

Palaeocene–Eocene paratropical floral change in North America: responses to climate change and plant immigration

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Abstract: The Initial Eocene Thermal Maximum (IETM) at *c.* 55 Ma represents a period of rapid global warming that lasted less than 200 ka. The response of vegetation to such an event, and particularly warm-adapted highly diverse vegetation types, is poorly understood. Using pollen floral, clay mineral and stable carbon isotope analyses of sediments from the upper Tuscaloosa Formation on the eastern US Gulf Coast (eastern Mississippi and western Alabama), we document paratropical floral changes across the Palaeocene–Eocene boundary from the Wahalak #2 and lower Harrell cores. Data indicate strong changes in the abundance of kaolinite that correlate with changes in relative abundance of native pollen taxa. There is no evidence for a transient, extra-tropical flora on the US Gulf Coast that may characterize the IETM. Immigration and extinction are not associated with this event. Instead, Early Eocene plant immigration occurs in pulses and therefore is not associated directly with climate change during the IETM. The two cores share the same regional species pool but compositional differences are stronger between cores than they are either through changes in environment, increased soil erosion or chemical weathering, or through the introduction of non-native plants. Our data suggest that vegetation change across the Palaeocene–Eocene boundary is not a single event but rather a sequence of cascading events.

Keywords: lower Eocene, US Gulf Coast, ¹³C, kaolinite, palynology, vegetation.

This paper documents the response of a paratropical flora to climate warming and plant immigration across the Initial Eocene Thermal Maximum (IETM). The IETM at about 55 Ma was a rapid climate warming event that lasted between 84 and 220 ka (Röhl *et al.* 2000; Bowen *et al.* 2001). It is recognized in the stratigraphic record by a carbon cycle perturbation manifest as a $\delta^{13}\text{C}$ excursion of -2 to -8% (Kennett & Stott 1991; Koch *et al.* 1992, 1995; Bowen *et al.* 2001; Zachos *et al.* 2001). During the IETM, high-latitude deep oceans warmed by 4–8 °C (Kennett & Stott 1991; Zachos *et al.* 2001), and the one well-studied record on land (at high mid-latitudes in the Bighorn Basin, Wyoming, USA) suggests that mean annual temperatures rose by up to 4 °C (Fricke *et al.* 1999). Shifts in clay mineral composition during the IETM have been used qualitatively to assess regional changes in humidity, seasonality of precipitation, temperature and soil erosion (Robert & Chamley 1991; Schmitz *et al.* 2001). In some studies, the shifts in clay mineral assemblages have been used to identify the position of the Palaeocene–Eocene boundary (Gibson *et al.* 2000; Bolle & Adatte 2001).

In the oceans, benthic foraminifera suffered an extinction of between 30 and 50% (Kennett & Stott 1991; Thomas 1998), the dinoflagellate *Apectodinium* bloomed in high latitudes (Crouch *et al.* 2001), pelagic foraminifera diversified (Kelly *et al.* 1996) and ostracodes experienced extinction and community turnover (Speijer & Morsi 2002). On land, the IETM led to major mammalian turnover on the three Holarctic continents, with associated shifts in geographical range and trophic levels

(Gingerich 1989; Clyde & Gingerich 1998; Beard & Dawson 1999; Bowen *et al.* 2002). In North America, where the mammalian record has been studied in the greatest detail, the IETM is characterized by faunas that contain the first representatives of three mammalian orders (Artiodactyla, Perissodactyla, Primates), as well as unusual ‘dwarfed’ versions of range-through taxa (Gingerich 2003).

In contrast to the clear response seen in land vertebrate faunas and marine fauna and flora, land plants record neither major turnover nor massive extinction across the Palaeocene–Eocene boundary (Frederiksen 1998; Wing 1998; McIver & Basinger 1999; Rull 1999; Harrington 2001; Jaramillo & Dilcher 2001; Wing & Harrington 2001; Harrington 2003a). In all studied areas, there is limited extinction and only minimal immigration that is tied to the Early Eocene (Harrington 2003a; Wing *et al.* 2003). According to many ecological studies, the introduction of non-native plants should have a deleterious effect on the native flora (e.g. Lonsdale 1999; Levine *et al.* 2003) but the only strong pattern to emerge so far from the Palaeogene data is a reorganization in native plant associations across the boundary (Harrington 2001, 2003b; Wing & Harrington 2001). An important consideration for understanding this vegetation response is that embedded within the global climate perturbations are regional environmental changes that play a fundamental role in governing floral membership of a regional vegetation type.

In this paper we examine the floral response to the IETM on the eastern US Gulf Coast. This region is significant because it had a paratropical climate in the Late Palaeocene–Early Eocene

with mean annual temperatures of about 27 °C and mean annual range of temperatures of about 2 °C (Wolfe & Dilcher 2000). Most studies on Palaeocene–Eocene plant records emanate from high latitudes so it is important to understand the responses of high-diversity vegetation types to the perturbations in the global climate during and across the IETM. We present pollen and spore (sporomorph), isotopic and clay mineral data from the Late Palaeocene–Early Eocene, and attempt to identify the stratigraphic position of the IETM. We test whether vegetation change correlates with the introduction of immigrant plants and we also examine whether kaolinite abundance is correlated with changes in vegetation because clay mineral changes may provide a climate proxy. A summary is provided of both floral and clay mineral changes from literature sources to facilitate a greater understanding of our results.

Vegetation records in the IETM

There are few sections globally that contain vegetation records from within the IETM (Table 1). In all cases, pollen and spores are the only plant organs preserved in known boundary sections, and the Powder River Basin is the only terrestrial locality. Vegetation records from the Powder River Basin indicate that pollen floras in the IETM are more similar to those of the Palaeocene than the Early Eocene (Wing *et al.* 2003). The sole difference in floral response between New Zealand and North America is that one taxon, a mangrove palm, first occurs within the IETM in New Zealand (Table 1); all the North American immigrants arrive after the IETM (Wing *et al.* 2003). Hence, Wing *et al.* (2003) proposed that floral change across the Palaeocene–Eocene boundary is composed of two phases: changes in abundance of native range-through vegetation, followed by arrival of immigrants. The model of Wing *et al.* (2003) requires more data to test its relevance because it is based on a very small sample size (Table 1). Sections in Spain and the UK do not add greatly to this debate. In Spain, the pollen data come from offshore marine sediments and contain high proportions of gymnosperm pollen and fern spores that are prone to long-distance dispersal in marine sediments (van der Kaars 2001). In the UK, the position of the IETM is not well known in plant-bearing strata, although recent attempts have identified a candidate section called the Cobham Lignite that embraces the IETM (Collinson *et al.* 2003). The trend leading to increased abundance of paratropical sporomorph taxa, as noted by Beerling & Jolley (1998), may relate to longer-term warming in the last 1 Ma of the Late Palaeocene (e.g. Wing 1998; Zachos *et al.* 2001), especially because other high-latitude records with robust time constraint indicate minimal floral change within the IETM (Table 1).

Clay mineral records in the Late Palaeocene to Early Eocene

Clay mineral assemblages can offer a climate proxy that provides a context for examining biotic change. Possible interpretations of kaolinite abundance across the Palaeocene–Eocene boundary, for example, include increased humidity and chemical weathering (Robert & Chamley 1991; Robert & Kennett 1994; Gibson *et al.* 2000; Bolle & Adatte 2001). But a more favoured postulate is that kaolinite abundance in some areas of the world results from increased mechanical weathering of soils (Thiry 2000; Schmitz *et al.* 2001; Dickens *et al.* 2003) because kaolinite forms slowly and the quantities observed in the Late Palaeocene–Early Eocene are inconsistent with formation during a single, rapid warming interval such as the IETM (Thiry 2000; Dickens *et al.* 2003). In

Table 1. Palaeocene–Eocene boundary sections containing plant fossils

Area	δ ¹³ C	Additional constraint	Depositional environment	Comments	Reference
USA (Powder River Basin, WY)	Y	1	Terrestrial, subtropical–warm temperate floodplains and swamps	Two samples contained within the IETM. Both have characteristic ‘Palaeocene’ compositions. Eocene immigrants (<i>Platycarya</i> and <i>Intraiporopollenites instructus</i>) first occur after the IETM	Wing <i>et al.</i> (2003)
New Zealand (Tawanui)	Y	2,3	Marine, upper–middle bathyal depths (500–1000 m)	Twelve samples contained within the IETM. Only <i>Spinizonocolpites prominatus</i> (<i>Nypa</i> mangrove) first appears near the beginning of the IETM but not at the base. Vegetation communities do not change significantly across the IETM. There are no extinctions	Crouch & Visscher (2003)
Spain (Ernuva)	Y	2	Marine, offshore basin slope	Four samples contained within the IETM but are dominated (85–90%) by marine phytoplankton. Pollen floras are dominated by gymnosperms, ferns and reworked taxa such as <i>Cranwellia</i> , <i>Expressipollis</i> and <i>Kiurzipites</i>	Schmitz <i>et al.</i> (2001)
UK (North Sea–SE England)	?	?	Marine, marginal to offshore	Isotope data come from the North Sea (Shell/Esso 22/6-1 well) but pollen data appear to originate from SE England. Pollen floras appear to show an increased paratropical affinity	Beerling & Jolley (1998)

1, Mammal biostratigraphy; 2, *Apectodinium* acme; 3, benthic foraminiferal extinction event.

a recent review of clay mineral changes in Tethyan sediments, Bolle & Adatte (2001) observed that in some regions, such as the Arabian peninsula and west and north Africa, aridity marks the Late Palaeocene–Early Eocene interval. This aridity is expressed as an increased abundance of the clay mineral palygorskite. In addition to the sections noted by Bolle & Adatte (2001), globally there are other sequences with clay mineral records in the Late Palaeocene and Early Eocene (Table 2). The increase in kaolinite is variable in all sections and there is no agreement in the literature as to what represents a ‘significant’ increase in kaolinite. A compounding issue is that most sections cannot be correlated directly with the IETM; only Gebel Duwi in Egypt has an increase of 20% in kaolinite that can be tied directly with both the benthic foraminiferal extinction (BFE) and the carbon isotope excursion (Bolle & Adatte 2001; Speijer & Morsi 2002). However, even in Gebel Duwi, there is a noticeable increase in kaolinite in the Late Palaeocene that precedes the IETM (Bolle & Adatte 2001). Tawanui in New Zealand has isotopic control and the BFE, but the increase in kaolinite is minimal (Table 2) and limited to four samples that occur before the IETM (Kaiho *et al.* 1996). In Elles (Tunisia), Alamedilla (Spain) and Zumaia (Spain) kaolinite increases in the Late Palaeocene, *c.* 200 ka before the IETM (Gawenda *et al.* 1999; Bolle & Adatte 2001). In other regions, such as Antarctica (Robert & Kennett 1994), Virginia (Gibson *et al.* 2000) and SE England (Bolle & Adatte 2001), strong increases in kaolinite demonstrably postdate Palaeocene–Eocene boundary events such as the *Apectodinium* acme, the isotope excursion and the BFE. Some regions such as the Bighorn Basin in Wyoming, USA (Gibson *et al.* 2000) and Kaurtakapy in Kazakhstan (Bolle & Adatte 2001) have no changes in clay minerals across the Palaeocene–Eocene boundary. Changes in clay mineralogy and, by association, changes in weathering, environmental conditions or mechanical erosion are clearly regionally diverse in the Late

Palaeocene–Early Eocene and are not necessarily linked with the IETM.

Stratigraphy of the eastern US Gulf Coast

Sediments of early Palaeogene age are present across a wide area on the US Gulf Coast from Georgia to Mississippi and the general stratigraphy of the Late Palaeocene–Early Eocene interval (Fig. 1) is well understood (Frederiksen *et al.* 1982; Berggren *et al.* 1985; Gibson & Bybell 1994; Mancini & Tew 1995). Time constraints are provided by magnetostratigraphy (Rhodes 1995; Rhodes *et al.* 1999) and complemented by sequence stratigraphy (Mancini & Tew 1995). Biostratigraphy is provided by calcareous nannoplankton (Gibson *et al.* 1982; Gibson & Bybell 1994), planktonic foraminifera (Mancini & Oliver 1981; Berggren *et al.* 1985) and sporomorphs (Frederiksen 1988, 1991, 1998; Harrington 2001). Traditionally, the Palaeocene–Eocene boundary was placed at the base of the Bashi–Hatchetigbee formations in western Alabama and eastern Mississippi (Frederiksen *et al.* 1982). However, recent work on the US Gulf Coast, and the new placement of the Palaeocene–Eocene boundary at the IETM instead of the NP9–NP10 boundary (Aubry *et al.* 2003), now puts the Palaeocene–Eocene boundary within the upper Tuscaloosa Formation (Harrington & Kemp 2001; Harrington 2003*b*). This represents more than 80 m of section. Unfortunately, the upper Tuscaloosa Formation represents brackish-water depositional environments with emergent swamp deposits that do not preserve marine biota that can be used to identify the IETM. The middle Tuscaloosa Formation and Bashi–Hatchetigbee formations contain marine fossils (Gibson *et al.* 1982) but they are respectively too old and too young to contain the IETM (Harrington & Kemp 2001; Harrington 2003*b*).

Table 2. Late Palaeocene–early Eocene sites containing clay mineral data; comments indicate the stratigraphic control on the clay mineral data

Region	Kaolinite increase	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	BFE	Other	Comments	Reference
Antarctica Site 690B	?	Y	Y	Y	–	Strong increase in smectite (<i>c.</i> 30%) but not kaolinite. Changes in kaolinite/illite ratio correlate directly with IETM. Increase in kaolinite up to 25% after IETM	Kennett & Stott (1991); Robert & Kennett (1994); Röhl <i>et al.</i> (2000)
Central North Sea (UK)	60%	N	N	N	1	20% kaolinite is associated with 90% <i>Apectodinium</i> peak but increased kaolinite occurs with lower abundance (30%) of <i>Apectodinium</i>	Knox (1996, 1998)
New Zealand (Tawanui)	<i>c.</i> 5%	N	Y	Y	–	Kaolinite at <i>c.</i> 5% of clay suite before the BFE. Four samples cover the IETM and the small increase in kaolinite occurs immediately before the BFE. Kaolinite decrease to <i>c.</i> 7% during and after the BFE	Kaiho <i>et al.</i> (1996)
USA (New Jersey)	<i>c.</i> 30%	N	N	Y	–	Kaolinite increase coincides with Vincentown–Manasquan fms transition and with BFE	Gibson <i>et al.</i> (1993)
USA (Virginia)	20–40%	N	N	N	1	Marlboro Clay (NP9–NP10) contains abundant <i>Apectodinium</i> but is diachronous in Virginia	Edwards & Guex (1996); Gibson <i>et al.</i> (2000)
USA (Wyoming)	–	Y	Y	–	2	The Bighorn Basin has excellent time constraint but no kaolinite increase	Gibson <i>et al.</i> (2000)
USA (North Dakota)	>70%	N	N	–	2, 3	The Golden Valley Fm. is not accurately time-constrained but floras and mammals below and above the highly kaolinitic Bear Den member in the lower Golden Valley Fm. indicate a Palaeocene–Eocene transition	Hickey (1977)
Spain (Zumaia)	<i>c.</i> 75%	N	Y	Y	–	Increase in kaolinite precedes IETM by <i>c.</i> 270–325 ka	Gawenda <i>et al.</i> (1999)

1, *Apectodinium* acme; 2, mammalian biostratigraphy; 3, megafloal biostratigraphy; BFE, benthic foraminifera extinction.

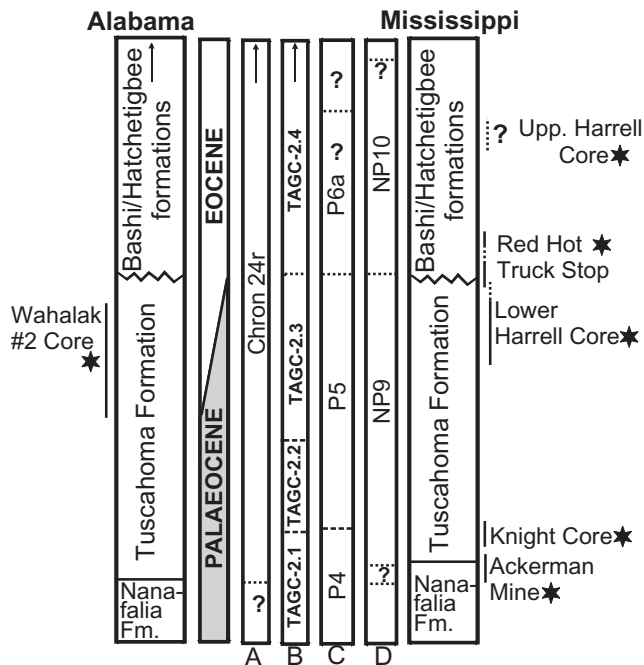


Fig. 1. Stratigraphy of the eastern US Gulf Coast adapted from Harrington (2001). A, magnetostratigraphy (Rhodes 1995; Rhodes *et al.* 1999); B, sequence stratigraphy (Mancini & Tew 1995); C, planktonic foraminifera (Mancini & Oliver 1981; Berggren *et al.* 1985); D, nannofossils (Gibson & Bybell 1994); stars indicate position of lignites used in isotope analysis.

Methods and materials

Study sections

Palynological, isotopic and clay mineral data are presented from the Wahalak #2 Core, western Alabama, and the lower Harrell Core, eastern Mississippi (Figs 1 and 2). In addition, isotope data are also presented from the Ackerman Mine, the Knight Core, the Red Hot Truck Stop and the upper Harrell Core (Figs 1 and 2). We divide the Harrell Core into two sections; the lower Harrell Core contains only the Tuscahoma Formation whereas the upper Harrell Core contains lignites from the Bashi–Hatchetigbee formations that were not analysed for pollen and spores. Both the Wahalak #2 and lower Harrell cores contain the upper Tuscahoma Formation and lie above the Bells Landing Marl, which contains P5 Zone foraminifera (Mancini & Oliver 1981), and below the Bashi–Hatchetigbee formations, which lie unconformably on top of the

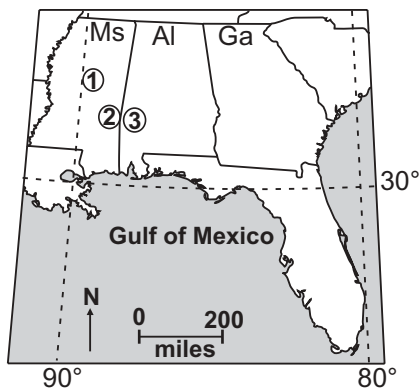


Fig. 2. Location map of the eastern US Gulf Coast. 1, Ackerman Mine; 2, Knight Core, Harrell Core and Red Hot Truck Stop; 3, Wahalak #2 Core.

Tuscahoma Formation in both the Wahalak #2 and lower Harrell cores. This contact represents a major sequence boundary across western Alabama and eastern Mississippi (Mancini & Tew 1995). The exact stratigraphic relationship between the lower Harrell and Wahalak #2 cores is unknown. The youngest known Tuscahoma sediments are at the Red Hot Truck Stop locality in Meridian, Mississippi, which is located near the Harrell Core. This site contains Early Eocene mammals and plant remains in the Tuscahoma Formation (Ingram 1991; Beard *et al.* 1995; Frederiksen 1998; Harrington 2003b). The Bashi–Hatchetigbee formations are also present at this locality, although in this paper we present only isotope data from this part of the section. The results from a previous pollen investigation from the Red Hot Truck Stop are included in some statistical and comparative analyses of the pollen composition in the Wahalak #2 and lower Harrell cores using the data from Harrington (2003b).

Isotope analysis

Isotope analysis was undertaken on 20 samples from 14 lignites from throughout the Tuscahoma and Bashi–Hatchetigbee formations (Figs 1 and 3). These samples include sections potentially embracing the IETM (Wahalak #2 and lower Harrell cores) as well as those younger and older than the IETM. These samples delimit the range of isotopic variability in Palaeocene–Eocene swamps from the US Gulf Coast. Samples were ground in a mortar and pestle, soaked in HCl to remove carbonates, rinsed to neutrality with distilled water, and then oven dried. Powders (*c.* 2 mg) were sealed in Sn foil capsules, and then analysed using a Carlo Erba elemental analyser interfaced with a Micromass Optima gas source mass spectrometer. Carbon isotope values are reported as normalized part per thousand (‰) deviations from an international standard using the standard notation: $\delta^{13}\text{C} = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000$, where *R* is the $^{13}\text{C}/^{12}\text{C}$ ratio, and the standard is V-PDB. One standard deviation for repeated analysis of a laboratory C standard is $\pm 0.15\%$.

Clay mineral analysis

Clay mineral identification and quantification was carried out using XRD analysis on 11 samples from the Wahalak #2 Core and on 27 samples from the lower Harrell Core. A $< 2 \mu\text{m}$ separate was isolated to identify clay minerals present in each sample. XRD analysis was carried out using a Philips PW1700 series diffractometer equipped with a cobalt-target tube and operating at 45 kV and 40 mA. Diffraction data were analysed using the International Centre for Diffraction Data (ICDD) database. Clay mineralogies were then determined after scanning Ca-saturated oriented samples as air-dry and glycol-solvated mounts and after heating the mounts to 550 °C for 2 h. To gain further information about the clay minerals present in the samples, modelling of XRD profiles was carried out using newmod-for-windows™ (Reynolds & Reynolds 1996). Modelling was also used to assess the relative proportions of clay minerals present in the $< 2 \mu\text{m}$ fractions by comparison of sample XRD traces with newmod-for-windows™ modelled profiles. The modelling process requires the input of diffractometer, scan parameters and a quartz intensity factor (instrumental conditions), and the selection of different sheet compositions and chemistries. An estimate of the crystallite size distribution of the species may be determined by comparing peak profiles of calculated diffraction profiles with experimental data. By modelling the individual clay mineral species in this way, mineral reference intensities were established and used for quantitative standardization following the method outlined by Moore & Reynolds (1997).

Sporomorph analysis

A total of 92 samples were taken for palynological analysis from the Wahalak #2 Core ($n = 15$) and the lower Harrell Core ($n = 77$). Most palynological samples are from estuarine or brackish-water deposits that yield regional pollen floras. Some lignites are also present in both cores in the Tuscahoma Formation (Fig. 3a and b) but are excluded from pollen analysis because they contain a predominantly local pollen flora. Sample preparation followed a basic procedure of maceration with mortar and

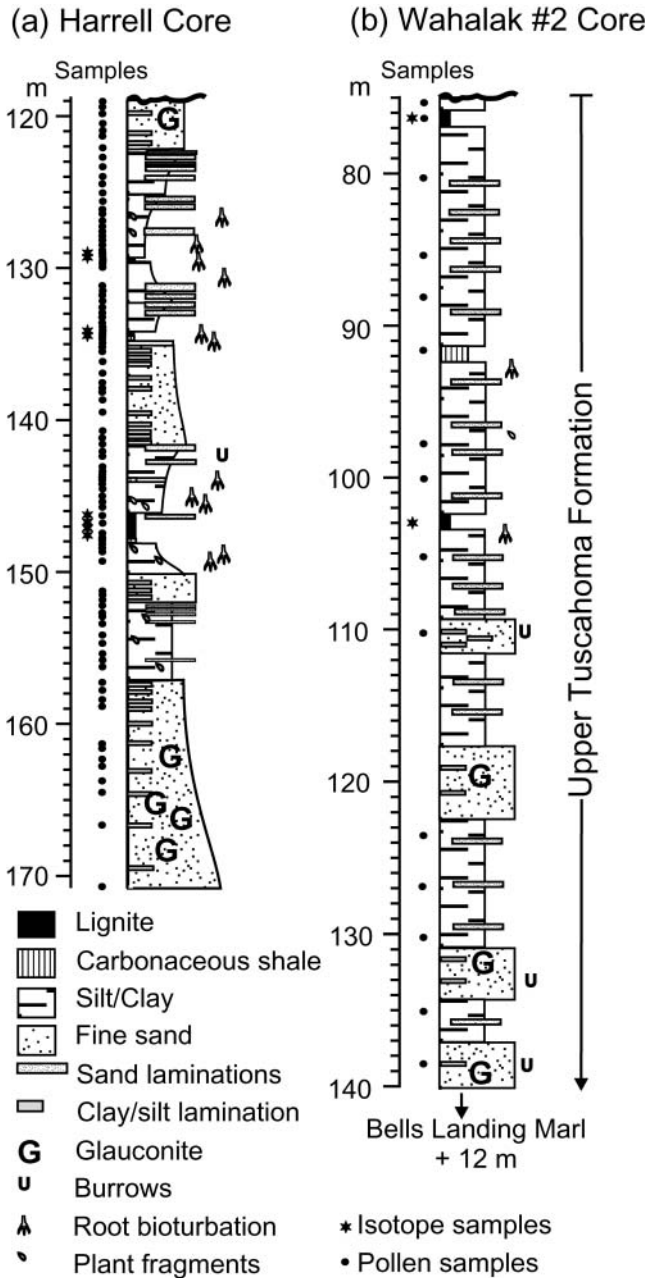


Fig. 3. (a) Measured section through the upper Tuscalooha Formation in the lower Harrell Core indicating major facies types and sampling position for both isotopes and sporomorphs. (b) Measured section through the upper Tuscalooha Formation in the Wahalak #2 Core indicating major facies types and sampling positions. Section redrawn from Mancini (1981). In both (a) and (b), the top represents the contact with the Bashi–Hatchetigbee formations.

pestle, chemical digestion of carbonates (HCl) and silicates (30% HF), followed by light oxidation to remove excess amorphous organic material (2 min in 70% HNO₃). Residues were stained with safranin and aliquots were mounted evenly onto two coverslips. Between most stages, residues were sieved with a 10 µm mesh. More than 400 spore and pollen grains were counted for each sample. Both composition and diversity are of interest in this paper and we use a variety of techniques to explore these components of the sporomorph assemblages. The Bray–Curtis index of similarity and the squared chords metric of measuring dissimilarity between samples were used to assess compositional change over time.

The Bray–Curtis index of similarity uses presence–absence data and the squared chord dissimilarity metric requires relative abundance data. Rare taxa are excluded from the squared chord dissimilarity analyses; we define these taxa as those that are absent from the top 25 taxa rankings in any one sample. In presence–absence matrices, all taxa are included because they are equally weighted. For both metrics, similarity–dissimilarity is measured relative to the oldest sample in each section. Detrended correspondence analysis (DCA) was used on both presence–absence and the modified relative abundance data to assess compositional differences between sections. In this case rare taxa are defined as those present in <20% of samples and they were downweighted during ordination of relative abundance data; downweighting is not required for the presence–absence matrix. The MVSP program (Kovach 1998) computed similarity–dissimilarity metrics and DCA.

Rarefaction analysis was used to examine within-sample diversity as a function of numbers of taxa per sample. Rarefaction was required because all the samples have slightly different count sizes. Rarefaction allows the standardization of all taxon counts through interpolation to the same number of specimens (Miller & Foote 1996). biodiversity pro calculated these within-sample diversity statistics (McAleese *et al.* 1997). Another useful approach is the study of among-sample diversity patterns because diverse datasets can have many taxa that are rare and not present consistently in every sample. The changes in among-sample diversity were determined by Chao 2 estimation because this method is sensitive to high-diversity datasets and to low numbers of samples (Colwell & Coddington 1994). The Chao 2 estimates were calculated using estimates (Colwell 2000).

Confidence intervals on the stratigraphic ranges of taxa with first and last occurrences were calculated using the Strauss & Sadler (1989) equation published by Marshall (1990). The significance level is calculated at 50%. Statistical significance was tested using the nonparametric Mann–Whitney U-test, Kruskal–Wallis ANOVA and Spearman rank correlation because the distribution of the counted pollen data is difficult to determine even after statistical manipulation.

Results

Isotope geochemistry

None of the samples from the lower Harrell or Wahalak #2 cores have carbon isotope values significantly more negative than those from other lignites of Late Palaeocene or Early Eocene age (Table 3). Samples from both the Wahalak #2 and lower Harrell cores show dispersion of $\delta^{13}\text{C}$ values from -26.9‰ to -25.2‰ . There is considerable variation in the isotopic signature from the lignites and even within the same lignite (Fig. 4a). For example, variations of more than 1‰ are recorded in lignite numbers 6 and 7 (Table 3). Given the coarse isotopic sampling in the upper Tuscalooha Formation, the IETM probably occurs between lignites, assuming that lignites are capable of recording faithfully the $\delta^{13}\text{C}$ excursion at the Palaeocene–Eocene boundary.

Clay mineralogy

The abundance of kaolinite in the lower Wahalak #2 Core is typical of that in the lower–middle Tuscalooha Formation, which averages 5–11% of the clay mineral assemblages (Harrington & Kemp 2001). The two samples with *c.* 60% kaolinite and the samples higher in the core with *c.* 20% kaolinite (Fig. 4b) are therefore significantly different. Lignites bracketing this interval are 26 m apart and have typical $\delta^{13}\text{C}$ values for Late Palaeocene–Early Eocene lignites (Table 3). Sedimentation rates are difficult to reconstruct in the upper Tuscalooha Formation because there are few data points but this interval is probably sufficient to encompass the entire IETM. In contrast, there is no kaolinite peak in the lower Harrell Core, but values are the same as those in the upper Wahalak #2 Core and consistently greater

Table 3. Stable carbon isotope results from 14 lignites on the eastern US Gulf Coast tabulated from youngest (1) to oldest (14)

Section	Sample	Metre level	Lignite number	$\delta^{13}\text{C}$ (‰)
Upper Harrell Core (MS)	Ht/76*	80.65	1	-27.1
	Ht/39*	80.77	1	-27.0
	Ht/71*	84.66	2	-26.2
Red Hot Truck Stop (MS)	Rh/05c*	-	3	-26.3
	Rh/04c*	-	4	-27.6
Lower Harrell Core (MS)	Ha/19†	129.08	5	-25.6
	Tu/21†	129.15	5	-26.4
	Ha/29†	133.95	6	-25.8
	Tu/17†	134.16	6	-26.9
	Ha/46†	146.15	7	-26.3
	Ha/47†	146.76	7	-25.6
	Ha/48†	147.37	7	-26.3
	Tu/05†	147.62	7	-26.9
	Wahalak #2 Core (AL)	Wa†	76.94	8
Wa†		103.33	9	-26.4
Knight Core (MS)	Kn/01‡	47.0	10	-25.9
Ackerman Mine (MS)	AC/12 I seam‡	-	11	-27.2
	AC/09 H seam‡	-	12	-25.7
	AC/03 G seam‡	-	13	-25.4
	AC/06 F seam‡	-	14	-27.2

The Harrell Core is split into two because the upper section is within the Bashi–Hatchetigbee formations whereas the lower section is within the Tuscahoma Formation. Metre levels are provided only for core samples. $\delta^{13}\text{C}$ values are relative to V-PDB. MS, Mississippi; AL, Alabama; -, outcrop value.

*Eocene.

†Palaeocene or Eocene.

‡Palaeocene.

than 20% (Fig. 4a). The Tuscahoma Formation at the Red Hot Truck Stop has low kaolinite abundance of about 5% of the clay mineral assemblage (Gibson *et al.* 2000). Hence, changes in clay mineralogy are restricted to a confined interval in the upper Tuscahoma Formation, but an interval that is probably significantly greater in duration than the IETM.

Floral composition

A total of 167 taxonomic groups are present in both cores, with particular dominance in Taxodiaceae (sequoia family) and Myricaceae–Betulaceae (sweet gale–birch) pollen (Fig. 4b and c). Many taxa are present in very low abundance and the top 10 ranked taxa account for 80% of all counted specimens. Families with present-day subtropical to tropical affinity are represented by Anacardiaceae (mangoes–cashews), Annonaceae (sweetsop), Apocynaceae (oleanders), Bombacaceae (balsa trees), Loranthaceae (mistletoes), Palmae (palms), Sterculiaceae (cocoa) and Symplocaceae (tea trees). Wind-pollinated families are represented in abundance by Myricaceae–Betulaceae, Juglandaceae (walnut), Taxodiaceae and Ulmaceae (elms). Many of the sporomorph taxa cannot be placed into modern systematic groups or can be placed, at best, into three or more possible modern families (Harrington & Kemp 2001; Harrington 2003b).

First and last occurrences

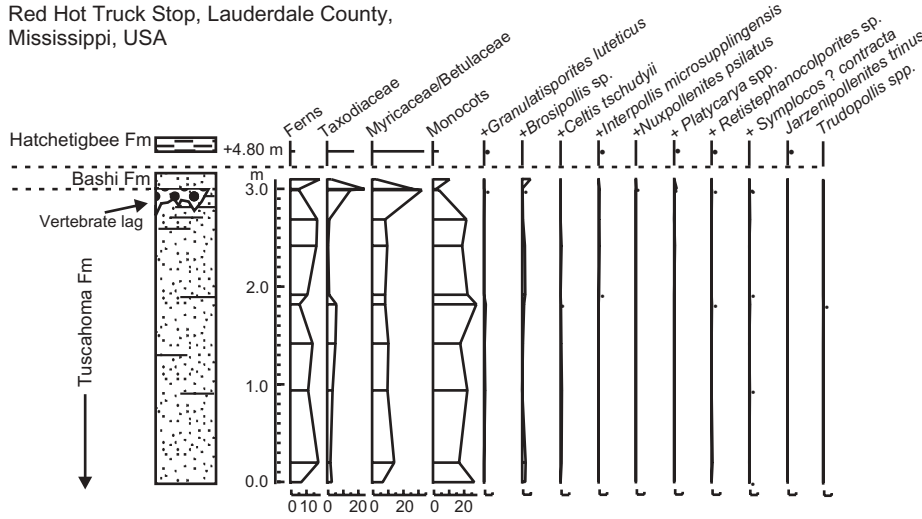
First occurrences of some 'Eocene' taxa (Tschudy 1973; Frederiksen *et al.* 1982; Harrington 2003a,b) are observed in the lower Harrell Core (Fig. 4b) and are represented by *Granulatisporites luteticus*, *Interpollis microsuplicingensis*, *Celtis tschudyii*, *Symplocos? contracta* and *Brosipollis* spp. Most of these first appear within an interval of 7 m at 145 m depth and some represent taxa that immigrated from Europe (e.g. *Interpollis microsuplicingensis*) and possibly Asia (e.g. *Celtispollenites* sp.)

(Frederiksen 1993; Harrington 2003a). The only potential Eocene immigrant in the Wahalak #2 Core is *Symplocos? contracta* (Fig. 4c). Some Eocene immigrant taxa are missing from the lower Harrell Core and include *Nuxpollenites psilatus*, *Platycarya* spp. and *Retistephanocolporites* sp., which all occur at the Red Hot Truck Stop locality (Fig. 4a) (Harrington 2003b), and *Dicolpollis* and *Intratropipollenites instructus*, which occur only in the Bashi–Hatchetigbee formations (Tschudy 1973; Frederiksen *et al.* 1982; Frederiksen 1988; Harrington 2001). The high sampling intensity in the lower Harrell Core and at the Red Hot Truck Stop means that collection failure does not explain this lag in appearance times. With the exception of both *Cranwellia* and *Intratropipollenites* sp. A, which are absent from both cores, many taxa with last occurrences noted by Frederiksen (1998) and Harrington (2001) in the Late Palaeocene, such as *Insulapollenites rugulatus*, *Jarzenipollenites trinus*, *Pseudoplicapollis limitata*, *Tricolpites crassus*, *Tricolporopollenites* sp. C and *Trudopollis* spp., are either present at the Red Hot Truck Stop locality (Fig. 4a; Harrington 2003b) or have 50% confidence intervals that extend above the Tuscahoma Formation in both the Wahalak #2 and lower Harrell cores. A sharp extinction horizon is lacking but reworking of sporomorphs is a possibility, which may extend artificially a taxon's apparent stratigraphic range. However, reworking will not affect first appearance datum points.

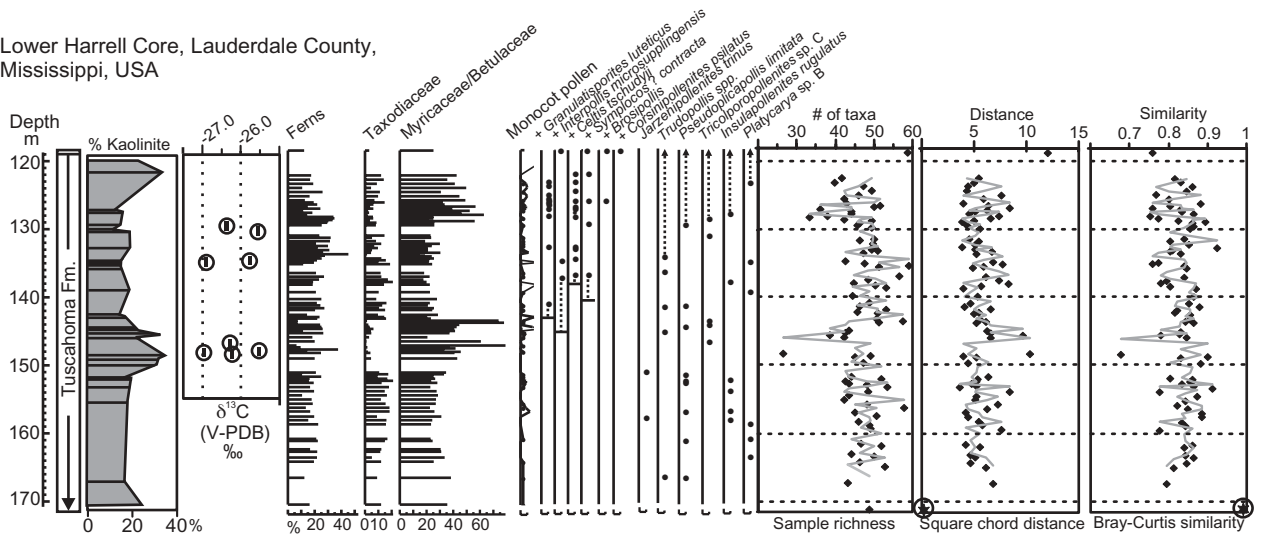
Composition change

In the Wahalak #2 Core (Fig. 4c), there is a changeover in dominant taxa at about 100 m between Taxodiaceae pollen, which is characteristic of middle and lower Tuscahoma assemblages (Harrington & Kemp 2001), to Myricaceae–Betulaceae pollen. In the lower Harrell Core, myricaceous pollen is the top ranked taxon and ferns are more abundant (Fig. 4b). The squared chord distance metric demonstrates that samples in the kaolinite-rich upper Wahalak #2 Core (Fig. 4c), from the 100 m level to

A Red Hot Truck Stop, Lauderdale County, Mississippi, USA



B Lower Harrell Core, Lauderdale County, Mississippi, USA



C Wahalak #2 Core, Choctaw County, Alabama, USA

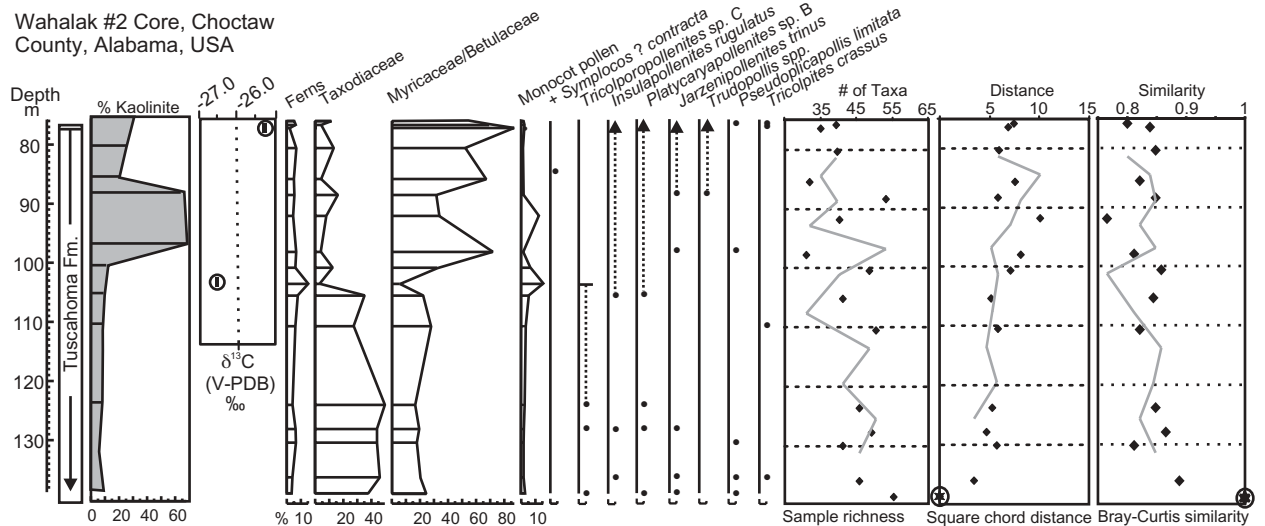


Fig. 4. Summary diagrams of the upper Tuscahoma Formation at (a) the Red Hot Truck Stop (data from Harrington 2003b), (b) the lower Harrell Core and (c) the Wahalak #2 Core. Also shown in (b) and (c), from left to right, are kaolinite content (per cent of clay mineral suite), $\delta^{13}\text{C}$ content of lignites, major vegetation types and dominant taxa, Eocene first occurrence taxa (marked with \pm and with 50% confidence intervals plotted on their bases), Palaeocene last occurrences (with 50% confidence intervals), rarefied sample richness at 401 grains, square chord distance from the lowest sample in the section (marked by a circled star) and Bray–Curtis similarity from the lowest sample in the section (marked by a circled star). Grey lines represent a five-point moving average through the samples.

the Tusahoma and Bashi–Hatchetigbee boundary at 75 m, belong to a different population from those in the lower half of the core ($U_{(7,7)} = 45$, $P = 0.007$). This reflects the change in the relative abundance of taxa that range through the section. However, the Bray–Curtis metric is not significantly different ($U_{(7,7)} = 11$, $P = 0.09$), demonstrating that changes in relative abundance are not correlated with new patterns of co-occurrence in native plant associations. Detrended correspondence analysis shows that the lower Harrell Core, the Wahalak #2 Core and the Red Hot Truck Stop are all compositionally different from one another in terms of both relative abundance and the co-occurrences of taxa (Fig. 5a and b). A one-way Kruskal–Wallis ANOVA on axis 1 sample scores from presence–absence data (Fig. 5b) demonstrates that a sample from one section is more similar to other samples from the same section than it is to samples from any other section (KW statistic $_{(77,15,12)} = 59.24$, $P < 0.0001$). The results from relative abundance data (Fig. 5a) on axis 1 sample scores are also statistically significant (KW statistic $_{(77,15,12)} = 58.52$, $P < 0.0001$). This suggests that relative abundances of dominant taxa are different in all sections and is seen in Fig. 4a–c. It also suggests that sporomorph co-occurrences are different, even though the sections share essentially the same species pool. However, nested within this pattern, there are subtle differences in the distribution of samples in the ordination space from the Wahalak #2 Core that correlate with

the abundance of kaolinite. In the relative abundance ordination (Fig. 5a), samples during and after the kaolinite peak are clearly defined on axis 2 whereas in the presence–absence ordination (Fig. 5b) there is no significant distinction. This supports results from the Bray–Curtis and square chord metrics. However, axis 2 captures significantly less variation in both ordinations than axis 1 (Fig. 5a and b) hence compositional differences between sections are stronger than environmental changes over time.

The distinct composition of samples from the Red Hot Truck Stop reflects in part the introduction of several immigrant taxa in the Early Eocene (Fig. 4a; Harrington 2003a) and it should therefore be compositionally dissimilar to Palaeocene floras. However, the initial introduction of immigrant taxa on the US Gulf Coast in the lower Harrell Core appears to have little impact upon the composition of the flora. If the assemblages before the introduction of immigrants (samples from 171 m to 147 m) are compared in the lower Harrell Core (Fig. 4b) with assemblages after the first occurrence of Eocene immigrants (samples from 145 m to 119 m), both square chord ($U_{(27,49)} = 720$, $P = 0.525$) and Bray–Curtis metrics ($U_{(27,49)} = 805$, $P = 0.119$) show no significant differences in composition. The same pattern is also demonstrated from DCA on the relative abundance data (Fig. 5c), which shows no significant differences on axis 1 between samples before the arrival of immigrants (171 m to 147 m) and those after (above 145 m). The ordination on presence–absence

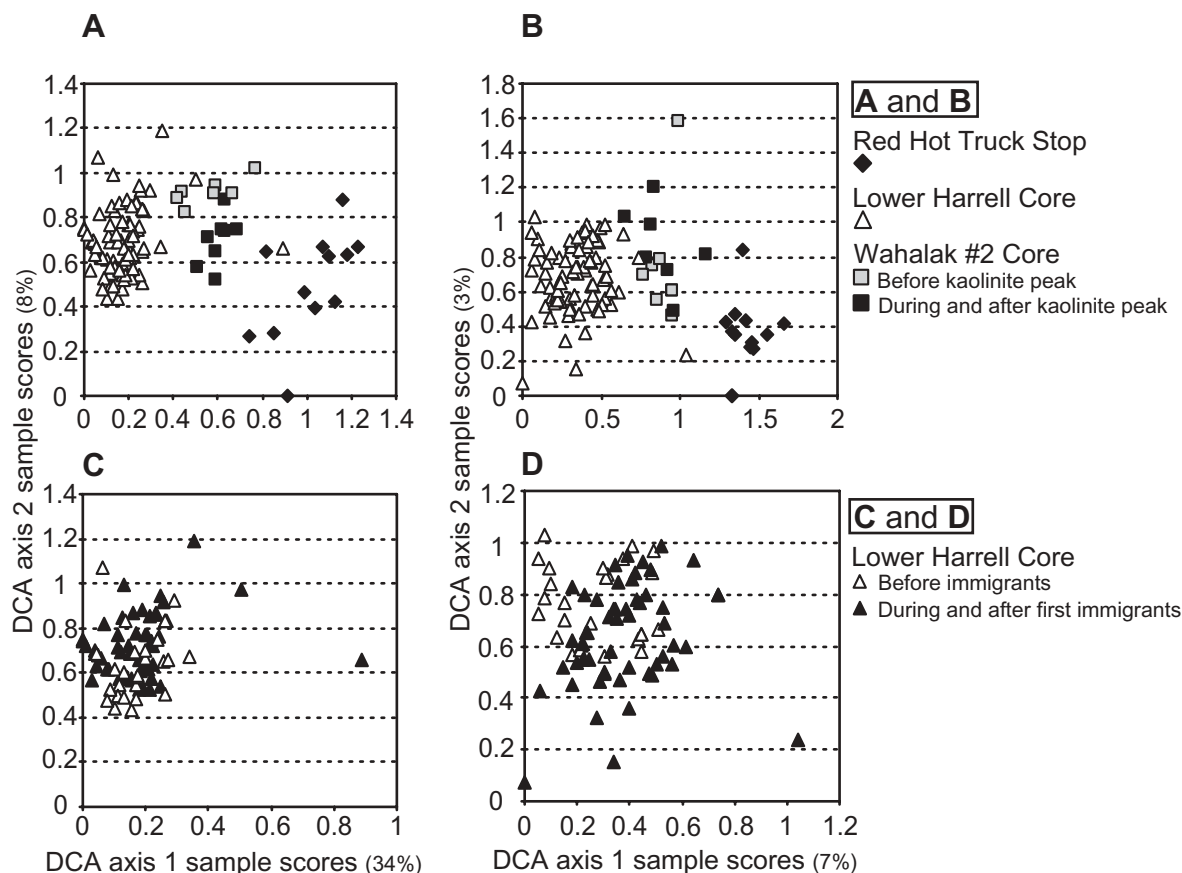


Fig. 5. Detrended correspondence analysis of clastic samples from the lower Harrell Core, Wahalak #2 Core and the Red Hot Truck Stop. (a) Relative abundance data; (b) presence–absence data. In both (a) and (b) samples from the Wahalak #2 Core are split to show those that occur before the kaolinite peak and those that occur during and after the kaolinite peak. (c) Lower Harrell Core relative abundance replotted from (a), indicating the samples that occur before the arrival of immigrant taxa and those during and after the arrival of the first immigrants; (d) lower Harrell Core presence–absence data replotted from (b), also indicating the samples that occur before the arrival of immigrant taxa and those during and after the arrival of the first immigrants. Data values are not re-ordinated in (c) and (d).

data (Fig. 5d) in the lower Harrell Core indicates a weak difference that is statistically significant ($U_{(28,49)} = 947.5$, $P = 0.006$) because samples before the arrival of immigrants have mean axis 1 sample scores of 0.27 and those after the arrival of immigrants have mean axis 1 sample scores of 0.38. The sample scores after the arrival of immigrants are therefore more similar to the Eocene samples from the Red Hot Truck Stop that have high axis 1 scores (Fig. 5b). However, all the lower Harrell Core samples are strongly clustered in both relative abundance and presence–absence ordinations (Fig. 5a and b) so this is only a minor change in taxa co-occurrences.

Diversity change

Within-sample diversity is high in both the Wahalak #2 and lower Harrell cores (Fig. 4b and c), with an average of 46 (SD 5) taxa in 401 counted grains in the lower Harrell Core and 43 taxa (SD 7) in the Wahalak #2 Core. However, there are changes in the Wahalak #2 Core that correlate with changes in kaolinite abundance. Samples in the lower part of the Wahalak #2 Core (100–138 m), below the peak kaolinite values, have an average of 47 taxa v. 39 taxa in the kaolinite-rich sediments above 100 m ($U_{(7,7)} = 7$, $P = 0.01$). This reflects the change in dominants, because within-sample richness is negatively correlated with the abundance of Myricaceae–Betulaceae ($r_s = -0.65$, $P < 0.008$) that becomes the dominant taxon from Taxodiaceae in the upper part of the core (Fig. 4b). Among-sample diversity does not change across the same interval; Chao 2 estimation expects 120 taxa (SD 9) before the kaolinite peak if seven samples were sampled against 115 taxa (SD 13) during and after the kaolinite peak if the same number of samples were sampled (Fig. 6a).

In contrast, the introduction of immigrants has no effect on within-sample diversity in the lower Harrell Core because samples below the lowest possible occurrence of Eocene taxa (145 m) yield 41 taxa on average and those after yield 42 taxa ($U_{(28,49)} = 688$, $P = 0.98$). Among-sample differences are not strongly significant either, because if 30 samples were taken from the lower part of the lower Harrell Core, 150 (SD 8) taxa would be expected v. 165 (SD 10) in the upper part of the lower Harrell Core for the same number of samples (Fig. 6b).

Discussion

The data show two patterns that are of interest here: (1) changes in clay minerals that are coupled with changes in sporomorph

relative abundance; (2) first occurrences of Eocene immigrants that do not correlate strongly with changes in composition, diversity or clay minerals. Without an isotope excursion it is difficult to tie accurately these events to the IETM but the strong, sharp changes in kaolinite concomitant with a vegetation shift suggest that environmental and vegetation changes are not responding to long-term warming in the Late Palaeocene. Significantly, this shift in vegetation and clay minerals is not correlated with the introduction of Eocene taxa, which means that the two events (shifts in relative abundance and arrival of immigrants) are different events occurring at different times. Therefore this also suggests that the Wahalak #2 and lower Harrell cores represent slightly different time intervals with younger Tusahoma sediments preserved in the lower Harrell Core because there are no European immigrants in the Wahalak #2 Core. The time scale over which the US Gulf Coast immigrants arrive demonstrates that they are not directly related to the events of the IETM. The IETM probably facilitated plant access to North America by making the Holarctic landbridges hospitable for plant habitation (Wing & Harrington 2001), but the pace at which these plants spread through the continent was not controlled by the IETM. For example, *Dicolpopollis* (Palmae), *Platycarya* (Juglandaceae) and *Intratripopollenites instructus* (Bombacaceae–Sterculiaceae–Tiliaceae) first occur in sediments that demonstrably postdate the IETM but other European immigrants such as *Interpollis microsuplicingensis* (Frederiksen 1988) are present in the first pulse of immigration. This implies that little correlation exists between the site of origin of a taxon and how long it took to spread through North America. Other variables such as cooling in the Early Eocene and processes operating on ecological time scales probably had stronger influences on the rate and tempo with which plant communities changed in the Early Eocene. The controls on last occurrences may follow the same pattern because regional extinction is correlated neither with changes in environment nor with the arrival of non-native taxa.

Data from this study complement the model of Wing *et al.* (2003) even though the Gulf Coast flora was completely different in the early Palaeocene from the western Interior floras for which the model was derived. Our expanded dataset suggests that plant turnover across the Palaeocene–Eocene boundary essentially relies on the IETM precipitating a cascade response. First, there is a shift in abundance of selected native taxa in response to some aspect of climate change (warming or rainfall). This is most noticeable in Taxodiaceae and Myricaceae–Betulaceae

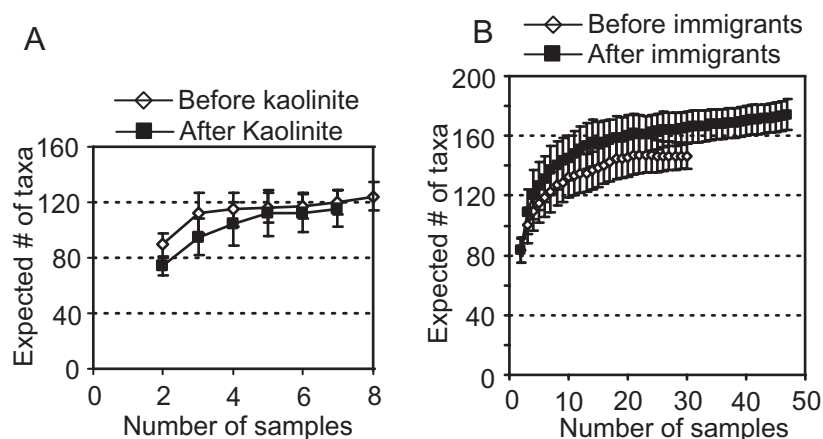


Fig. 6. (a) Chao 2 estimated sample richness for the Wahalak #2 Core comparing samples from before the peak kaolinite values with those from within and after peak kaolinite abundance. (b) Chao 2 estimated sample richness for the lower Harrell Core comparing samples from below the lowest possible occurrence of Eocene immigrants with those samples from after the arrival of immigrants. Error bars represent one standard deviation.

pollen because they are abundant. This is not a transient, extra-tropical, high-diversity flora because it is composed of native taxa and marks a long-lasting change in vegetation. At this stage, plant co-occurrences are not affected by this reorganization. This phase of plant turnover needs further testing with data from sections capable of yielding both high-quality plant records and an isotope record. Second, immigrants arrive in different stages. Some immigrants are initially rare, such as *Interpollis micro-supplingensis* and *Brosipollis* (Fig. 4b), so establishing their first occurrence is difficult. However, they do become more abundant in the Early Eocene (Fig. 4a) and some taxa, such as *Dicolpollis* and *Platycarya*, are numerically abundant in the Early Eocene (Harrington 2001) and they are not present in the Tuscahoma Formation in the Wahalak #2 and lower Harrell cores. The establishment of non-native plants does not lead to immediate change in the vegetation type, which implies that these plant taxa complemented the native vegetation. Extinction is not linked to immigration and this suggests that extinction is related more to separate events during the Early Eocene. Finally, the co-occurrences of native plant associations change. Whether these changes correlate directly with the arrival of immigrants is equivocal but data from well-dated sections in the continental interior (the Bighorn and Powder River basins) show that plant associations are different immediately after the IETM (Wing & Harrington 2001; Wing *et al.* 2003). The processes that lead to this change are unknown but could include any sort of climate change in the Early Eocene or new plant–animal interactions caused by the major turnover in terrestrial mammals.

Conclusions

(1) Paratropical pollen and spore data from the Wahalak #2 Core (upper Tuscahoma Formation) in western Alabama, USA, show that there is a shift in pollen assemblages from those dominated by Taxodiaceae to those dominated by Myricaceae–Betulaceae pollen. This shift is not associated with among-sample diversity changes or changes in plant co-occurrences. Eocene first occurrences are not correlated with this shift and there is no evidence for extinction.

(2) The shift in dominant taxa correlates directly with changes in the abundance of kaolinite. In the Wahalak #2 Core, peak kaolinite values temporarily reach >50% of the total clay assemblages before decreasing to values of *c.* 20%. Carbon isotope analyses of lignites bracketing this interval of elevated kaolinite do not record excursion values that would indicate the IETM. Even though many sections in the Late Palaeocene–Early Eocene interval show clay mineral changes that are not correlated precisely with the IETM, our section is unique because it demonstrates that vegetation shifts are coupled with changes in environment through more intense weathering, climate warming or changes in the seasonality of precipitation leading to increased mechanical weathering. This flora is not an excursion phenomenon because composition does not return to its original state.

(3) The lower Harrell Core in eastern Mississippi also yields excellent pollen floras from the upper Tuscahoma Formation. This core has no shift in relative abundance of dominant taxa or kaolinite in excess of 50%. However, the core does record the first occurrence of Eocene immigrant taxa including, in order, *Granulatisporites luteticus*, *Interpollis microsupplingensis*, *Celtis tschudyii*, *Symplocos? contracta*, *Brosipollis* sp. and *Corsinipollenites psilatus*. No last occurrences correlate with the introduction of Eocene immigrants. Kaolinite consistently forms 20–30% of the clay assemblages in the core, which is significantly greater than in known Upper Palaeocene sections. Lignites throughout

the core have $\delta^{13}\text{C}$ values within the normal range of –26.9‰ to –25.2‰ for Upper Palaeocene–Lower Eocene lignites on the eastern US Gulf Coast.

(4) The introduction of Eocene immigrants on the eastern US Gulf Coast does not affect diversity either within or among samples. The composition of the flora, in terms both of relative abundance of native taxa and the co-occurrences of native taxa with one another, does not change immediately with the introduction of new taxa. The whole pattern of immigration is complex and spans a considerable time period in the Early Eocene. This suggests that the changes in paratropical floras are not controlled directly by warming at the Palaeocene–Eocene boundary but by processes operating on ecological time scales within a framework of longer-term climate changes in the Early Eocene.

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