

Results for the nearest neighbor analysis, inclusive of the African data, are shown in Table 2c.

Discussion

For the two localities, the results reveal differences in abundance, diversity, and fragmentation grade. At Sanctorum, theoretically one could expect a greater number of complete leaves because deposition was within fine-grained sediments, and thus it is likely that the energy of deposition was low compared to that at Los Baños. This difference in energy could also have had a differential effect on the preservation of leaf apices because, in higher energy situations, some apex morphologies would be more prone to damage and loss than others. The majority of leaves correspond to the microphyll size II and III (see the CLAMP website for size templates) and have very acute and attenuate apexes that in turn are highly susceptible to degradation. For the majority of incomplete leaves, these structures are precisely those that are missing. Fortunately, apex loss has a minimal affect on CLAMP predictions, provided other characters are present (Spicer et al. 2005), but to avoid the effect of any possible character loss on CLAMP's ability to reliably predict temperature, only complete leaves were used in this analysis. From the large number of specimens available, and examination of fragments, we determined that the complete leaves captured the full morphological range present in the preserved assemblage.

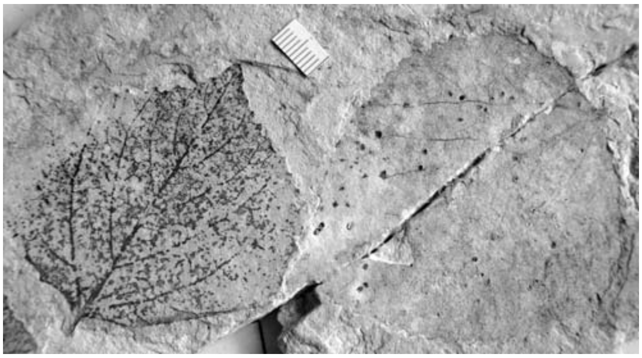


Fig. 8 Examples of *Populus* leaves (Sanctorum). *Scale* in mm

For the Los Baños locality, the higher number of fragmented leaves is explained by the higher energy level in the depositional environment as indicated by medium- to coarse-grained sandstone. Iron staining on the leaf surfaces may have formed during transport and before final burial (Spicer 1977), or as a result of iron chelating on the original organic material and subsequent release during weathering. The nature of the fragmentation (mechanical as distinct from biological degradation) and the sedimentary context suggest allochthonous origins for both assemblages.

CLAMP predicted temperature parameters for both Sanctorum and Los Baños, suggesting that during the Pliocene a mesothermal woodland (Wolfe 1985) bearing microphyllous leaves developed within a maximum range of mean annual temperatures 12–22ºC (including 2 sigma uncertainties and rounding up) with the MAT of Los Baños being 14.4°C and that of Sanctorum 16.6°C. Taking both sites together, the mean is 15.5°C. Although the various CLAMP datasets and the nearest neighbor methodology used here indicate Sanctorum was slightly warmer than Los Baños, the differences are all within 2 sigma uncertainties and thus should not be regarded as significant. The mean annual range of temperature, calculated as the mean difference across all CLAMP analyses between the WMMT and the CMMT and taking into account uncertainties, is 21°C. Similarly, the growing season length of around 9 months is remarkably consistent across the analyses.

Where differences are to be expected is within the precipitation estimates. Here, Sanctorum is consistently indicated to be the wettest, but again the inherently large 2 sigma uncertainties overlap between the two fossil sites. Unsurprisingly, the gridded data show drier predictions than the ungridded which is a function of spatial averaging inherent in the gridding process. All analyses, though, show a marked differentiation between the three driest and three wettest months, and this is most noticable with the gridded data. With the ungridded data, the differences are just within the 2 sigma overlap, but gridded data indicate distinct differences with the driest season receiving less than a third of the precipitation of the wet season. Average annual relative humidity of around 66% is remarkably consistent across all analyses. Gridded data indicate an enthalpy figure of 320±10 kJ/kg (maximum) for both fossil sites, while the ungridded calibration yields 310±6 kJ/kg. These values are therefore to be regarded as identical.

Table 2 CLAMP results using *MET3BR* (ungridded) meteorological data, *GRIDMET3BR* (gridded) meteorological data, and the nearest neighbor methodology of Stranks and England (1997) and additional African sites

	MET3BR			GRIDMET3BR			Nearest neighbor methodology			
Climate variable	SD residuals	Los Baños	Sanctorum	SD residuals	Los Baños	Sanctorum	Los Baños		Sanctorum	
							SD residuals	Climate variable	SD Residuals	Climate variable
MAT (°C)	1.2	15.1	18.2	1.2	13.9	15.9	1.2	14.3	0.9	15.7
WMMT (°C)	1.6	24.6	27.2	1.4	23.3	25.2	1.5	23.6	1.3	22.8
CMMT (°C)	1.9	6.8	9.7	1.9	5.4	7.3	1.8	6.0	1.5	8.0
LGS (months)	0.7	8.7	10.3	0.7	7.9	8.8	0.8	9.5	0.8	9.8
GSP (mm x 10)	33.8	152.8	247.9	19.5	113.8	160.1	21	102	25	142
MMGSP (mm x 10)	3.7	17.1	25.4	2.6	13.6	18.3	3.3	11.6	3.5	15.5
3-WET (mm x 10)	14.1	72.2	108.0	13.9	69.9	85.2	15.6	76	13.9	55.3
3-DRY (mm x 10)	9.4	32.0	51.4	3.2	15.7	18.5	4.4	14	5.0	14.7
RH (%)	7.3	66.2	66.0	5.3	68.4	67.9	3.1	66.0	4.0	66.2
SH (g/kg)	0.9	7.3	8.0	1.0	7.5	8.4	0.9	7.7	0.8	8.0
ENTHAL (kJ/kg x 10)	0.3	30.7	31.2	0.5	31.6	32.2	0.4	31.9	0.4	32

SD Standard deviation, MAT mean annual temperature, *WMMT* warm month mean temperature, *CMMT* cold month mean temperature, *LGS* length of the growing season, *GSP* mean growing season precipitation, *MMGSP* mean monthly growing season precipitation, *3-WET* precipitation during the three wettest months, *3-DRY* precipitation during the three driest months, *RH* relative humidity, *SH* specific humidity, *ENTHAL* enthalpy

Using the classification of Köppen, modified by Garcia (1988), both sites appear to have experienced a temperate-humid climate, but at present in this region a megathermal vegetation is observed (MAT >20 ºC) where a xerophytic scrub-vegetation contains abundant leguminous plants with a predominantly notophyll leaf size. In the classification of Köppen and modified by Garcia (1988), this corresponds to a dry-temperate climate.

At Los Baños, repeated episodes of flooding and drought occurred as indicated by the mud-rich succession containing mudcracks. In these sediments, raindrop impact “craters” have been preserved (Arellano et al. 2005). This is consistent with the seasonal variations in rainfall suggested by CLAMP and a distinct dry season. This and the frost-free thermal regime supported the development of a *Quercus* forest with subsidiary elements such as *Juniperus* and *Cercocarpus* (Fig. 5). Entire margins predominate and microphyll size categories II and III account for 65% of the total.

The Sanctorum section represents a quieter lacustrine depositional environment represented by finer sediments containing diatoms and ostracods (Arellano et al. 2005). In this locality, the leaves of *Salix* (Fig. 7), *Populus*, and *Platanus* predominate as riparian/lacustrine margin elements relatively free of flooding events since they develop in the external facies at the edges of the basin. The percentage of morphotypes with entire margins is high (66%), and because toothed margins tend to predominate in riparian communities (Wolfe 1977, 1979, 1993), this would indicate that morphotypes with a non-riparian habitat are well represented and are likely to have been sourced from better-drained sites either along inflow streams or by wind transport.

LMA superficially indicates markedly different MATs, but taking into account the uncertainties, the two values of 14 and 20°C overlap. Single character (leaf margin type in this case) analysis is highly susceptible to taphonomic effects (e.g., selection for toothed margined species due to stream courses passing through communities rich in those taxa), and without the uncertainty estimate it would be easy to conclude that markedly different MATs were experienced at the two sites. The multivariate analyses used here (CLAMP with different calibration data and analytical protocols) are more taphonomically robust because a more complete suite of environment-correlated physiognomic characters are utilized. CLAMP analyses indicate a high degree of thermal similarity between the sites.

The similarities in the climate regimes suggest that differences in floral composition may indicate spatial differences in community structure and composition rather than any fundamental climatic differences. Undoubtedly, edaphic and taphonomic differences exist between the two sites as recorded in the differences between the sampled sections.

The Pliocene climate clearly favored the presence of taxa such as *Populus, Quercus,* and *Cercocarpus* that are not found in any abundance in this area today, which, by comparison with the Pliocene, is now much drier. Some taxa, e.g., *Quercus*, *Cercocarpus*, and *Salix*, were not only more abundant but were also more diverse in the Pliocene (Ortiz and Velasco-de León 2006). It is likely that the marked climatic change between the Pliocene and today was due to the uplift of the Sierra Madre Oriental, generating an orogenic shadow and a decrease in the precipitation in this area. Subsequently, the disappearance of the Amajac palaeolake, most likely related to this drying, was associated with a drastic change in the type of vegetation. Oaks and gallery forests were replaced by a xeromorphic scrubland.

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