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South American palaeobotany and the origins of neotropical rainforests

Robyn J. Burnham[1*] **and Kirk R. Johnson**[2]

[1]*Museum of Paleontology, 1109 Geddes Road, University of Michigan, Ann Arbor, MI 48109-1079, USA*
[2]*Department of Earth Sciences, Denver Museum of Nature and Science, Denver, CO 80205, USA*

Extant neotropical rainforest biomes are characterized by a high diversity and abundance of angiosperm trees and vines, high proportions of entire-margined leaves, high proportions of large leaves (larger than 4500 mm^2), high abundance of drip tips and a suite of characteristic dominant families: Sapotaceae, Lauraceae, Leguminosae (Fabaceae), Melastomataceae and Palmae (Arecaceae). Our aim is to define parameters of extant rainforests that will allow their recognition in the fossil record of South America and to evaluate all known South American plant fossil assemblages for first evidence and continued presence of those parameters. We ask when did these critical rainforest characters arise? When did vegetative parameters reach the level of abundance that we see in neotropical forests? Also, when do specific lineages become common in neotropical forests?

Our review indicates that evidence of neotropical rainforest is exceedingly rare and equivocal before the Palaeocene. Even in the Palaeocene, the only evidence for tropical rainforest in South America is the appearance of moderately high pollen diversity. By contrast, North American sites provide evidence that rainforest leaf physiognomy was established early in the Palaeocene. By the Eocene in South America, several lines of evidence suggest that neotropical rainforests were diverse, physiognomically recognizable as rainforest and taxonomically allied to modern neotropical rainforests. A mismatch of evidence regarding the age of origin between sites of palaeobotanical high diversity and sites of predicted tropical climates should be reconciled with intensified collecting efforts in South America. We identify several lines of promising research that will help to coalesce previously disparate approaches to the origin, longevity and maintenance of high diversity floras of South America.

Keywords: Cretaceous; Palaeocene; Eocene; fossils; neotropics; biodiversity

1. INTRODUCTION

Our aims in this paper are to define modern tropical rainforests using distinctive features that can be addressed using evidence preserved in the fossil plant record, to evaluate those features of tropical rainforest from a standpoint of availability and reliability from the fossil record, and then to review the accumulated evidence for tropical rainforest from the Early Cretaceous until the Late Eocene in the neotropics, with a special emphasis on South America.

(a) *What is a tropical rainforest? Climate and vegetation*

Tropical rainforests today, regardless of where they grow geographically, are defined on both climatic and vegetational criteria (Richards 1996; Whitmore 1998; Leigh 1999; Morley 2000). Climatic criteria tend to be quantifiable, whereas vegetational criteria for tropical rainforest are qualitative and variable. Both sets of criteria vary from place to place and from authority to authority. In general, climatic conditions required to support a tropical rainforest can be found today between *ca.* 30° S to 30° N, and are limited to areas having annual rainfall of 1800 mm or greater (up to 9000 mm). If seasonal dryness occurs, the period of time during which rainfall is less than 100 mm per month is limited to three months. Mean annual temperature in tropical rainforests of the world varies between 18 °C and 28 °C per year, but at any one site diurnal fluctuations are larger than seasonal fluctuations, resulting in a very equable temperature throughout the year. Frost is almost never encountered; in fact, an 18 °C cold month mean has been used as one defining climatic criterion (Wolfe 1979; Morley 2000).

Subtypes of tropical rainforest are almost universally recognized because the climatic criteria mentioned above, although uniform and relatively simple for temperature, are quite variable in rainfall distribution and quantity. Elevation, in addition to three important moisture criteria (length of the dry season, relative humidity, total rainfall), allow tropical rainforest to be classified into the well-known of montane, superwet, wet seasonal and wet–dry (Richards 1996; Whitmore 1998; Leigh 1999; Morley 2000). Precipitation and temperature distribution at selected sites typical of lowland tropical climatic subzones in the extant neotropics are depicted in figure 1.

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[*] Author for correspondence (rburnham@umich.edu).

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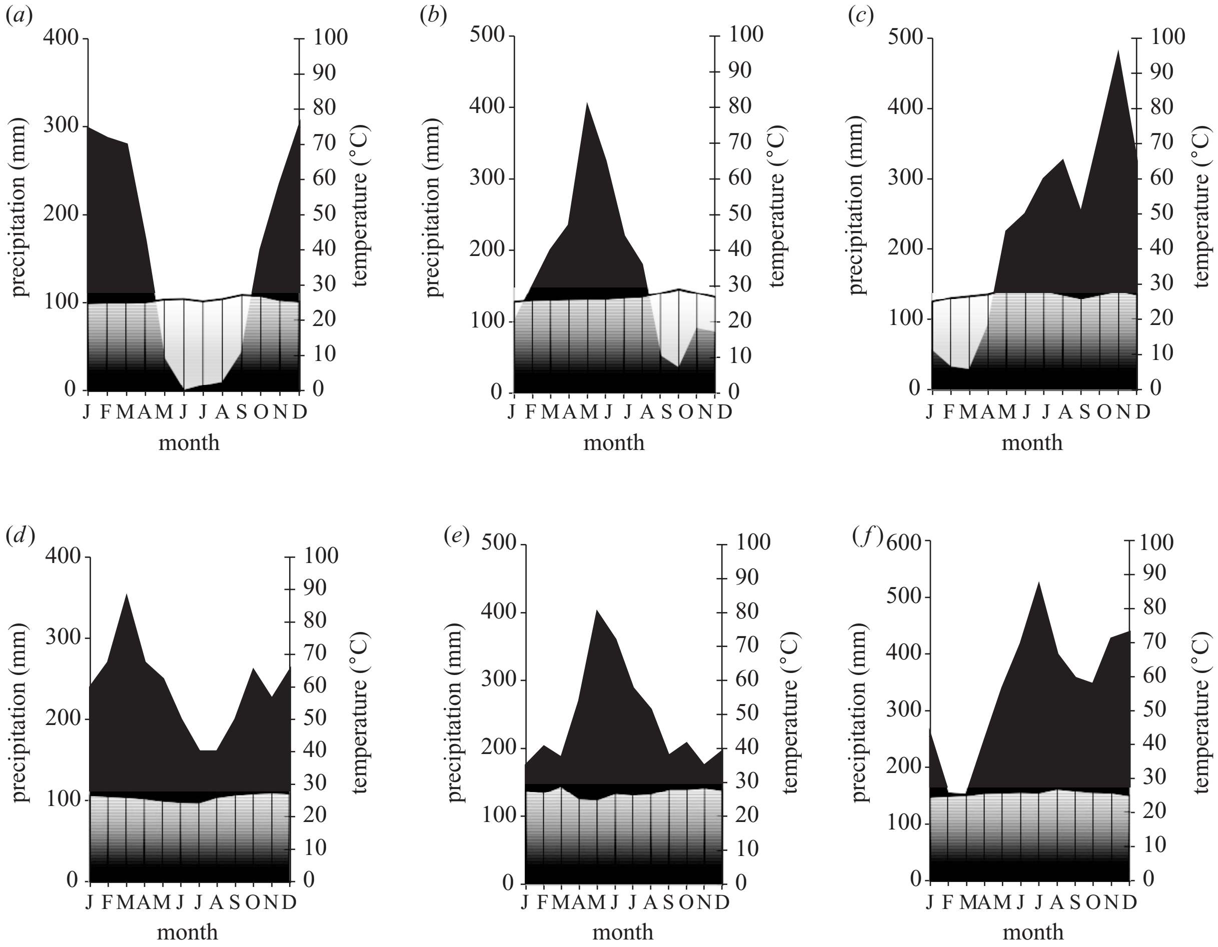

Figure 1. Climate diagrams showing precipitation and mean monthly temperature for six neotropical rainforest sites. (*a*) Porto Nacional, Brasil (237 m) MAT = 25.6 °C, 1831 mm MAP, wet–dry; (*b*) Sipaliwini, Suriname (253 m) MAT = 26.8 °C, 2071 mm MAP, seasonal wet; (*c*) Barro Colorado, Panama (64 m) MAT = 27.0 °C, 2718 mm MAP, tropical wet; (*d*) Iquitos, Peru (104 m) MAT = 26.0 °C, 2845 mm MAP, tropical wet; (*e*) Yasuni, Equador (250 m) MAT = 27.2 °C, 2904 mm MAP, tropical wet; and (*f*) La Selva, Costa Rica (40 m) MAT = 25.7 °C, 4035 mm MAP, tropical superwet. Temperatures are the essentially flat lines and values are read from the right *y*-axis. Precipitation is represented by the shaded black areas and values are read from the left *y*-axis. Elevations are all below 500 m.

Taxonomically, tropical rainforest climates today are dominated by angiosperms. Palaeotropical and neotropical rainforests, even seasonally wet forests, are comprised of over 90% angiosperm taxa, from the shrub to canopy levels. Disturbed tropical habitats can support dense covers of pteridophytes or gymnosperms, but even here angiosperms dominate species lists. However, in light of our focus on ancient biomes recognizable as equivalent to those extant on Earth today, we restrict our discussion to tropical rainforest biomes in which angiosperms were speciose, if not absolutely dominant. We stress, however, that the age of climatic and structural characteristics typical of tropical rainforest are probably as old as the Palaeozoic, in contrast to inferences that tropical rainforest is only *ca.* 65 Myr old based on angiosperm dominance (Leigh 1999). For example, 'liana abundance' is often cited as characteristic of tropical angiosperm-dominated forests, and today climbing plants in tropical rainforests are almost exclusively angiosperms (out of all lianas today, more than 90% are angiosperms). Examples of successful non-angiosperm rainforest climbers today include species in the gymnosperm genus *Gnetum*, as well as ferns like *Lygodium*, *Drynaria*, *Lomariopsis* and *Stenochlaena*. Climbers are well known in the Palaeozoic fossil record (e.g. *Blanzyopteris*, *Karinopteris* and *Mariopteris*; see reviews in Kerp & Krings (1998); Krings *et al.* (2001, 2003)); so not all climbers are angiosperms. Thus abundant angiospermous lianas do not necessarily indicate modern tropical rainforest because ferns, seed ferns and gymnosperms are or were successful and abundant climbers.

2. DEFINITION OF THE ARCHETYPAL TROPICAL RAINFOREST

We outline here features of a modern archetypal tropical rainforest (ATR) ecosystem, in which characters of the climate, plant habit and floristics point to tropical rainforest. Using these characteristics as the 'gold standard' or 'Cadillac rainforest' against which any fossil deposit can be compared will allow us to evaluate records of fossil occurrences since the Mid-Cretaceous for evidence of tropical rainforest biome. The characters and their states are summarized in table 1.

Neotropical lowland rainforest today is located at low elevation, 700 m or lower above sea level (Harling 1979;

Table 1. Archetypal rainforest (ATR) characteristics and their availability in the fossil record.

major character category	specific character	accessibility in the fossil record	preservation limitations	data quality in application to ATR recognition
elevation	$\leqslant$ 700 m	accessible via proxies: foliage or sediments	sedimentological data	spotty
climate	high precipitation	accessible, semi-reliable	leaf data only	good on a relative scale; less reliable for absolute precipitation
	high temperature	accessible, semi-reliable	leaf data only	good on a relative scale; moderate for absolute temperature
	high equability	accessible, semi-reliable	leaf morphology or proxy via modern relatives	good on a relative scale; moderate for absolute values
vegetation	productivity	not accessible	uninterpretable?	not available
	angiosperm species dominance	accessible, reliable	generally no limitations	available from pollen, wood and leaf data
	angiosperm dominance by individual	accessible, semi-reliable	leaf data (pollen data unreliable)	leaf (large collections needed)
	species diversity	absolute values inaccessible; relative levels (hi–med–low) possible	leaf or pollen data	moderate (relative levels can be determined)
	species heterogeneity	accessible, semi-reliable	need intense and controlled sampling techniques (leaves and *in situ* wood)	few studies focus on this; lack of data the biggest problem
	common and abundant families in tropical rainforests	accessible to inaccessible, depending on the family	extremely variable	pollen (low taxonomic resolution, abundant data); leaves (better resolution, fewer sites); flowers and fruits (rare)
	palm diversity high	accessible; good preservation, reliable	megafossils commonly preserved; identification problems	highly applicable, palm pollen not differentiable for all genera
	evergreen (asynchronously deciduous)	almost unknowable, except via identification inference	fossil texture is not a reliable indicator of evergreen state	low
habit	many lianas and trees	only accessible via identification and inference; dependent on taxonomy	little direct evidence, even of liana wood	highly variable (if present, high potential for interpretation)
	emergents	almost unknowable, except via identification inference	no direct evidence	low
	many large leaved monocots (other than palms)	reliable when preserved; sampling needs to be controlled and intense	impressions and compressions common; inferences from phytoliths and pollen, with taxonomic identification	pollen (poor resolution); leaves (good but rare); phytoliths (potential exists)
	many epiphytes	virtually no data (pollen for some broad groups?)	no direct evidence; inferences made for Palaeozoic plants	poor
	many hemi-epiphytes	almost unknowable, except via identification inference	rarely recognizable as hemi-epiphytes via direct evidence	poor

(*Continued*.)

Table 1. (*Continued*.)

major character category	specific character	accessibility in the fossil record	preservation limitations	data quality in application to ATR recognition
foliage	entire margins > 60%	accessible, reliable	compressions and impressions only; angiosperm dicots only; reliable species count needed	impressions and compressions good, otherwise nothing
	drip tips > 25%	semi-accessible, semi-reliable	compressions and impressions only; angiosperm dicots only; high species count needed; tips least often recovered in the fossil record	leaf compression: moderate, otherwise nothing
	large leaf size	accessible, semi-reliable	compressions and impressions only; dicots only; large sample needed; whole leaves important	leaf impressions and compressions good
fruits, flowers	cauliflory and ramiflory common	almost unknowable, except via identification inference	rarely recognizable as cauliflory/ramiflory via direct evidence	poor
	average fruit or seed size large	accessible, reliable	petrifaction floras are best	moderate
pollen, wood, phytoliths	pollination by insects common	almost unknowable, except via identification inference	almost never preserved	none to poor
	pollen and fruit/seed diversity high	accessible but quantitative analyses needed: these are rare	pollen commonly preserved, fruit and seed deposits can be rich: little limitation	moderate: relative diversity possible, absolute impossible
	wood with high vulnerability index; rare growth rings	accessible	spotty geographical distribution of deposits. Data accessible	vulnerability index > 2–3
	Phytoliths indicate closed, moist forest	accessible; technique new but well documented	taxonomically variable: some plants lack them	good when used in combination with other evidence
plant–animal interaction	insect herbivory common; plant defenses, etc.	accessible	spotty geographical distribution of deposits and studies	modern reference points are understudied
	high diversity of arboreal mammals	accessible	taphonomic limitations in acidic sediments (low preservation)	data high quality, but rarely deposited in sediments along with macrofossil plants

Jørgensen & León-Yánez 1999). Climate is characterized by high rainfall, with 1800 mm or greater annually, during which nine months receive more than 100 mm each; temperature is warm with a MAT of 18 °C or greater and a mean annual range of less than 7 °C.

Tropical forests are highly productive, collectively producing 49 billion tons of biomass annually (Leigh 1999), and over recent years in the neotropics an excess of almost three-quarters of a ton of biomass has been accumulated per year per hectare (1 hectare $= 10^4\ \mathrm{m}^2$; Phillips *et al.* 1998). They are dominated by angiosperms, with more than 80% of the individuals and species of over 10 cm in diameter belonging to either the palm family (Arecaceae) or to dicotyledonous angiosperm families. Species diversity is high, with more than 40 tree species per hectare (and up to 300 tree species per hectare in hyperdiverse forests; reviewed in Wright (2002)). Rarely, tree species diversity can be even lower than 40 species per hectare, specifically in 'monodominant forests' (Connell & Lowman 1989; Henkel 2003). Species heterogeneity, as measured by β-diversity (between habitat or between regions), tends to be high but varies depending on the scale over which it is measured (Arita & Rodríguez 2002; Condit *et al.* 2002).

Archetypal rainforest in the neotropics can be characterized by a suite of 'most abundant' families to which more than 50% of the species belong in an average hectare of forest. This list was derived from species counts on six plots of forest ranging from seasonally dry tropical forest in Costa Rica (moist gallery forest within this biome) to superwet forests of Amazonia. The most important families are (in order of decreasing importance) Leguminosae, Moraceae, Annonaceae, Euphorbiaceae, Lauraceae, Sapotaceae, Myristicaceae and Palmae. Twelve additional families comprise another 25% of the species found in the

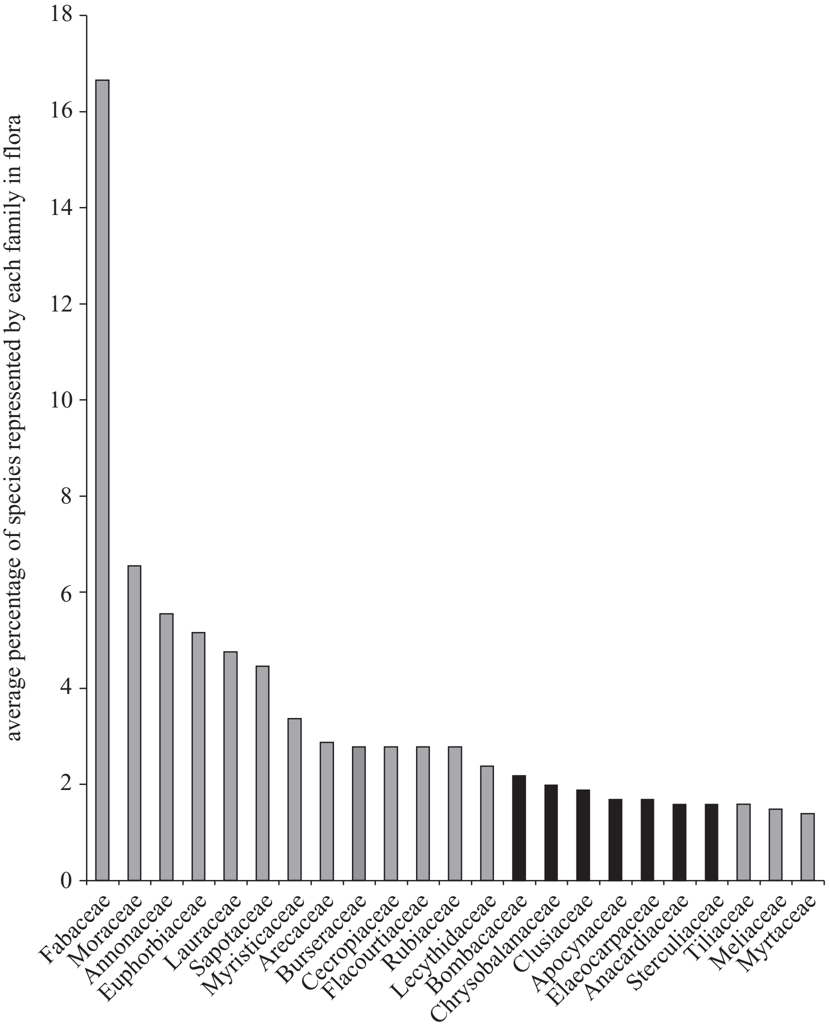

Figure 2. Diversity and dominance in modern neotropical floras. All families shown include 80% of all species averaged across six neotropical rainforest 1 ha plots (climates ranging from wet–dry to super wet tropical rainforest). Grey bars indicate families that include an average of 80% of all stems (dominance counts). The first eight families shown include 57% of all stems. The floras used for this compilation were derived from plots in the following areas: Guanacaste, Costa Rica (moist gallery forest); Barro Colorado Island, Panama; Allpahuayo, Peru; Yasuní, Ecuador (swamp forest); Yasuní, Ecuador (floodplain forest); Pakitsa, Peru (floodplain forest).

archetypal neotropical tree plots (Burseraceae, Cecropiaceae, Flacourtiaceae, Rubiaceae, Lecythidaceae, Bombacaceae (= Malvaceae s. l. 'baobabs'), Chrysobalanaceae, Guttiferae (Clusiaceae), Apocynaceae, Elaeocarpaceae, Anacardiaceae and Sterculiaceae; figure 2). By stem abundance of species (which may more accurately reflect fossilization potential of specific families), eight families represent 57% of all stems on the six plots surveyed in the neotropics. In order of decreasing importance, those families are: Leguminosae, Palmae, Rubiaceae, Violaceae, Euphorbiaceae, Meliaceae, Sapotaceae and Moraceae. Seven additional families increase the proportion of stems represented on neotropical hectares to 75% (Annonaceae, Flacourtiaceae, Myristicaceae, Lauraceae, Tiliaceae, Cecropiaceae, Polygonaceae; figure 2). These data are comparable with those presented by Ter Steege *et al.* (2000) and by Terborgh & Andresen (1998). Their analyses show that over 80% of tree individuals belong to only 16 families (out of 292 possible families represented in Amazonia). De Oliveira & Mori (1999) found that only four families comprise more than 50% of the species in a very diverse area near Manaus, Brazil. The point to note is that a very small number of families dominate an otherwise staggeringly rich tree flora over a wide area of the neotropics. Because this number of families is small and manageable, it should be possible to focus on records of abundance of these families in the fossil record to document the presence of tropical rainforests in the past.

In the ATR, species are primarily 'evergreen', or more appropriately, non-synchronously deciduous. A rough estimate of 80% (R. J. Burnham, personal observation) of the tree species shed leaves sequentially rather than synchronously, although some of the forest giants can be deciduous (e.g. species in the genera *Schizolobium*, *Ceiba*, *Cavanillesia*, *Pseudobombax*, *Tabebuia*, *Dipteryx*, *Vatairea*). A large deciduous tree will contribute significantly to the quantity of leaf litter that is potentially available for fossilization.

Neotropical rainforest plant habits include herbs, shrubs, epiphytes, hemiepiphytes, lianas and trees. Palms contribute significantly to tree and shrub richness in neotropical plant communities. On average, four to seven species of palms with individuals more than 10 cm diameter at breast height coexist per hectare when areas with rainfall over 2000 mm are censused, and many more species are present as shrubs and understorey plants (Scariot 1999; Phillips & Miller 2002). In rich tropical rainforest, as many as 20% of all woody species may be represented by lianas (Gentry 1991*a*), and another 20–30% may be added by epiphytes and hemiepiphytes (Hammel 1990). Large-leaved monocots can form dense stands in the understorey (Zingiberaceae, Marantaceae, Costaceae and Cannaceae) or along river meanders where inundation creates a constantly silting environment (Dahlgren *et al.* 1985; R. J. Burnham, personal observation). The forest canopy is closed; from the forest floor the canopy appears to be an even cover of plants with as many as four to five leaves of different plants shading one another at any vertical point. However, a view across the canopy of the rainforest reveals a three-dimensional topography that is derived from influences of high winds, catastrophic tree falls, river meandering and the topography of the land surface itself.

Vegetatively, ATR is characterized by entire-margined, mesophyllous leaves (of a size larger than 4500 mm^2), with a high abundance of species with drip tips (25–70% of the species: R. J. Burnham, unpublished data from Yasuní, Ecuador). Leaves can be coriaceous or chartaceous in texture, but generally a high proportion of species in ATR bear coriaceous leaves. Our minimum values to qualify as ATR for these parameters (as measured from leaf litter, herbarium samples or fossilized leaves) are: more than 60% species with entire-margined leaves; more than 50% mesophyllous-leaved species; more than 25% species bearing leaves with drip tips; and *ca.* 50% species with coriaceous leaves. The classically held belief that tropical rainforest wood does not bear growth rings has been set aside by recent study of many more species of modern tropical trees, but in general the absence of growth rings in several species from a single flora does point to ATR. To our knowledge, the taxonomic distribution of buttresses in tropical rainforests has not been carefully documented, nor does a morphological definition of buttresses consistent from family to family exist. Nonetheless, the presence of multiple species with buttresses in a single flora is rarely found beyond the limits of ATR (reviewed in Clair *et al.* (2003)).

Reproductively, few flower or fruit types can be considered absolutely exclusive to ATR. Cauliflory and ramiflory are far more common in ATR than in other biomes but their presence outside of ATR (especially in dry tropical forests) restricts their utility as a defining characteristic of the forest. Insect and bird pollination predominate in ATR over wind pollination, particularly in low disturbance environments (Bush & Rivera 2001). The high proportion of animal-distributed pollen was documented as slightly lower for the liana community, even in ATR (Gentry 1991*b*). Average size of dispersal units (fruits or seeds) of species in the neotropical rain forests is large, especially compared with seasonal dry and temperate forests (Tiffney 1984; Foster & Janson 1985; Foster 1986; Grubb & Metcalfe 1996; Lord *et al.* 1997).

Plant–animal interactions have been proposed to be substantially greater in ATR, thus evidence of those interactions via herbivory, increased defences and elaborate dispersal adaptations should be more prevalent in ATR. Arboreal mammals, while potentially no more numerous in ATR than in other forested biomes, are far more diverse, with species richness of non-volant rainforest mammals reaching as high as 60 species using standard trapping methodologies (Voss *et al.* 2001).

These characteristics are summarized for the ATR in table 1, where we have also indicated the probability of their retrieval in the fossil record, covered in § 3.

Fossilized plant parts (organs and pieces of organs) are deposited in decreasing abundance from pollen and phytoliths through to leaves, wood, fruits, and finally flowers. Although phytoliths have received scant attention from only a few researchers over the years, they show great promise for interpretation of palaeoenvironments (Piperno 1985; Piperno & Pearsall 1993; Stromberg 2004). Leaves and pollen have been the mainstay of data contributing to the history of angiosperm plant life. Pollen data are dense and reliable where collected, quantified and interpreted carefully in reconstructing source vegetation diversity. Although the provenance of any one pollen sample is highly variable, the consensus of opinion is that in tropical vegetation, pollen source is likely to be from vegetation relatively close to the site of collection (Bush *et al.* 2001). However, pollen is notoriously variable in its taxonomic utility. Many grains are identifiable only to the family level, others are identifiable to genus, and relatively few are identifiable to species using standard means (light microscopy). The result is that tracing lineages through time using pollen will be coarse, and the larger the taxonomic group, the more likely the chance of misinterpretation. Pollen grains, being short-lived and without function outside of the flower, do not contribute morphological detail on which to reconstruct climate. Instead, identifications are made of the pollen grains and subsequent correlation is made with distributions of modern relatives. Pollen of some taxonomically important families (e.g. Lauraceae) do not preserve well.

Leaves are produced in large quantity by their source plants, but relative to pollen grains, fewer reach a depositional basin and even fewer are retrieved from the rock record. Leaf fossils are often known from few individuals, can only be quantified with a large collecting effort, are bulky to store and manage, and are difficult to place accurately in taxonomic groups. Recent advances in methodologies for describing foliar features by the Leaf Architecture Working Group (Ash *et al.* 1999) have streamlined the process of describing taxa based on leaves (morphotyping), but we are still lacking a means for researchers to place leaves accurately in broad taxonomic groups (i.e. identify their affinities to modern genera, families and orders). By contrast, leaves do bear many morphological characters and, relative to pollen, can be readily placed into groups that represent species, thus allowing quantification of diversity based on solid characters. Leaves are sensitive to environmental conditions and will reflect the palaeoclimate of the source flora, within the genetically determined phenotype constraints of each lineage. With some features, the larger problem involves excavation of foliar features from the rock itself, such as drip tips, which are only narrow extensions of the leaf lamina. Drip tips cause little bedding-plane disruption and thus do not encourage rocks to break naturally along their outlines. The very same quality that makes a drip tip useful to a live leaf is the quality that discourages its retrieval from the rock record!

Wood and the reproductive parts of plants (flowers, fruits, seeds) are somewhat similar in their relatively low abundance in the fossil record, although they can be found in dense accumulations in certain types of deposits, such as petrifaction or mummifications sites (see Jacobs 2004). Great progress has been made on Mid-Cretaceous floras using data from the spectacular preservation of fruits and flowers from eastern Brasil, New Jersey, Sweden and Portugal (Crepet & Nixon 1988; Friis *et al.* 2000, 2003; Mohr & Friis 2000; Schonenberger *et al.* 2001; Hermsen *et al.* 2003; Rydin *et al.* 2003), but surprisingly few accumulations of reproductive parts or wood have been described from anywhere outside of Brazil in the neotropics. We suspect that this gap results from lack of study, not absence from the record.

The most reliable and accessible characteristics that can document tropical rainforest in the fossil record fall into two broad categories: climatic indicators and taxonomic lineage indicators. Physiognomic features of leaves have been used for almost 100 years to reconstruct palaeoclimates (Bailey & Sinnott 1915, 1916). Recently, more quantitative methods have been applied to the reconstruction of palaeoclimates using leaf physiognomy (e.g. Wolfe 1979, 1993). The recognition of variability of leaf morphology within biomes, measurement and sampling error, and lack of correspondence of species to specific climatic conditions have stimulated the application of error estimates to climate reconstructions, particularly palaeotemperature (Wilf 1997; Wilf *et al.* 1998; Burnham *et al.* 2001). In addition, use of sedimentological criteria (evaporites, coals, carbonates, etc.) can help to constrain the potential types of climate that were present at specific areas in the past. Using pollen to reconstruct climate uses taxonomic identification of the pollen grains to determine possible climatic ranges, based on the climatic range of modern relatives. A similar approach is used for leaves, with the additional application of the presence of palms as indicators of rare frost as an example that has been used with good result (Wing & Greenwood 1993; Mosbrugger & Utescher 1997). Many additional lines of evidence can be brought to bear on the development of tropical rainforest, but these two broad approaches (climatic indicators and taxonomic lineages) are used more often than others because of their application to a broad range of fossil deposits.

3. CRETACEOUS RECORD OF TROPICAL RAINFOREST AT LOW LATITUDES (WESTERN HEMISPHERE)

Data on biomes in the Cretaceous at low palaeolatitudes (20° N to 20° S) are rare in the Western Hemisphere. The record was reviewed by Burnham & Graham (1999), but their approach was simply to report the numbers of floras known and the emphasis was on macrofloral evidence. Some additional data have come to light, palynological evidence is added to the Cretaceous through to the Eocene record, and new evidence has been published in the last 5 years. Even so, the record is disappointingly scant.

With the exception of reports of coals from the Aptian of Peru, the terrestrial sedimentological criteria for climates of any type in South America are entirely lacking from the Mid to Late Cretaceous maps of Ziegler *et al.* (2003). Sedimentological evidence indicating seasonal dryness during the Aptian and Albian comes from Brazil, where carbonates are found and pollen records document abundant *Classpolis* pollen, indicating Cheirolepidiaceous conifer-dominated forests. Even so, angiosperms are an evident component of the flora (Herngreen *et al.* 1996). Mangrove pollen is proposed to have been widespread in coastal areas throughout the equatorial region (Morley 2000). Herngreen & Duenas Jimenez (1990) report ‘common angiosperms’ in Colombian cores as old as the Late Aptian. By the Albian, the northern portion of South America is defined within a new pollen province (Elaterates Province), reflecting the change in composition of the dominants from conifer dominants to the taxonomically obscure ‘elaterates’ (Pons 1988; Srivastava 1994). Herngreen *et al.* (1996) report that the pollen flora from low palaeolatitude areas includes as much as 70% angiosperms, and Vakhrameev (1984) attributes a moist tropical climate to the coal-bearing area of northwest South America in the Mid-Cretaceous. For the remainder of the Cretaceous, a high proportion (10–50%) of presumed palm pollen is found in palaeoflora that are known and well studied. A rich diversity of other angiosperm pollen grains and some leaves are known, but very few have been allied with modern plant groups beyond ‘dicotyledonous angiosperms’ (Duarte & Japiassú 1971; Pons 1988; Guilland *et al.* 1990). Cretaceous silicified wood has been reported from almost every one of the northern states of Brazil, but with no determinations (Duarte & Japiassú 1971).

More northern regions bring information to bear on low latitudes by inference. Fossil leaf and wood evidence suggested to Upchurch & Wolfe (1987) that tropical wet forests were present at mid-latitudes at this time (north and south of 20° palaeolatitude). However, others have suggested that higher latitudes were xeric to sub-xeric (Spicer *et al.* 1993). Coals and high species diversity in pollen counts (Hotton 1988; Nichols 2002) do suggest abundant moisture at least in some areas of the USA, such as the Gulf Coastal Plain and sections of the Rocky Mountains (Ziegler *et al.* 2003).

Direct evidence of moist tropical floras in the Cretaceous at low latitudes is neither supported nor rejected by the scant data available. The records of taxa known from low-latitude macrofossils can be briefly summarized. From the Aptian of Brazil, cycads gnetaleans, araucarians, Cheirolepidiaceous conifers and moderately sized angiosperm leaves are known (De Lima 1980; Mohr & Friis 2000; Rydin *et al.* 2003). Also from Brazil, the Aptian Codo Formation includes probable Nympheaceae (Duarte & Silva Santos 1993). Pons (1988) reported on a diverse Colombian macro- and micro-fossil flora from the Eastern Cordillera of Colombia, but almost no macrofossils were placed in modern angiosperm orders. Pollen similar to the legume genus *Dinizia* has been reported from the Maestrichtian (Caccavari 1996) of Brazil, and wood and fruit samples with probable affinity to Lecythidaceae, Bombacaceae and Palmae were reported from Colombia (Huertas 1969), Peru (Mourier *et al.* 1992) and Brazil (Maury 1930; Duarte & Japiassú 1971). One of the very few Maestrichtian leaf floras known is from Colombia (Huertas 1960, 1969; Romero 1986), from which plants with affinities to Moraceae, Lauraceae, Sterculiaceae, Palmae and Cecropiaceae were reported. It is astounding that a summary of the known macrofossil localities from the neotropics can be summarized so completely in this single paragraph. The compilation of Duarte & Japiassú (1971) is in need of careful re-evaluation for potentially productive sites in many areas of Brazil.

A monumental summary of 10 Maestrichtian biomes worldwide by Horrell (1991) is disappointingly thin in data relevant to the issues addressed here. Out of 205 palaeobotanical records (pollen and macrofloras), only 10 come from any area between Mexico and southern Bolivia. Those records are not entirely independent because some represent duplicate reports of work on the same deposit by separate authors or even the same author. Sedimentological evidence from coals and evaporites in his study is even more scant, with over 100 records but not one from the region between Mexico and southern Bolivia. The neotropics, can only be included in his summary of tropical rainforest biome by assumption that latitudinal bands of climate did exist in the past, rather than on direct evidence.

Despite this lack of data from the neotropics, it may be possible to extrapolate climatic conditions to the neotropics based on other equivalent-aged records from similar latitudes. Horrell (1991) documents moderate diversities of palms and angiospermous pollen from Nigeria and Malaysia, but contends that the limited distribution of coals and palaeobotanical data suggestive of tropical rainforest biome indicates that tropical rainforest was far more limited in the Maestrichtian than it is today. By contrast, the relatively dry tropical forest biome (Horrell's Biome 2) is documented both by macrofossil remains of palm wood in Brazil as well as calcretes indicative of seasonal rains. The majority of the palynologically defined Palmae Province is thus assigned to a dry tropical forest, in which temperatures may have been high but rainfall was lacking at least part of the year. We believe that re-evaluation of the variability within the Palmae Province may well reveal some areas where rainfall was sufficiently high to generate a moist tropical forest.

In summary, to our knowledge there are virtually no characters diagnostic of ATR present in data published from the Cretaceous of the neotropics. We hasten to stress the poverty of the record and the inadvisability of drawing conclusions based on the lack of data. In spite of isolated pollen records (which are equivocal in climatic interpretation), this is not simply a case of negative evidence (data confirming lack of rainforest); it is a case of missing evidence (no data are available).

4. EARLY CENOZOIC RECORD OF TROPICAL RAINFOREST AT LOW LATITUDES

(a) *Palaeocene*

Until recently, the Palaeogene plant fossil record from South America was largely based on pollen records accumulated by petroleum, coal and bauxite companies from wells and boreholes under the direction of petroleum, coal and bauxite exploration companies. These records create an image of the coastal areas of northern South America, with abundant mangroves, especially *Nypa* palms, and a diverse but relatively unknown *terra firme* flora that contributed to the diversity of the assemblages. Pollen data from Colombia, Guyana and Venezuela have contributed substantially to the evidence for warm, equable climates at low latitudes (Van der Hammen & Wymstra 1964; Van der Hammen & Garcia 1966; Germeraad *et al.* 1968; Colmenares & Teran 1993; Jaramillo & Dilcher 2000, 2001). Many of these pollen assemblages are dominated by palm pollen of various types. Significant family records from these pollen floras are Annonaceae, Palmae, Araceae, Bombacaceae, Burseraceae, Euphorbiaceae, Leguminosae, Melastomataceae, Myrtaceae and Sapotaceae (table 2). Our expectation is that rich palaeofloras represented by macrofossils will be discovered that better indicate the diversity anticipated from an archetypal rainforest in the Palaeocene. Work currently underway in the El Cerrejon Coal Mine in northern Colombia (C. A. Jaramillo and S. L. Wing, unpublished data) on pollen and macrofossils suggests a pattern of relatively low diversity of the palaeofloras through to the Late Palaeocene (C. A. Jaramillo, personal communication). Included in this flora are species with drip tips, large leaf size and affinities to classic rainforest families (Palmae, Araceae, Bombacaceae and Leguminosae). The potential for the El Cerrejon flora to give detailed information was suggested more than 30 years ago when the leaf cuticle of six species from El Cerrejon was described by Doubinger & Pons (1970).

A single palm fruit assignable to the Palaeocene has been described by Dolianiti (1955) from Brazil (Maria Farinha Fmn, Pernambuco), but the flora has not been reinvestigated, nor the age verified, to our knowledge. A single palm fruit, which had probably floated into the depositional setting from some distance, is relatively uninformative for our purposes here.

The Palaeocene climate at equatorial latitudes was, by most estimates, significantly wetter than that of the Cretaceous, and probably somewhat warmer, particularly soon after the Cretaceous–Tertiary boundary. Peat accumulation, mostly documented in coastal mangrove habitats (Leidelmeyer 1966), was widespread and is purported to be derived from a *Nypa*-dominated community. Although Romero (1993) has reconstructed two large biogeographical microfloral provinces for this time period ('palm' and 'mixed'), there was probably a zonation caused by Hadley cell circulation (see Parrish 1998) at mid-latitudes in South America.

Morley (2000) boldly asserts that closed-canopy multistratal rainforest became widespread in lower and middle latitude areas in the Early Palaeocene (66–60 Myr ago). Direct evidence for the widespread nature of these forests is scant in South America, but the record is lacking, rather than contradictory. Ziegler *et al.* (2003) propose that Morley's reconstruction of the extent of tropical rainforest is unrealistic, and instead propose that transitional tropical, but potentially seasonally dry areas, would reduce the potential size of tropical rainforest during the Early Palaeocene. Even a more limited tropical rainforest distribution, as depicted by Ziegler *et al.* (2003) would reconstruct the large majority of northern South America as tropical forest in the Palaeocene. The solid documentation of ATR at higher northern latitudes (Castle Rock, CO; Johnson & Ellis 2002) is intriguing and a complete reanalysis of climate patterns with their temperature estimates included is needed.

Table 2. Palaeocene taxonomic data on common neotropical Angiosperm families.

family	genus and species	source of evidence	reference
Annonaceae	*Proxapertites tertiaria*, *Longapertites microfoveolatus. vaneendenburgi*	pollen	Van der Hammen & Garcia (1966); Jaramillo & Dilcher (2001)
Araceae (?)	*Echimonocolpites ruedae*	pollen	Van der Hammen & Garcia (1966)
Arecaceae	*Gemmastephanocolpites*, *Mauritiidites*, *Proxapertites operculatus* and *P. tertiarius*, *Retimonocolpites microreticulatus* and *R. regio*, *Psilamonocolpites* and *Proxapertites cursus*	pollen: Lebrija, Colombia and Los Cuervos Formation, Venezuela	Van der Hammen & Garcia (1966); Colmenares & Teran (1993)
Arecaceae	*Nypa pernambucensis*	fruit: possibly drifted	Dolianiti (1955)
Bombacaceae	*Bombax ceiba* (*Bombacacidites annae*)	pollen: Colombia, Caribbean and Los Cuervos Fmn, Venezuela	Germeraad *et al.* (1968); Colmenares & Teran (1993)
Ctenolophonaceae	*Ctenolophonites lismae*	pollen: El Cerrejon Mine, Colombia	Van der Kaars (1983)
Ctenolophonaceae	*Verrustephanocolpites rugulatus*	pollen: Catatumbo and El Limbo, Colombia	Van der Hammen & Garcia (1966)
Fabaceae	*Striatopollis catatumbus*	pollen: Piñalerita, Colombia	Jaramillo & Dilcher (2001)
Euphorbiaceae	*Psilatricolpites operculatus*	pollen: Los Cuervos Fmn, Colombia	Gonzalez-Guzman (1967)
Melastomataceae	*Heterocolpites palaeocenica*	pollen: Lebrija, Colombia	Van der Hammen & Garcia (1966)
Myrtaceae	*Syncolporites lisamae*, *S. poricostatus*	pollen: Colombia	Van der Hammen & Garcia (1966); Jaramillo & Dilcher (2001)
Proteaceae	*Retidiporites magdalenensis*, *Echitriporites trianguliformis*	pollen: Lebrija,Colombia and Los Cuervos Fmn, Venezuela	Van der Hammen & Garcia (1966); Colmenares & Teran (1993); Jaramillo & Dilcher (2001)

(b) *The Palaeocene–Eocene transition*

The Palaeocene–Eocene boundary has been a focus of several worldwide palaeontological correlations and reconstructions recently. It is a period of apparent mid-latitude warming with substantial environmental changes that affected life, especially vertebrates, on land (Clyde 2001; Gingerich 2001). The effect on plants is equivocal because the record is frustratingly absent at many sections that span this time period (Harrington 2001; Harrington & Wing 2001). The apparent changes in neotropical plants across the boundary are highlighted here, based on palynological evidence from Colmenares & Teran (1993), Rull (1999), Jaramillo & Dilcher (2001) and Jaramillo (2002). Rull (1999) recognized an increasing provincialization across the boundary, with pantropical taxa dominating before the boundary and taxa with modern neotropical affinities dominating after the boundary. He noted an increase in diversity in the Eocene relative to typical Palaeocene levels as well as ecological differences between samples from the two time periods. Sample diversity was not reported, so an interpretation of tropical rainforest based on diversity alone cannot be made from the data; too few taxa have confirmed botanical affinities from the flora to be able to make judgements based on those reported. Substantial floral turnover appears to have occurred, with the extirpation of some taxa now absent in South America (e.g. *Ctenolophonites* spp.). In other areas of South America (Jaramillo 2002), diversity increases and dominant taxa are different across the boundary, but the rapidity of the transition is unclear.

(c) *Eocene*

By the Eocene, the question about tropical rainforest at low latitudes is no longer 'was it there?', but rather 'how extensive was it?' and 'which modern lineages are recognizable?' A relative wealth of macro- and microfossil data are available to address these questions, as though the depositional settings in the lowlands of Central and South America had finally fixed on a configuration in which they received consistently accumulating sediment.

In the Eocene, the fossil record in the neotropics begins to show depth in data on both pollen and macrofossils (Burnham & Graham 1999). Great strides have been made in using regional palynological zonations in coastal settings of northern South America and in Central American localities (Germeraad *et al.* 1968; Muller *et al.* 1987; Graham 1995; Jaramillo & Dilcher 2001). However, many of the macrofossil palaeobotanical contributions published prior to the 1960s from Peru, Bolivia, Ecuador and Brazil are left with only 'Eocene' as their age. Thus any details of the progression of lineage diversification during the Eocene must wait until each flora is independently dated, correlated and re-evaluated. Even those floras assigned here to the Eocene were dated by general stratigraphic means in the 1920s and 1930s and should now be carefully re-examined for an accurate age determination. Many of the fossiliferous deposits from Andean countries are intercalated with volcanic ashes, such that any future reassessment of ages can be based on radiometric dating.

5. EOCENE PLANT MORPHOLOGY: A CLUE TO NEOTROPICAL RAINFORESTS

Plant morphology, which should show some correlation with temperature and precipitation, is used here to interpret the presence of tropical rainforest. Eocene macrofossil floras (leaves and/or fruits) are known from Brazil, Colombia, Ecuador, Venezuela and Peru, and can be analysed by using standard characters that have palaeoclimate applications (entire margins, drip tips, coriaceous leaves, large leaf size, etc.). Pollen floras of Eocene age have been recovered from all of those countries, as well as from the Greater Antilles and Panama. Very few of these macrofossil floras have been adequately collected or described, but an accumulation of data on the Fonseca and Gandarela (Duarte & Mello Filha 1980; De Lima & Salard-Cheboldaeff 1981) floras of Minas Gerais, Brazil is used here to demonstrate that the morphological signature of archetypal rainforest was in place during the Eocene. The flora (Fonseca Formation) is largely comprised of compression material and has attracted recent attention because of the presence of lignites, fishes, insects, and especially fossil plants. Deposition was in oxbow lakes and quiet river stretches of a tropical lowland river system. Thirty-one species of dicotyledons have been gleaned from the literature based on macrofossil remains. Out of those dicotyledonous species, the leaves of 24 species are entire-margined, two are serrate-margined, and the remaining five have not been evaluated yet because of a lack of information. Thus, 92% out of the 26 species that could be evaluated had entire-margined species, and of those species for which size data could be obtained (19 out of 31), average leaf size was *ca.* 3700 mm^2, a value that is relatively high for a poorly known fossil flora. Using calculations provided by Wilf *et al.* (1998) derived from modern leaf and climate data, this leaf size predicts a precipitation of *ca.* 1200 mm yr^{-1}. These preliminary indicators all point to relatively high species richness in a tropical flora living under conditions of warm temperature and abundant precipitation. Other than this flora, there are few macrofossil leaf floras published from this time period that can be analysed using leaf morphology data.

6. EOCENE PLANT SYSTEMATICS: A CLUE TO NEOTROPICAL RAINFORESTS

A major step forward in understanding the complex palynological signal in tropical areas was made when Germeraad *et al.* (1968) published a work spanning more than 13 sites in Colombia and Venezuela, and drawn from a range of prior unpublished reports. In addition to a stratigraphic framework, they presented detailed information on the modern botanical affinities of many of the pollen taxa that they used in their assessment. While acknowledging that thousands of different species are present in their samples, and that 200 are certainly important, they focus on just 49 species based on their stratigraphic importance and dominance in samples. This work set a standard for other researchers to take a more plant-based approach to their stratigraphic data and has genuinely revolutionized the integration of palynology with modern tropical ecology and evolution. A recent compilation of the distribution and ecology of pollen found in Quaternary cores (Marchant *et al.* 2002) provides a standard reference for ecological interpretations of pollen genera recognized from at least the Eocene to the present.

A large number of families and genera that indicate rainforest conditions are present in Eocene sediments from the neotropics (table 3).

Based on Eocene leaf deposits in the Fonseca Basin of Minas Gerais, Brazil (De Lima & Salard-Cheboldaeff 1981; Mello *et al.* 2000), a wide range of tropical plant families are represented in Eocene sediments of northern South America: Annonaceae, Bignoniaceae, Bombacaceae, Combretaceae, Euphorbiaceae, Fabaceae, Malphighiaceae, Melastomataceae, Meliaceae, Menispermaceae, Monimiaceae, Myrsinaceae, Myrtaceae, Rutaceae, Sapindaceae, Sapotaceae and Tiliaceae (table 3). These families provide good evidence for well-developed ATR by the Eocene at 20° S. In Ecuador (Ancon) and Peru (Belen and Parinas), rich fossil fruit and seed deposits include the following families: Anacardiaceae, Annonaceae, Palmae, Combretaceae, Dilleniaceae, Ebenaceae, Moraceae, Myristicaceae and Sapindaceae (Berry 1929*a*,*b*). It should be emphasized that these taxonomic summaries are by no means complete and most macrofossil sites have not been recollected or revised for half a century. This is true particularly of the potentially rich sites (of Eocene age) in Venezuela and Peru.

Jaramillo (2002) has suggested that increases in tropical palm pollen (*Proxapertites*) and woody Bombacaceae in the Eocene of Colombia are indications of increased temperatures and precipitation. In addition, his analysis suggests higher heterogeneity among samples in Eocene sediments, which would support tropical rainforest interpretations. However, multiple causes for sample heterogeneity can be proposed, so this might be best interpreted as supporting rather than primary evidence.

7. SEDIMENTOLOGY AND MODELLING: CLUES TO EOCENE NEOTROPICAL RAINFORESTS

Climatic reconstructions for the Eocene, based on global climate modelling (Frakes *et al.* 1992; Beerling & Woodward 2001; Ziegler *et al.* 2003), indicate tropical temperatures (18–30° MAT) encompassing from one-third to two-thirds of the continent of South America. Central American palaeoclimates are reconstructed differently by palaeobotanical versus global climate model approaches. Palaeobotanical-based reconstructions show the most generalized pattern, with tropical rainforest extending uninterrupted from southern Bolivia to New Mexico (Frakes *et al.* 1992). By contrast, Ziegler's group proposes dry conditions throughout Central America and Mexico, based on evaporite distribution. Some models indicate that precipitation of at least 100 mm per month occurred only in northern South America and eastern Brazil, with the rest of the South American continent being probably too dry to support closed-canopy tropical rainforest. The Atlantic coast of Brazil (including the area of the Fonseca site, mentioned in § 5 above) appears in Beerling & Woodward's (2001) models as sufficiently wet to maintain tropical rainforest. In South America, much larger areas of a moist tropical rainforest biome were indicated by both Wolfe (1985) and Morley (2000), although neither source is based on sufficient data to do more than connect very widely separated dots. Ziegler *et al.* (2003) propose that the evidence for low latitude rainforests is restricted to 5–10° from the equator during the early Tertiary, which may be at odds with the Fonseca site data, but allow that

Table 3. Eocene records of Angiosperm taxa potentially indicative of tropical rainforest.
(The authors did not reverify records by inspection of pollen grains or macrofossils. Instead, these records are listed to give a summary of the citations of tropical taxa that have been presented in the fossil record. Records that have been rejected by other authors subsequent to initial publication are omitted.)

family represented	genus, species	evidence from	reference
Araceae (or Arecaceae)	*Longapertites* spp.	pollen: Colombia	Jaramillo & Dilcher (2001); Zetter (2001)
Anacardiaceae	*Anacardium peruvianum*	fruit: Ecuador	Berry (1929*b*)
Annonaceae	*Annona perubiana*	fruit: Ecuador	Berry (1929*b*)
Annonaceae	*Oxandra emygdiana*	leaves: Brazil, Fonseca	Duarte (1958)
Annonaceae	*Annona oliveirae*, *A. lamergoi*, *A. carnavalii*	leaves: Brazil, Fonseca	Duarte (1958)
Apocynaceae	*Apocynophyllum texensis*	leaves: Venezuela	Berry (1936)
Arecaceae	*Arecipites regio*	pollen: Colombia	Jaramillo & Dilcher (2001)
Arecaceae	*Iriartites restinensis*	fruit: Peru	Berry (1929*a*)
Arecaceae	*Mauritiidites franciscoi*	pollen: Colombia	Jaramillo & Dilcher (2001)
Arecaceae	*Proxapertites* spp.	pollen: Colombia	Jaramillo & Dilcher (2001)
Arecaceae	*Palmocarpon bravoi*	fruit: Ecuador	Berry (1929*b*)
Arecaceae	*Astrocayum sheppardi*	fruit: Ecuador	Berry (1929*b*)
Bignoniaceae	*Jacaranda tertiaria*	leaves: Brazil, Fonseca	Berry (1935); De Lima & Cheboldaeff (1981)
Bignoniaceae	*Arrabidaea* sp.	leaves: Brazil, Fonseca	Berry (1935); De Lima & Cheboldaeff (1981)
Bombacaceae	*Eriotheca prima*	flower: Brazil	Duarte (1974)
Bombacaceae	*Bombax ceiba* (*Bombacacidites annae*)	pollen: Colombia, Caribbean	Germeraad *et al.* (1968)
Bombacaceae	*Catostemma* (*Jandufouria seamrogiformia*)	pollen: Colombia, Caribbean	Germeraad *et al.* (1968)
Burseraceae	*Burserites fayettensis*	leaves: Venezuela	Berry (1936)
Burseraceae	*Protium* (*Tetracolporopollenties transversalis*)	pollen: Colombia	Jaramillo & Dilcher (2001)
Chrysobalanaceae	*Licania angustata*	leaves: Brazil, Gandarela	Duarte & Mello Filha (1980)
Chrysobalanaceae	*Licania gandarelensis*	leaves: Brazil, Gandarela	Duarte & Mello Filha (1980)
Chrysobalanaceae	*Hirtella perfecta*	leaves: Brazil, Gandarela	Duarte & Mello Filha (1980)
Combretaceae	*Combretum boggsi*	fruit: Brazil	Berry (1929*b*)
Combretaceae	*Combretum fonsacanensis*	leaves: Brazil, Fonseca	Berry (1935)
Combretaceae	*Terminalia maxima*	leaves: Brazil, Fonseca	Berry (1935)
Dilleniaceae	*Tetracera belensis*		
Euphorbiaceae	*Homalanthus prenutans*	leaves: Brazil, Fonseca	Berry (1935)
Euphorbiaceae	*Alchornea* (*Psilatricolpites* and *Ranunculadicites operculatus*)	pollen: Caribbean	Germeraad *et al.* (1968)
Euphorbiaceae	*Amanoa* (*Retitricolporites irregularis*)	pollen: Caribbean	Germeraad *et al.* (1968)
Euphorbiaceae	*Jatropha tertiaria*	fruits: Peru	Berry (1929*a*)
Fabaceae	*Caesalpinia echinatiformis*	leaves: Brazil, Fonseca	Berry (1935)
Fabaceae	*Cassia adumbrata*	leaves: Brazil, Gandarela	Duarte & Mello Filha (1980)
Fabaceae	*Cassia fonsecana*	leaves: Brazil, Fonseca	Berry (1935)
Fabaceae	*Cassia otustafolia*	leaves: Brazil, Fonseca	Berry (1935)
Fabaceae	*Mimosa calodendrum*	leaves: Brazil, Fonseca	Berry (1935)
Fabaceae	*Schizolobium excelsum*	leaves: Brazil, Fonseca	Berry (1935)
Fabaceae	*Triptolemaea tertiaria*	leaves: Brazil, Fonseca	Berry (1935)
Ctenolophonac.	*Ctenolophon*	pollen: Caribbean	Germeraad *et al.* (1968)
Humiriaceae	*Sacoglottis cipaconensis*	fruit: Peru	Berry (1927, 1929*a*)

(*Continued*.)

Table 3. (*Continued*.)

family represented	genus, species	evidence from	reference
Humiriaceae	*Vantanea sheppardi*	fruit: Ecuador	Berry (1929*b*)
Malpighiaceae	*Banisteria oblongifolia*	leaves: Brazil, Fonseca	Berry (1935)
Malpighiaceae	*Brachypteris*	pollen: Caribbean	Germeraad *et al.* (1968)
Malpighiaceae	*Perisyncolporites pokornyi*	pollen: Caribbean, Colombia	Germeraad *et al.* (1968); Jaramillo & Dilcher (2001)
Melastomataceae	*Miconia ligustroides*	leaves: Brazil, Fonseca	De Lima & Cheboldaeff (1981)
Melastomataceae	*Tibouchina dolianitii*	leaves: Brazil, Fonseca	Duarte (1956)
Melastomataceae	*Tibouchina santosii*	leaves: Brazil, Fonseca	Duarte (1956)
Meliaceae	*Cedrela jacksoniana*	leaves: Venezuela	Berry (1936)
Meliaceae	*Cedrela campbeli*	leaves: Brazil, Fonseca	Berry (1935)
Menispermaceae	*Chondrodendron brasilense*	leaves: Brazil, Fonseca	Dolianiti (1949)
Monimiaceae	*Siparuna preguayense*	leaves: Brazil, Fonseca	Berry (1935)
Moraceae	*Psildiporites redundantis*	pollen: Panama	Graham (1985)
Moraceae	*Ficus americanafolia*	leaves: Venezuela	Berry (1936)
Moraceae	*Ficus sphericus*	fruits: Peru	Berry (1929*a*)
Myristicaceae	*Virola tertiaria*	fruits: Peru	Berry (1929*a*)
Myrsinaceae	*Myrsine braziliana*	leaves: Brazil, Fonseca	Berry (1935)
Myrtaceae	*Eugenia* sp.	leaves: Venezuela	Berry (1936)
Myrtaceae	*Myrciaria abscondita*	leaves: Brazil, Gandarela	Duarte & Mello Filha (1980)
Myrtaceae	*Syncolporites proicostatus*	pollen: Colombia	Jaramillo & Dilcher (2001)
Olacaceae	*Anacalosa* (*Anacolosidites* spp.)	pollen: Caribbean	Germeraad *et al.* (1968); Jaramillo & Dilcher (2001)
Pelliceriaceae	*Lanagiopollis crassa*	pollen: Colombia	Jaramillo & Dilcher (2001)
Rhizophoraceae	*Rhizophoa* sp.	pollen: Panama	Graham (1985)
Rubiaceae	*Psychotria eogenica*	fruits: Peru	Berry (1929*a*)
Rubiaceae	*Uragoga tertiaria*	fruits: Peru	Berry (1929*a*)
Rutaceae	*Calodendrum* sp.	leaves: Brazil, Fonseca	De Lima & Cheboldaeff (1981)
Rutaceae	*Dictyoloma beckeri*	fruits: Brazil, Gandarela	Duarte & Mello Filha (1980)
Rutaceae	*Erythrochiton bahiense*	leaves: Brazil, Fonseca	Berry (1935)
Sapindaceae	*Cupaniodes peruvianus*	seeds: Peru	Berry (1929*a*)
Sapindaceae	*Sapindoides peruvianus*	fruit: Ecuador, Peru	Berry (1929*b*)
Sapindaceae	*Sapindus* spp.	leaves: Brazil	Berry (1935)
Sapindaceae	*Sapindus ferreirai*	leaves: Brazil, Gandarela	Duarte & Mello Filha (1980)
Sapotaceae	*Tetracolporopollenties maclosus*	pollen: Colombia	Jaramillo & Dilcher (2001)
Sapotaceae	*Chrysophyllum preoliviforme*	pollen: Venezuela	Berry (1936)
Sapotaceae	*Labatia fonsecana*	leaves: Brazil, Fonseca	Berry (1935)
Tiliaceae	*Luehea roxoii*	leaves: Brazil, Fonseca	Berry (1935); Dolianiti (1950)
Vitaceae	*Ampelocissus bravoi*	fruits: Peru	Berry (1929*a*)
Vitaceae	*Cissus willardi*	fruits: Peru	Berry (1929*a*)
Vochysiaceae	*Qualea incisa*	leaves: Brazil, Gandarela	Duarte & Mello Filha (1980)

rainforest biomes may have spread along coastal areas beyond the well-defined bands that they propose.

In summary, although the Eocene data are sparse, with few taxa collected and described from the large majority of fossil-bearing sites, it is clear that rainforest taxa were present, climatic conditions were adequate and leaf morphology is reflective of tropical rainforest in the neotropics, particularly in eastern Amazonia. Indications that these conditions also existed in the Palaeocene cannot be rejected, but palynological evidence, in particular, seems to indicate consistently that tropical habitats had lower diversity than in the Eocene.

8. OTHER INDIRECT EVIDENCE FOR THE AGE OF NEOTROPICAL RAINFOREST BIOMES

Given the acknowledged gaps in the fossil record for many biomes, especially those not closely associated with depositional settings, we briefly present here additional lines of evidence that do not specifically depend on fossil evidence of plants from the biome in question. Our reasoning is that if there is a large mismatch between indications from the fossil record versus those from other approaches, both records should then be viewed with some caution with regard to the timing of appearance. However, data from other lines of evidence, consistent with the palaeobotanical record, may support the timing of neotropical rainforest origin. This approach should highlight geographical areas where continued prospecting for fossil evidence would be worthwhile.

(a) *Ages of tropical lineages using modern molecular analyses*

One promising approach has been to estimate the absolute age of plant lineages currently restricted to the tropical rainforest biome, thus shedding light on the origin of the biome indirectly. Although this approach requires some assumptions (see below), it can be used to indicate a maximum potential age of the biome. Evidence accumulating from molecular-based phylogenies of several lineages within the Malpighiales (Davis *et al.* 2002, 2004) has indicated that several lineages of angiosperms, whose modern representatives are now largely restricted to tropical rainforest, have origins of approximately Cenomanian age (114–98 Myr ago). These results are tentative, based on assumptions involving the consistency of ecological tolerances, the accuracy of dating of fossils anchoring the phylogenies, the methods used for interpolation of dates and the robustness of the phylogenetic patterns. However, they do suggest that a higher density of records and sites of Cretaceous age would reveal greater diversity among angiosperms, even though they may not have been dominant taxa in the rainforests of the neotropics. This approach is widely used among contributors to this Discussion issue (e.g. Pennington & Dick 2004; Plana 2004; Richardson *et al.* 2004).

(b) *Global symmetry argument*

One might argue, on the basis of a symmetrical pattern of climate north and south of the equator, and broadly similar uplift patterns in North and South America, that there must have been equivalent-age tropical rainforest in both places at similar latitudes. The Castle Rock Flora of early Palaeocene age in Colorado is an excellent example of early modern tropical rainforest in North America. Orogeny has been linked to the appearance of the tropical rainforest in Castle Rock (Johnson & Ellis 2002). One mechanism proposed is generation of diverse habitats via orogeny (elevational and/or depositional) in which diversification would occur. Alternatively, orogeny can provide isolation and corridors as causeways for migration. South America may well fit a similar model of orogenic stimulation of diversity with a continuous, relatively low-lying Andean highland lying to the west of the Amazon basin starting in the Eocene. Thus, in climatologically similar areas in South America, the uplift of the Andes and the increased heterogeneity of habitats had an effect on the assembly of high diversity tropical rainforests. This uplift timing is substantially later in South America (Eocene to Present) than in North America (Late Cretaceous to Eocene).

(c) *Supporting patterns in reptiles and mammals*

Animals characteristic of tropical rainforest have been reported from deposits as old as the Cretaceous in South America. Caecilians were reported from the Cretaceous (Maestrichtian) of Bolivia (Rage 1986), and the Palaeocene of Brazil (Estes & Wake 1972) and Bolivia (Rage 1986). These records cannot support the existence of closed tropical forest by themselves, but their presence adds weight to the idea that tropical rainforest is probably older than the currently published fossil record indicates.

9. SUMMARY COMMENTS

We have reviewed here the evidence for tropical rainforest in South America from the Mid-Cretaceous through to the Eocene in light of the quality of the fossil record. We conclude that evidence is very limited for ATR until the end of the Cretaceous. Evidence for a closed-canopy tropical rainforest in the Maestrichtian is limited, but a high abundance and moderate diversity of palm pollen are suggestive of areas that should be investigated more intensely in the future. By the Late Palaeocene, there is growing evidence for tropical rainforest, although diversity still appears to be rather lower than for ATR. Preservational biases may influence these records, and in areas of eastern Brazil and coastal Colombia, Ecuador and Peru we suggest that prospecting intensity should be increased to resolve this question. By the Eocene there is little doubt that closed-canopy tropical rainforest was present in South America, but additional data are needed. Quantitative palynological sampling, exploratory phytolith analysis and quantitative macrofossil sampling are critical avenues that must be followed in the future to document the presence of tropical rainforest in the current neotropical realm.

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GLOSSARY

ATR: archetypal tropical rainforest
MAP: mean annual precipitation
MAT: mean annual temperature