

Fossil angiosperm leaves and climate: from Wolfe and Dilcher to Burnham and Wilf

With 5 figs, 2 tabs

David R. GREENWOOD

Abstract

Eocene climates have become a preoccupation for some paleobotanists, geoscientists and climatologists interested in ‘hothouse earth’ times, and in particular how the past may provide insight into future climate change driven by changed concentrations of atmospheric greenhouse gases. The foundations for this interest in the Eocene were laid down by David DILCHER and Jack WOLFE in the 1960s–1970s through their use of leaf physiognomy to reconstruct trends in climate, primarily mean annual temperature (MAT), over the Tertiary. Reviewed here are the seminal works authored by these paleobotanists, and also lesser-known works that pointed the way, conceptually and methodologically, to the importance of understanding the Eocene, but significantly also, to the importance of understanding the factors that may confound the paleobotanical record of past climates. Leaf margin analysis (LMA) and leaf size analysis, CLAMP, and taphonomy were all topics explored by DILCHER and WOLFE, their contemporaries and those whom they mentored. A fundamental shift towards publishing quantitative estimates of MAT, cold month mean temperatures and precipitation was driven in part by the development by WOLFE of CLAMP, but also by the challenge of reconciling new computer models of Cretaceous and Eocene climates that were at odds with what paleontologists understood were times of frost-free climates across North America. The relationship between leaf margin proportion and MAT has been shown to be essentially global, although subject to regional variation (*cf.* New Zealand). Recent papers have also sought to better quantify the taphonomic biases inherent in LMA and CLAMP, while others have sought ever more accurate or more precise leaf-climate correlations, topics first raised in papers written by Jack WOLFE and David DILCHER, 40+ years ago. New data are presented to show that one key element in obtaining estimates of past temperatures that are both accurate and precise remains largely overlooked – how well is the climate signal shown in the forest canopies preserved in the fossil assemblages?

Key words: paleobotany, leaf physiognomy, paleoclimate, taphonomy, Cenozoic, Australia, North America

Introduction

It is now part of the accepted understanding of the Cenozoic that global temperatures declined stepwise, with intervals of warming between cooling steps, from late Cretaceous times to the Pleistocene ice ages (fig. 1). Within the Cenozoic, the early Eocene is now recognized from a variety of paleontological proxies as being the warmest geological interval in the past 65 million years, with clear evidence that not only were both poles un-glaciated for much of the Eocene, but that they were covered by forests. The causes of global warm temperatures in the Eocene, and peak warmth in the early Eocene in particular, are thought to be due to a combination of factors including high levels of atmospheric carbon dioxide and other greenhouse gases, as well as the lack of a circum-

Antarctic oceanic current (ZACHOS et al. 2001, PAGANI et al. 2005). Our current understanding of early Cenozoic (Paleogene, or formerly ‘early Tertiary’) climate change, and the nature of Eocene climate in particular, originated from two revolutions in geology – each developed in the context of an increasingly more refined geochronology; the isotopic record of sea-surface temperatures from marine microfossils (e.g., WOLFE & POORE 1982, ZACHOS et al. 2001), and the paleobotanical record of land temperatures (e.g., WOLFE & HOPKINS 1967, WOLFE 1971, 1978, DILCHER 1973, WOLFE & POORE 1982).

In the 1960s and 1970s, WOLFE (1971, 1978, 1979, WOLFE & HOPKINS 1967), and DILCHER (1973, DOLPH & DILCHER 1979) provided new insights into the known relationship between leaf form and climate (e.g., BAILEY & SINNOTT 1915), and used their data to interpret Cenozoic

Author’s address: David R. GREENWOOD, Environmental Science, Brandon University, 270 18th Street, Brandon, Manitoba, R7A 6A9, Canada,
<greenwoodD@brandu.ca>

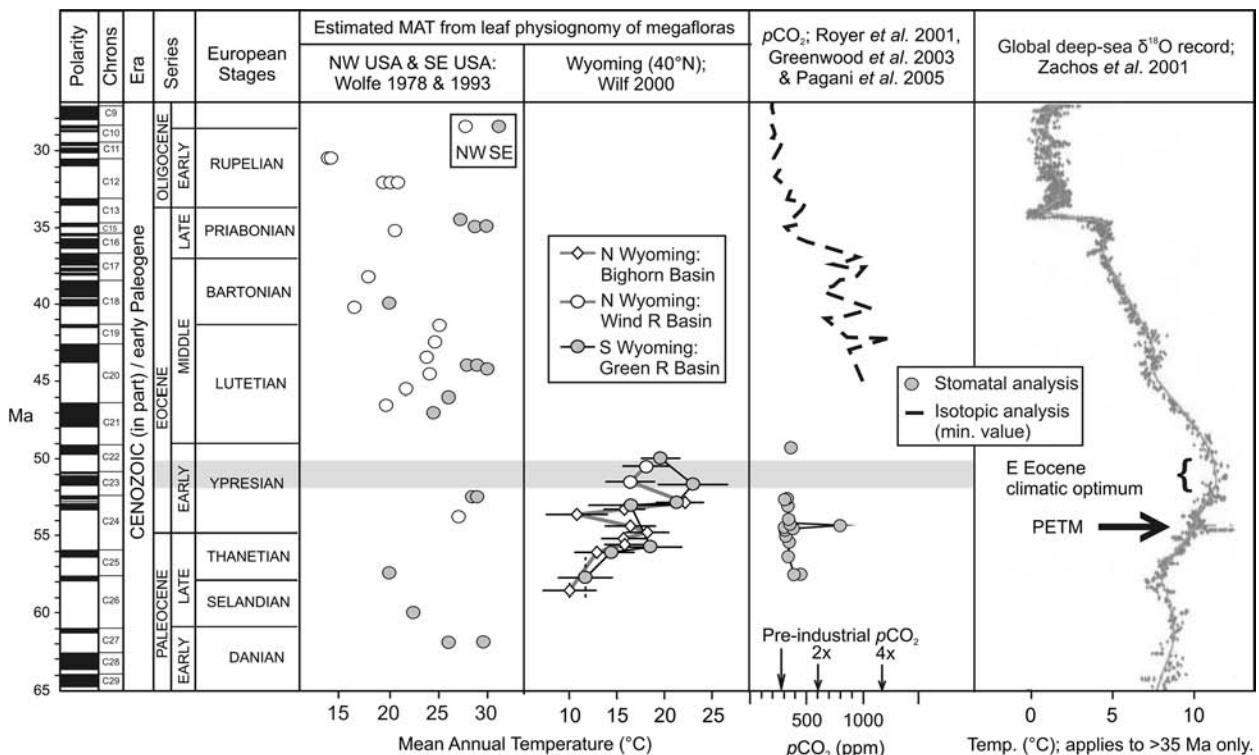


Fig. 1: North American Paleogene climates and atmospheric conditions, based primarily on leaf physiognomy, contrasted against the refined geochronometric scale (BERGGREN et al. 1995) and the marine isotopic record. Data sources: MAT from megaflora, WOLFE (1978, 1993), WILF (2000) and WING et al. (2000); $p\text{CO}_2$ from megaflora, ROYER (2001) and GREENWOOD et al. (2003a); marine temperatures and $p\text{CO}_2$ from isotopic analyses, ZACHOS et al. (2001) and PAGANI et al. (2005) respectively.

climates. WOLFE's work in particular demonstrated the now familiar fluctuations between warm and cool intervals in the Paleogene (fig. 1) at a time when it was generally thought that global temperatures had declined steadily over the 'Tertiary' (WOLFE 1971, 1978, 1979, 2001, WOLFE & HOPKINS 1967). The use of leaf form or physiognomy (i.e., the presence of drip tips and other traits, leaf size, shape and margin type) from fossil leaf floras to interpret climates was not universally accepted, and a number of concerns were raised by contemporary paleobotanists and geoscientists (see paper by SPICER, this volume). Nonetheless, the basic pattern of climatic fluctuations through the Cenozoic derived from paleobotanical indices such as leaf margin analysis have become part of our general knowledge of Cenozoic climate change. In the past 10 to 15 years, paleoclimate proxies based on leaf physiognomy have become more widely accepted; however, some concerns with this approach continue to be raised in the literature. These concerns and the responses of practitioners in the field are developed in this paper, and can be summarized as follows:

1. WOLFE's (1971, 1979) calibration of leaf margin proportion and MAT (fig. 2) – leaf margin analysis (LMA) – was based on floral lists.

Did this compilation obscure habitat (i.e., local site) ecological effects, such as the expectation that riparian

vegetation would have different sized leaves or a greater proportion of toothed species than other areas (MACGINITIE 1953, DOLPH 1979, BURNHAM et al. 2001, KOWALSKI & DILCHER 2003)?

2. WOLFE's (1971, 1979) leaf margin analysis data set was based on east Asian vegetation.

Was this relationship applicable to vegetation on other continents and in the geological past? BAILEY and SINNOTT (1915) had flagged in their work that Australian vegetation was somehow 'different', but also that vegetation from cold and dry environments did not follow their trends. UPCHURCH and WOLFE (1987) suggested – for the purposes of applying leaf physiognomy to paleoclimates – that Australian broad-leaf evergreen vegetation, with its paucity of temperate deciduous trees, its lack of seasonally very cold climates and generally highly seasonal rainfall, may offer a better analog for Late Cretaceous vegetation than did extant northern hemisphere vegetation.

3. What should we measure – leaf margin, leaf size, or a list of characters?

DILCHER (1973, DOLPH & DILCHER 1979) and earlier workers had shown that leaf physiognomy was likely responding to multiple environmental factors, and that many leaf traits co-varied with multiple climate variables.

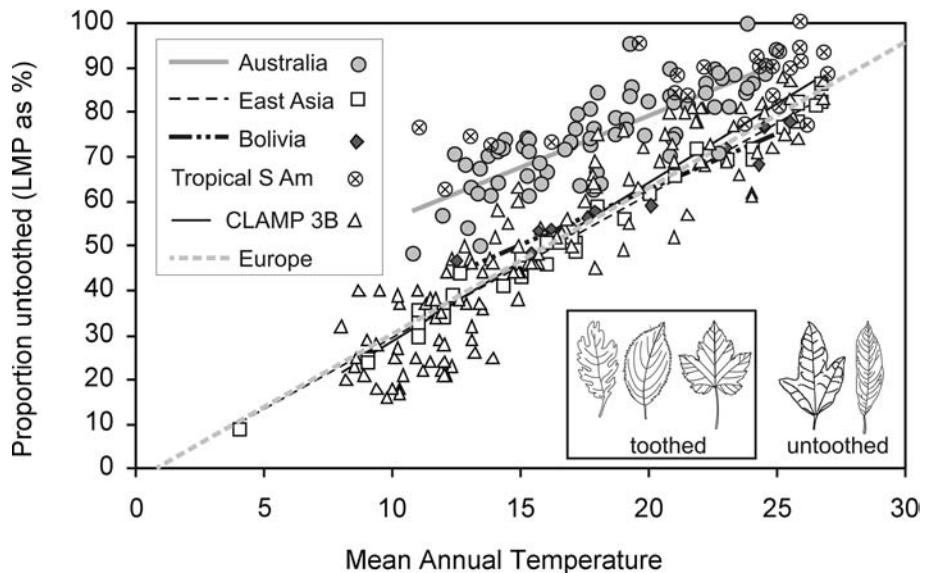


Fig. 2: Plot showing the main LMA studies excluding New Zealand and Africa, showing the relationship between LMP and MAT, based on GREENWOOD (2005b; fig. 1). Data sources: Australia, GREENWOOD et al. (2004); east Asia, WOLFE (1979) as presented in WING and GREENWOOD (1993); Bolivia, GREGORY-WODZICKI (2000); Tropical South America, KOWALSKI (2002); CLAMP 3B, WOLFE (1995 and pers. comm., 1992); Europe, TRAISER et al. (2005).

This issue would lead to the development of a multivariate approach – CLAMP (Wolfe 1990, 1993, 1995).

4. Quantification, accuracy and precision.

WOLFE'S (1971, 1978) early papers had graphically indicated temperature trends within the Cenozoic, and did not state a measure or uncertainty or error for the numerical estimates of MAT. Later papers by WOLFE, particularly those using CLAMP (Climate Leaf Analysis Multivariate program), and papers by his successors (e.g., WING & GREENWOOD 1993, GREENWOOD & WING 1995) published estimates of MAT using LMA expressed to the nearest whole tenth of a degree and stated errors of ± 2 °C or less based on the standard error of the estimates from regression analysis. WILF (1997) addressed the issue of error; however, recent papers (e.g., BURNHAM et al. 2001, 2005, KOWALSKI & DILCHER 2003) have considered various aspects that encompass the issue of precision versus accuracy, and why both are important.

5. Would taphonomic biases – such as the mixing of leaves from more than one forest type in a single deposit (e.g., MACGINITIE 1969), or the selective transport and preservation of leaf taxa and/or key leaf traits (e.g., ROTH & DILCHER 1978, GREENWOOD 1991, 1992, 2005a, WOLFE 1995, SPICER et al. 2005) – so alter the pattern of leaf physiognomy preserved in a fossil assemblage that any climate signal was so degraded as to be not meaningful?

Leaf Physiognomy and Climate

Leaf Margin Analysis and Leaf Size Analysis

BAILEY and SINNOTT (1915, 1916) had noted that both the proportion of entire-margined leaves and the proportion

of large leaves in forests increased with decreasing latitude and suggested that this relationship could be used to interpret past climates. Wet tropical forests were rich in large smooth edged leaves, whereas temperate forests had mostly smaller leaves with toothed and/or lobed margins. General patterns of the relative abundance of toothed leaves and different size classes of leaves were therefore used by paleobotanists to make comparisons between Tertiary megafloras and modern vegetation, allowing qualitative inferences about climate and vegetation type (e.g., MACGINITIE 1953, 1969, WOLFE & HOPKINS 1967). BAILEY and SINNOTT (1916) noted, however, 1. that Australian vegetation showed a much lower proportion of toothed species than did the floras at comparable latitudes in the northern hemisphere, and 2. that vegetation from cold and dry environments did not follow their trends.

WOLFE (1971, 1978, 1979) developed leaf margin analysis based on the strong positive relationship between mean annual temperature (MAT) and the proportion of woody dicot species in a floral sample that has entire leaf margins (leaf-margin proportion, LMP) based on floral lists for sites in east Asia (fig. 2). This method allowed for quantitative estimates of MAT. Unfortunately, WOLFE never published the regression equation for the relationship based on the east Asian data set, although WING and GREENWOOD (1993) later re-plotted the data from WOLFE's (1979) original LMA chart and published both the inverted regression equation for application to fossil floras, and the regression statistics, including the standard error of the estimate (± 0.8 °C). All subsequent use of the 'east Asian LMA equation' have been based on WING and GREENWOOD's (1993) recalculation of WOLFE's (1979) regression, and not his original data. Since then, a number of other univariate equations for leaf margin analysis have been published based on other regional data sets (fig. 2).

DILCHER'S (1973) first contribution to the application of leaf physiognomy to paleoclimates did not have the

same impact as WOLFE's work. While DILCHER (1973) did consider both leaf margin proportion and leaf size, his principal contribution was leaf size analysis, the semi-quantification of the relative proportion of discrete leaf size classes that could be used to determine latitudinal or altitudinal climate zones (e.g., DOLPH & DILCHER 1980a). Nonetheless, some critical observations made in that work are worth revisiting: 1. large entire leaves are dominant in warm-moist environments; 2. small toothed leaves are dominant in cool and also in dry environments; and 3. leaf characters co-vary with more than one climate variable. Leaf size analysis has largely been sidelined, although UPCHURCH and WOLFE (1987, 1993) qualitatively reconstructed rainfall trends over the Late Cretaceous and Tertiary, and WILF et al. (1998, WILF 2000) developed a correlation between a leaf size index and mean annual precipitation that picks up on points 1. and 2. above. ROTH and DILCHER (1978) also considered taphonomic effects with respect to both leaf size analysis and leaf margin proportion in lake sediments, which will be discussed later in this paper.

Later work by DILCHER's student DOLPH (1979, DOLPH & DILCHER 1979, 1980a, 1980b) cast doubt on the application of leaf margin analysis in a quantitative manner, by highlighting the influence of local site-to-site variation in leaf margin proportion as a source of greater variance in LMP between sites of similar MAT than the pseudo-precision implied by the east Asian calibration. A problem with DOLPH's (1979) examination of leaf margin analysis, however, was that it did not truly examine the variables used in WOLFE's (1971, 1978, 1979) analysis, nor did it provide a valid statistical appraisal, as 1. DOLPH used biotemperature – a novel recalculation of MAT where days $<0^{\circ}$ and $>30^{\circ}\text{C}$ were recalculated to 0° and 30°C (HOLDRIDGE 1967), rather than MAT which is the simple average of daily maxima and minima, 2. some of his sites had as few as 2 species (8/38 had <10 spp.), whereas WOLFE had expressed concern over using sites with <20 spp., 3. DOLPH did not apply regression analysis to his data, either graphically or statistically, and 4. the range of biotemperature considered was small.

Outside of paleobotany, the marked fluctuations in MAT in the Paleogene determined by WOLFE using leaf margin analysis (WOLFE 1978, 1979) were adopted as the 'gold standard' for the climate record of the Cenozoic. More significantly perhaps, WOLFE (1990, 1993, 1995) responded to concerns about the covariance of leaf characters with climate variables (e.g., DILCHER 1973, DOLPH & DILCHER 1980a, 1980b) and proceeded to develop a multivariate approach – the Climate Leaf Analysis Multivariate Program or 'CLAMP'.

The CLAMP approach to quantitative estimation of paleoclimates is reviewed elsewhere in this volume (see SPICER 2007) and so will not be described in detail here. WOLFE's (1990, 1993, 1995) method applied correspondence analysis to the scored samples of leaves from >100 sites, each with > 20 species of woody dicots, to

demonstrate the multi-character mapping of 31 leaf traits in environmental space. In practical terms, paleoclimate estimates are calculated by projecting the position of the fossil flora onto each of the climate variable vectors calibrated using the modern CLAMP data set. Estimates of MAT, cold month mean temperature (CMMT), mean annual precipitation (MAP) and other variables such as growing season precipitation and paleoelevation have been derived using CLAMP (e.g., WOLFE 1994, HERMAN & SPICER 1996, 1997, WOLFE et al. 1997, KENNEDY et al. 2002). Rather than apply this approach, a number of authors have opted instead to directly analyze the CLAMP data set, or develop comparable data sets to derive regression models as predictors of paleoclimate (e.g., GREGORY & CHASE 1992, WING & GREENWOOD 1993, GREGORY 1994, GREGORY & MCINTOSH 1996, JACOBS & DEINO 1996, WIEMANN et al. 1998, 2001, WILF et al. 1998, JACOBS 1999, 2002, KOWALSKI & DILCHER 2003, JACOBS & HERENDEEN 2004). In part, this latter approach arose from the apparent complexity of the CLAMP ordination approach, and the perception that some characters were subjectively defined, resulting in potential measurement errors between different researchers scoring the same fossil flora (WILF 1997, WIEMANN et al. 1998, 2001). Whatever the approach used – univariate leaf margin (to estimate MAT) and leaf size analysis (e.g., to estimate MAP; WILF et al. 1998), multiple regression and ordination – the provision of tools to quantitatively estimate paleoclimates has revolutionized our understanding of Late Cretaceous and Paleogene climates.

Why do we care about climates of the past?

There are three primary reasons paleontologists are interested in paleoclimates: 1. coal deposits and other economically important geological formations are climatically controlled in time and space; 2. to a very large extent climate determines the geographical distribution of plant taxa; and 3. climate change can facilitate and mediate evolution, as well as the introduction and extirpation of taxa from continents (e.g., WOLFE 1987a, 1990). WOLFE (2001) notes that the prevailing paradigm amongst paleobotanists up to the 1960s (and for some, well after this date) was a simple model of maximum warmth in the early Tertiary followed by gradual cooling from moderate warmth to present-day conditions. In his recollections, WOLFE (2001) also relates the lesson learned that we must be open to new ideas and that gradualism and catastrophism can both be applied in interpreting the record of environmental change. An account of WOLFE's impact on our understanding of the events at the end of the Cretaceous are beyond the scope of this paper, but the role played by megafloral chronosequences analyzed to reconstruct North American climates, principally temperature, is summarized in fig. 1.

Since WOLFE's (1971, 1978) 'curves' were published, improved geochronological understanding of North American megafloras through improved radiometric dating and magnetostratigraphy, have permitted finer temporal resolution. For example, WILF (2000) was able to show cooler and warmer episodes through the late Paleocene to early Eocene of Wyoming (fig. 1), and WING et al. (2000) proposed the occurrence of a significant cooling episode in the early Eocene prior to the early Eocene thermal maximum. Analysis of multiple megafloral sites in the Okanagan Highlands of southern British Columbia, for example, has shown that these sites occupied a temperature-controlled ecotone in the early to middle Eocene that was potentially sensitive to climate change (GREENWOOD et al. 2005). These types of analysis of climate change at fine temporal scale are permitting better resolution of vegetation responses to past warming and cooling episodes in the late Cretaceous and Paleogene (e.g., WILF 2000, WILF et al. 2003).

In part the refinement in both the tools and interpretation of paleoclimates has been driven by the development of computer models of climate, or general circulation models (GCMs), models that are assessed using sensitivity analysis of past climates based on quantitative paleoclimate estimates such as those derived from leaf physiognomy (e.g., SLOAN & BARRON 1990, 1992, SEWALL et al. 2000, SHELLITO et al. 2003). In early climate model work, the Eocene had been targeted as a model for a 'warm earth', as qualitative paleontological proxy data had indicated ice-free poles and the presence of thermophilic taxa in the continental interiors of North America, Europe, Asia and Australia (SLOAN & BARRON 1990, 1992, WING & GREENWOOD 1993). The initial GCM results, however, predicted freezing conditions in the interior of North America and at the poles, prompting SLOAN and BARRON (1990) to claim that perhaps the fossil evidence had been incorrectly interpreted as indicating climates lacking freezing conditions. WING and GREENWOOD (1993, GREENWOOD & WING 1995), using a multiple regression model derived from WOLFE's (1993) CLAMP data set, however, were able to demonstrate that quantitative estimates of Eocene CMMT were markedly at variance with the initial GCM results; the continental interiors of North America and Australia and the polar regions were essentially free of frost in the early to middle Eocene.

In some ways, the discrepancy between the modeling results and the paleontological proxy data triggered an 'arms race' where both groups sought to better refine their data sets and their analytical tools. In recent modeling, continental interior and polar temperature fields generated by the models and estimated from paleontological proxies such as leaf physiognomy – within the errors of both approaches – are comparable (SHELLITO et al. 2003). Remaining discrepancies have been attributed respectively to either persistent inaccuracies – hidden or unrecognized errors or imprecision – in the paleontological proxies, or to persistent bias in the computer models

towards the boundary conditions of the modern world. The latter is beyond the scope of this paper; however, the former will be addressed here.

Precision, accuracy, and error

According to the standard dictionary definitions, precision and accuracy have the same meaning (SOANES & STEVENSON 2004). However, in the physical sciences accuracy can mean, "... the extent to which a given measurement agrees with the standard value for that measurement", whereas precision in this same usage is defined as "the extent to which a given set of measurements of the same sample agree with their mean" (RANDOM HOUSE 2000). This concept is graphically illustrated in fig. 3. In this paper, the distinction between accuracy and precision presented in this latter definition is used. The concept of significant figures deals with precision only. However, the accuracy of a measuring device is unknown unless it has been calibrated against a ruler with known accuracy. Following the advice of ROTH and DILCHER (1978), the measuring 'device' in this discussion is the leaf physiognomic character of sedimentary assemblages of leaves (i.e., fossil assemblages), and the 'ruler' against which it must be calibrated is the climate of the vegetated site from where the leaves came.

The effect of sample size on the error

The correct measurement of the uncertainty or error of the estimate from a regression model is a matter of precision. WOLFE's (1971, 1978) initial use of leaf margin analysis gave estimates of MAT without stating an error value. The 'accuracy' of the estimate of MAT using LMA has been shown to be improved when fossil floras with ≥ 30 dicot species were used (WOLFE 1971, 1978, UPCHURCH & WOLFE 1987, WILF 1997). In his application of CLAMP, WOLFE (1990) initially gave a standard error for MAT of 0.6 °C. In later papers using CLAMP the standard error of the residuals about the regression line for MAT estimates vs. the observed value was stated to be between 1.3 ° and 1.7 °C (WOLFE 1993, SPICER et al. 2005). These later values appear to be measures of accuracy as they seem to be attempts at calibration using CLAMP, but as will be discussed below their analysis ignores significant components of uncertainty.

WING and GREENWOOD (1993, GREENWOOD & WING 1995) calculated the standard error of LMA estimates of MAT as ± 0.8 °C based on their re-analysis of WOLFE's (1978, 1979) east Asian leaf margin proportion and MAT data, but ± 2.0 °C for a multiple linear regression model based on the CLAMP data set. Their values of the error for MAT estimates are consistent with those given by WOLFE for CLAMP using correspondence analysis, and

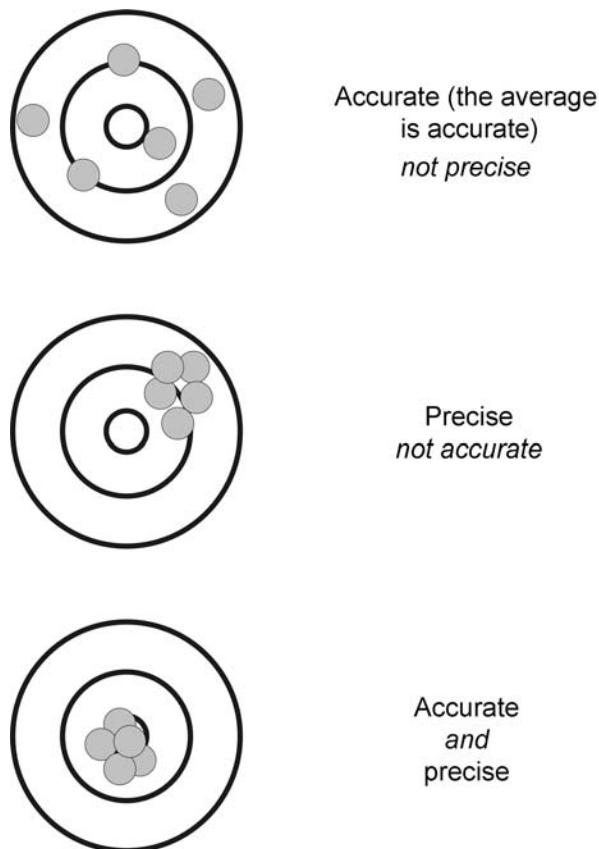


Fig. 3: Accuracy vs. precision. See text for explanation.

with other analyses (e.g., GREGORY & MCINTOSH 1996, WILF 1997). WILF (1997) considered the issue of error for LMA and calculated that by using standard errors alone and a simple rule about the minimum number of species scored, over-stated the degree of precision of the estimates. His introduction of the binomial sampling error for LMA estimates – where the larger of the two values of the sampling error and the standard error should apply to paleo-MAT estimates – provided a clearer measurement of the precision of an estimate as it incorporated the sample size used. Other factors play a significant role in the assessment of both accuracy and precision: for example, differences in LMP between local habitats contributing to leaf assemblages (i.e., how accurately is the climate reflected in the local canopy?); and sample size (i.e., how many species must be scored to precisely record the leaf physiognomic profile of the site?). BURNHAM et al. (2001, 2005) and KOWALSKI and DILCHER (2003) have rolled these factors into single studies, permitting coincident assessment of accuracy and precision.

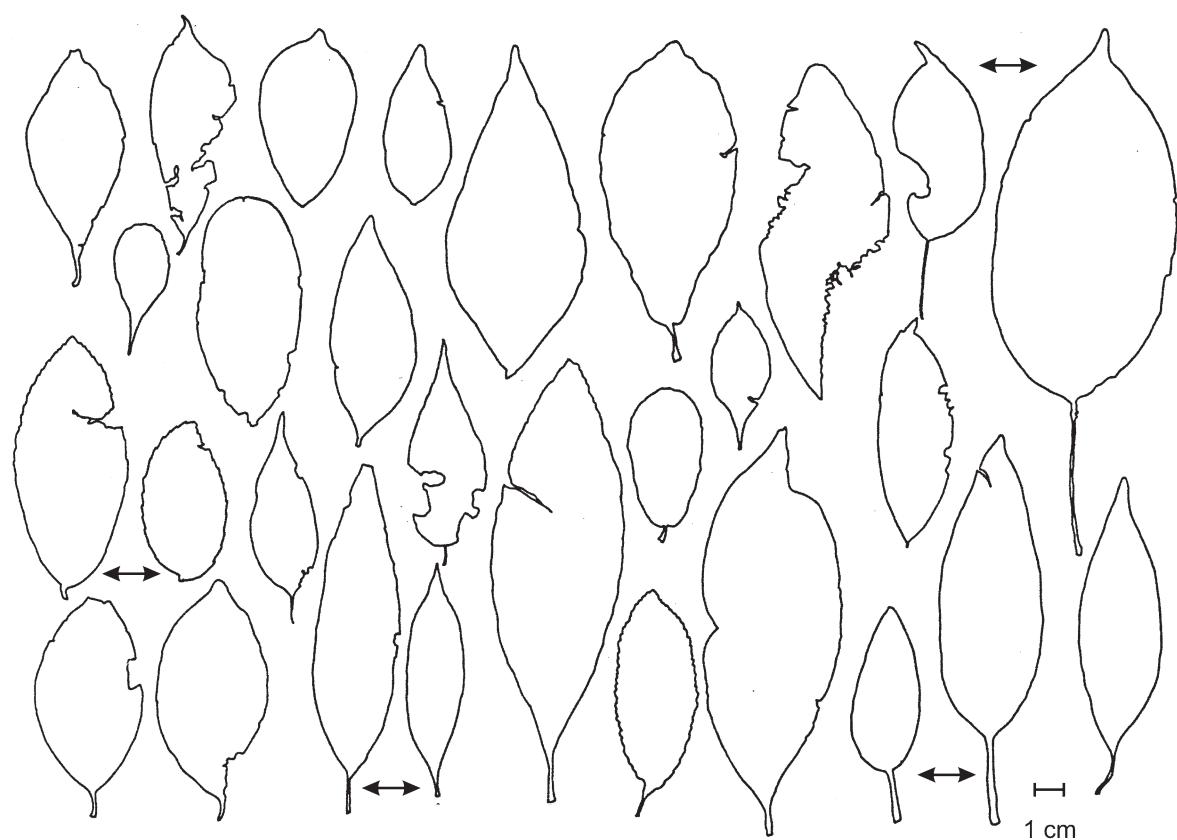
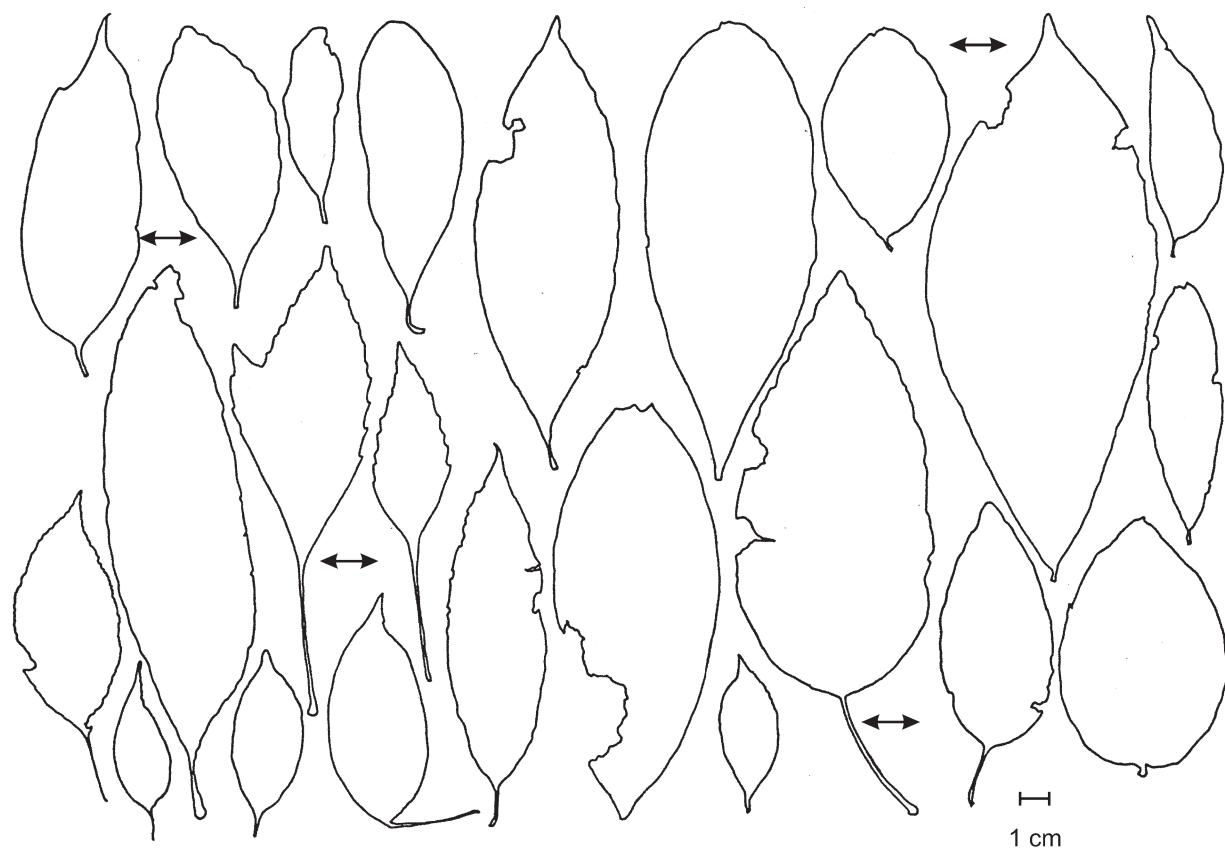
The recommended minimum number of species scored for leaf margin analysis represents a limitation in its application since many fossil leaf floras have fewer than 30 species of woody dicot (BURNHAM 1989, WILF 1997, BURNHAM et al. 2001, 2005). Based on an exploration of species-rich sites in the Neotropics (i.e., with 55 to >400 spp. per plot), BURNHAM et al. (2005) found that species richness does scale with the accuracy of reconstruction of MAT at a species richness of ≥ 25 , corroborating earlier recommendations (e.g., WOLFE 1993: 20–25), but they also recommended that an accuracy for MAT estimates greater than ± 3 °C was unreasonable.

Digital physiognomy

The accuracy of measuring leaf traits has attracted some attention, as WOLFE's (1993, 1995) CLAMP characters include a mixture of binary (e.g., toothed vs. non-toothed), multi-state (e.g., leaf size category), and qualitative characters (e.g., base and apex type). WILF (1997) argued that because leaf margin type (i.e. toothed vs. non-toothed) was unambiguous, it was less subject to observer error than other characters. But what is a tooth? Are leaves with suppressed teeth scored as toothed or non-toothed? At what point does a tooth become a ‘lobe’? WOLFE (1993, 1995) and others have argued that variation in the character of the tooth and the frequency of teeth along the margin contains climatically meaningful information. In order to remove perceived subjectivity in scoring leaf traits HUFF et al. (2003) proposed that leaf shape and teeth (shape, size and frequency) could be measured digitally, allowing greater precision in the measurement of leaf physiognomy (as continuous variables) and climate relationships in the modern world.

Later work (ROYER et al. 2005) demonstrated that colder sites will not only have more species with toothed margins, but that these species will also have more teeth, larger teeth, and more dissected leaf blades. The later study also offered a multiple regression model for MAT that was more accurate than leaf margin analysis. A fundamental limitation to this approach is the requirement for leaves with intact outlines, a condition poorly met in many fossil floras as fragmented leaves are typical in stream assemblages (fig. 4) and in the fossil record. ROYER et al. (2005) point out that leaf margin analysis produced greater errors (loss of accuracy) than their model where leaves were 50% intact. The greater loss of accuracy for LMA was due to leaves that had teeth only in the distal quarter or half that consequently were scored as non-toothed. An important point ROYER et al. (2005) make is that the incomplete pres-

Fig. 4: Silhouettes of the leaves from the Mt. Windsor stream-bed samples (GREENWOOD 1991, 1992, 2005a); upper panel is leaves from the upper beds (parautochthonous) and the lower panel is leaves from the lower beds (allochthonous). Some leaves are pairs, showing the largest and smallest leaf for that species (double-headed arrows); others are singlettons. Note the missing apices and interrupted margins on multiple specimens. Damage to lamina may represent pre-mortem insect damage (e.g., circular holes, healed marginal incisions), or mechanical damage during stream transport (e.g., tears and cracks, and broken apices). Chartaceous specimens required pressing prior to tracing.



ervation of leaves is probably a common and overlooked problem that can significantly affect the accuracy of paleo-temperature estimates, especially in low-diversity samples where some species are represented by a single specimen. The counter to this limitation, however, is their finding that only one leaf per species needs to be digitally measured for the continuous variables in their multiple regression model (ROYER et al. 2005).

Northern Hemisphere vs. the Southern Hemisphere?

The original calibration for leaf margin proportion and MAT from east Asian mesic vegetation showed a very precise correlation, i.e. the data points had a very good fit to a line (fig. 2), as evidenced by the very high r^2 value (WOLFE 1978, 1979, WING & GREENWOOD 1993). WOLFE also published a leaf margin proportion vs. MAT regression line – without data points – for the southern hemisphere, showing a different slope and intercept than for the east Asian calibration (UPCHURCH & WOLFE 1987). UPCHURCH and WOLFE (1987) argued that the ‘southern hemisphere curve’ was preferred over the East Asian calibration for late Cretaceous vegetation, owing to the prevalence of deciduous woody dicots in the extant northern hemisphere temperate vegetation, whereas extant southern hemisphere vegetation – like late Cretaceous vegetation – was predominantly broad-leaved evergreen forest. Subsequent to this *ad hoc* application of both a perception of difference between the northern and southern hemispheres today, and between predominantly deciduous and predominantly evergreen broadleaf forests, several studies have shown:

1. That predictive equations based on northern hemisphere vegetation are poor at predicting MAT for sites in tropical South America where $\text{MAT} \leq 21^\circ\text{C}$ (KOWALSKI 2002);
2. That there are differences between the Australian extant vegetation – a substantial part of the southern hemisphere – and that of the rest of the world (GREENWOOD et al. 2004), and;
3. That nonetheless (with the exception of New Zealand; STRANKS & ENGLAND 1997) the co-variation of LMP and MAT is an attribute of extant forests globally (fig. 2).

The data set that is the basis for the CLAMP method includes a wider range of geographical locales and climates than any other study. WING and GREENWOOD (1993), WILF (1997) and others found that the LMP scores at low MAT were substantially more scattered around the regression line than for sites at higher MAT (fig. 2). Many of these extant floras were from what WOLFE (1993, 1995) described as the ‘subalpine nest’; sites with leaf traits and climate correlations that were significantly different from sites at similar MAT, reflecting the unusual light (e.g., high UV) and other physical attributes at high altitudes.

Several studies have found that by excluding sites with a cold month mean $< -2^\circ\text{C}$ that much of the scatter disappeared and their multiple regression model statistics were improved (WING & GREENWOOD 1993, GREGORY & MCINTOSH 1996, WILF 1997). The reduced CLAMP data set for LMP vs. MAT (fig. 2) yields essentially the same regression line as all other regional datasets with the exception of tropical South America (KOWALSKI 2002), Australia and New Zealand (STRANKS & ENGLAND 1997), and converges on the Australian line at high MAT (GREENWOOD et al. 2004, GREENWOOD 2005b). Intriguingly, the Australian and tropical South American LMP vs. MAT calibrations are coincident with the ‘southern hemisphere curve’ regression line published without data points by UPCHURCH and WOLFE (1987). GREENWOOD et al. (2004) attributed the different slope and intercept of the Australian calibration to the lack of substantive evolutionary pressures in Australia over the Cenozoic or a extensive temperate source area to develop (or retain?) a substantial deciduous temperate broadleaf element in the extant flora. Their hypothesis mirrors WOLFE’s (1987b) idea that the catastrophic processes of the K-T event (i.e., the ‘impact winter’) had preferentially favored the survival of deciduous dicots in the northern hemisphere at the expense of mesothermal broadleaf evergreen dicots, whereas the southern hemisphere had largely escaped the impacts of the K-T extinction event.

Does the canopy reflect what is found in the fossil record?

Before the term was much in use in North American paleobotany, some paleobotanists asked whether the effects of taphonomic biases on leaf physiognomic analyses would so alter the pattern of leaf physiognomy preserved in a fossil assemblage that any climate signal was so degraded as to be not meaningful (see discussion in GREENWOOD 1991, 1992, 2005a). CHANEY (1924, CHANEY & SANBORN 1933) compared the leaf size character of Tertiary floras to that of forest floor leaf litter collections and noted the higher proportion of leaves over 10 cm in length in tropical forest litter than litter from temperate forests. MACGINITIE (1969) noted the presence of more than one community type in fossil floras, and expressed concern about leaf physiognomy as a paleoclimate proxy from such mixed floras. Canopy inventories of forest, river-bank, lake-shore sites and ‘wet-soil’ sites have now been shown to yield cooler estimates of MAT (due to more toothed species being present) than the forest interior (BURNHAM et al. 2001, KOWALSKI & DILCHER 2003). Experimental approaches – actualistic paleobotany or empirical taphonomic studies – in response to the concerns expressed by CHANEY (1924, CHANEY & SANBORN 1933) and MACGINITIE (1969) have largely focused on the selective transport and preservation of leaf taxa and/or key leaf traits (e.g., ROTH & DILCHER 1978, SPICER 1981,

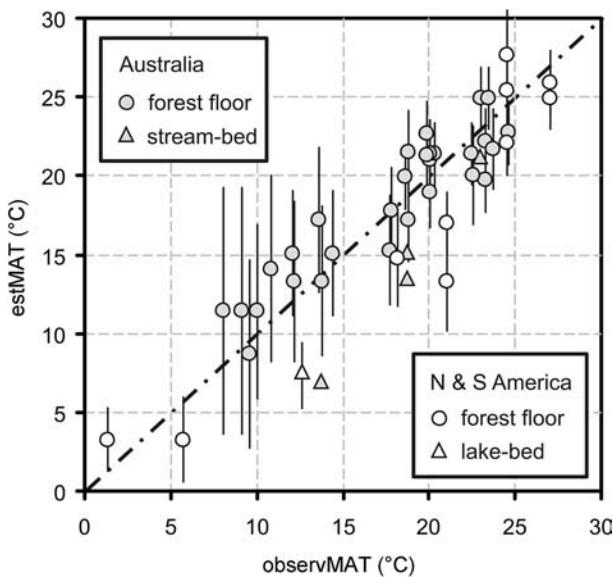


Fig. 5: Bivariate plot of estimated vs. observed MAT for litter samples from Australian, North American and South American forest-floor and stream- and lake-bed samples. Data sources (LMP and site MAT): Australian, GREENWOOD (2005a); North and South America, ROTH and DILCHER (1978), BURNHAM (1989) and GREENWOOD, JOHNSON and WING (unpublished). MAT estimated using LMA calibrated for Australia (GREENWOOD et al. 2004) for the Australian litter samples, and using WILF's (1997) CLAMP 3B LMA equation 'all sites' for the temperate North American sites (see tab. 1). The dashed angled line on the plot represents 1:1 correspondence between observMAT and estMAT.

GREENWOOD 1991, 1992, 2005a, WOLFE 1995, STEART et al. 2002, SPICER et al. 2005). For example, BURNHAM (1989) showed that litter samples from different floodplain sub-environments – channel, forebank, levee and back-levee – in Mexican paratropical forest reflected the site canopy leaf physiognomy, although the leaf size index of the channel samples was lower (i.e., smaller leaves were present) than that of the regional flora.

GREENWOOD (1991, 1992) and STEART et al. (2002) have shown that small leaves are preferentially transported down streams relative to much larger leaves, matching other studies including ROTH and DILCHER (1978) and SPICER (1981) who demonstrated that the small sun leaves of the upper forest canopy will preferentially be represented further from shore than the large shade leaves of lake-shore vegetation. Leaves in general travel laterally in forest settings little farther than the vertical height of the tree, and so forest floor litter largely reflects the floristic and foliar physiognomic character of the local canopy (FERGUSON 1985, SPICER 1989, BURNHAM et al. 1992, GREENWOOD 1992, STEART et al. 2006).

Using forest floor litter in Australian tropical and subtropical rainforests, GREENWOOD (1991, 1992) found that the leaf size index or LSI (sensu UPCHURCH & WOLFE

1987¹) from litter samples was consistently 2/3 lower than for the forest canopy and was further reduced in stream-transported deposits, the latter observation matching BURNHAM's (1989) findings. GREENWOOD's observations were consistent with ROTH and DILCHER's (1978) lake study (tab. 1), and SPICER's (1981) experimental work, and later substantiated experimentally by STEART et al. (2002). GREGORY (1994) applied GREENWOOD's (1991, 1992) observation of the preferential transport of smaller leaf classes within taxa by multiplying leaf area by 3/2 before determining the leaf size class for her multiple regression paleoclimate models. BURNHAM (1989, BURNHAM et al. 1992) had shown that the forest-floor litter reflected the taxonomic composition of the local forest quite faithfully, reflecting the local character of leaf-fall, and that the litter LMP in each of the subenvironments she sampled in her Mexican study was consistent with the local forest type. GREENWOOD (1992, 2005a) also demonstrated that the canopy floristics and LMP were accurately reflected in the forest-floor litter; LMA estimates of MAT based on a LMP scored from forest-floor litter samples were therefore within the error of the observed MAT for most species-rich sites (fig. 5).

The discussion above indicates that autochthonous (or perhaps, paraautochthonous) leaf deposits therefore reflect the foliar physiognomy of the canopy, although with a bias towards the smaller sun leaves. BURNHAM's work, and to a lesser extent that of GREENWOOD (1992) had also shown that particular synusiae, such as vines may be under-represented in forest floor samples, but over-represented in stream and lake samples due to their greater abundance in the forest-edge adjacent to water bodies. Scoring just vines, or just trees yields a LMP that returns an inaccurate MAT estimate; all woody dicot forest synusiae must be included in the inventory used to score LMP (BURNHAM et al. 2001, 2005). The forest-floor is an unusual site for fossilization, requiring an over-bank flood or volcanic ash-fall to bury the leaf litter in an autochthonous deposit. While forest-floor leaf fossil floras do occur (e.g., JOHNSON & ELLIS 2002), a more common site of deposition is in a lake-bed or in quiet water facies of streams (SPICER 1989, GREENWOOD 1991). Limited studies had shown that smaller canopy leaves were selectively over-represented in lake and stream deposits (ROTH & DILCHER 1978, SPICER 1981, GREENWOOD 1992). But the question remains, to what extent would taphonomic biases inherent in stream and lake-bed deposits affect paleoclimate estimates using leaf margin analysis or multivariate approaches such as CLAMP? That is, how are the accuracy and precision of the measurements and estimates affected? Two primary studies have considered this point, and additional data is presented here in support of these studies.

ROTH and DILCHER (1978) noted differences in the leaf physiognomy between lake bottom samples and the

¹ LSI = % microphylls + 2 x % notophylls + 3 x % mesophylls – 100 x 0.5

Table 1: Comparison of lake bottom leaf sample and hinterland forest canopy leaf physiognomy near Bloomington, Indiana. Data from ROTH & DILCHER (1978).

Sample	No. dicot spp.	LSI	LMP	MAT ^{1&2}
Forest canopy	27	12	26	9.6 ± 2.1 °C
Lake bottom	12	7.5	17	7.4 ± 2.6 °C

¹ Using MAT = 24.4*LMP + 3.25, and the binomial sampling error (from WILF, 1997 using CLAMP 3B). ² Bloomington, Indiana MAT = 12.6 °C.

forest canopy in Indiana (tab. 1). If MAT is calculated for their forest canopy and lake bed LMP values, both samples yield estimates that are cooler than the site MAT of 12.6 °C, and furthermore the lake bottom sample estimate is ~2 °C cooler than using the forest inventory, although both estimates overlap within the errors of their estimates (tab. 1 and fig. 5). The difference in LMP between the lake bottom sample and the forest canopy is within the range expected for a ‘wet site’ sample vs. a ‘dry site’ sample (KOWALSKI & DILCHER 2003), and so may represent different habitats being sampled; however, ROTH and DILCHER (1978) reported that the lake bottom sample contained a subset of the local forest, and lacked some riparian species including two vines. In contrast to the ROTH and DILCHER (1978) study, GREENWOOD (1992) demonstrated that stream-transported stream-bed samples from tropical rainforests showed an enrichment of species, but consistent with BURNHAM’s (1989) study, he found that LMP was largely unaffected. Both the ROTH and DILCHER (1978) and GREENWOOD (1992) studies found the selective loss of large leaves from within individual taxa. STEART et al. (2002) had shown that the loss of large leaves in streams is due in part to their entrapment by stream objects (logs, boulders), and mechanical damage leading to loss of intact lamina. In a later study, GREENWOOD (2005a) found that forest-floor litter yielded estimates (using LMA) of MAT that were consistent with the site MAT, but that stream-bed samples yielded lower MAT estimates than the site MAT (fig. 5). This effect was greater for temperate sites (i.e., sites where the canopy had low LMP) than for the tropical sites, and GREENWOOD (2005a) speculated that this ‘cool bias’ in stream-bed samples may reflect the ‘wet soil site’ bias shown in other studies (BURNHAM et al. 2001, 2005, KOWALSKI & DILCHER 2003) rather than the selective loss of entire leaf taxa or other taphonomic effects.

GREENWOOD’s (2005a) study was based on Australian mesic forest sites and streams, and the Australian LMP vs. MAT relationship has been shown to be different to that of northern hemisphere sites, including North America. In figure 5 are shown hitherto unpublished MAT estimates (estMAT) based on the LMP of forest-floor litter samples plotted against the actual site MAT (observMAT), for sites in North and South America, as well as the Australian data from GREENWOOD (2005a).

Sample methodology and analysis follow GREENWOOD (1992, 2005a), except for data points from BURNHAM (1989) and other published studies. As can be seen in the plot (fig. 5), the North and South American sites show a more mixed accuracy in estimated actual site MAT than do the Australian sites with a mild cool bias. The North and South American study shown here has far fewer sample points than the Australian study and the data are clumped, and so interpretation cannot be conclusive. Two of the sample points are informative though, on the issue of the so-called ‘wet site cool bias’ detected by KOWALSKI and DILCHER (2003) as they represent samples from one of the sites used in their study; ‘Dilcher’s Woods’ near Gainesville.

The litter samples from Dilcher’s Woods were collected by the author with David DILCHER, our spouses, and the DILCHERS’ dog in March 1993. Samples were collected at two points within the local site; a swamp site and a ridge site, in common with the KOWALSKI and DILCHER (2003) study. As can be seen in table 2, the estimates of MAT based on the litter samples using either the WING and GREENWOOD (1993) multiple linear regression equation or the LMA equation derived by KOWALSKI and DILCHER (2003) are cooler than both the site MAT and the estimate based on canopy samples. As would be predicted from BURNHAM et al. (2001) and KOWALSKI and DILCHER’s (2003) studies, the swamp site (i.e., the ‘wet soil’ site) yields a cooler estimate than the ridge site. Why a litter sample (ridge or swamp) should yield a cooler estimate than the canopy is unclear.

One possible answer to why the Dilcher’s Woods site yielded cool MAT estimates may lie in the primary difference between the Australian sites used in GREENWOOD (2005a) and the Florida site; the presence of both cool-season deciduous taxa (e.g., *Quercus* spp., *Corylus*) and broad-leaf evergreen taxa (e.g., *Gordonia*, *Persea*, *Magnolia*) in the canopy in the latter site. Deciduous leaves fall in a short space of time, typically a few days to weeks. The leaves of broad-leaf evergreens also often show a seasonal peak for leaf-fall (STEART et al. 2005), but spread over several weeks and the volume of leaves shed is markedly lower than that shown by deciduous trees. This difference in leaf phenology may result in a swamping of the forest-floor litter by the leaves of deciduous trees, such that the leaves of some broad-leaf evergreen taxa may be rendered ‘rare’ (e.g., BURNHAM et al. 1992) and missed in a count-limited methodology, such as was employed here (see GREENWOOD 1992). The leaves of some broad-leaf evergreen trees decay at a faster rate than chartaceous deciduous leaves (e.g., FERGUSON 1985, GREENWOOD 1992, STEART et al. 2002, 2005), and so may be quickly lost from the litter, especially where the soil remains wet. Rather than demonstrating a flaw in the analysis, differences in the transport potential and preservation of deciduous and broad-leaf evergreen leaves may draw attention to a potential bias; an over-representation of deciduous leaves (which tend to be toothed), at the

Table 2: Leaf physiognomy-based MAT estimates for Dilcher's Woods, Gainesville, Florida, USA. All data original to this report except where stated.

site	Actual ¹	LMA ¹	MLR ²	
Ridge	21 °	20.2 °	19.3°	canopy ³
		18.4 °	17.3°	litter
Swamp	21 °	18.6 °	17.3°	canopy ³

^{1 & 3} KOWALSKI & DILCHER (2003); ² Multiple linear regression from WING & GREENWOOD (1993).

expense of broad-leaf evergreen leaves (which tend to be entire margined). BURNHAM et al. (2005) have also shown that sample size in species-rich forests may affect MAT estimates, particularly where singletons represent families with mainly toothed margins (e.g., Sapindaceae).

In his early publications on CLAMP, WOLFE (1990, 1993) discussed taphonomic concerns anecdotally. In his 1995 paper he presented a small study – of the character advocated by ROTH and DILCHER (1978) – examining the accuracy of estimates of MAT and MAP for samples collected in stream-beds relative to sites based on canopy collections (WOLFE 1995). The MAT estimates for two of the ‘taphonomic samples’ were slightly cooler (Castle Creek & Santa Rita, 0.6 °C and 0.7 °C respectively) or slightly warmer (Payson, 0.2 °C) than the canopy sites. In each of these cases the differences were well within the error (however it is calculated) and so are insignificant. The precipitation estimates based on the taphonomic samples were also ‘slightly wetter’ (Payson & Santa Rita) or drier than the canopy sites (Castle Creek), but again these differences were not significant. The differences between the taphonomic and the canopy samples for precipitation were largely due to smaller leaf sizes being scored for some leaf taxa in the taphonomic samples relative to the canopy samples, consistent with prior studies (e.g., ROTH & DILCHER 1978, SPICER 1981, GREENWOOD 1992, 2005a).

SPICER et al. (2005) examined the impact on a CLAMP analysis of taphonomic processes on individual characters, such as the selective loss of large leaves and the tendency for some character states (e.g., drip tips) to be lost during transport due to mechanical damage. Their study was a simulation rather than an actualistic study as characters were scored as missing for taxa by computational removal. Those leaf traits most vulnerable to mechanical degradation are those at the leaf extremities, such as the apex, lobes, and certain forms of leaf base (see fig. 4). SPICER et al. (2005) found that the loss of any one of these features had little effect on CLAMP’s ability to estimate accurately any of the climate variables. They noted, however that the loss of margin characters significantly degraded the CLAMP estimates of temperature, which is a consequence of leaf margin proportion representing >80% of the variance for MAT (WING & GREENWOOD 1993, WILF 1997) and the auto-correlation

of CMMT, warm month mean temp. (WMMT) and MAT (SPICER et al. 2005). Their study is an artificial one – no leaves were harmed as no leaves were used. This study also appears to have confounded accuracy with precision. It would be interesting to repeat the exercise using actual taphonomic samples (e.g., WOLFE 1995) as it may be the case that the tendency for some taxa to decay quickly, or to have poor transport potential – factors discussed in the preceding text of this paper – may selectively control biases in character expression in actual leaf assemblages in different sedimentary facies (e.g., stream vs. lake or overbank deposits). Paradoxically, SPICER et al. (2005) discuss extensively the value of multivariate analyses versus univariate analyses (such as LMA), yet miss the potential for interactions between leaves and their environment during transport and preservation to be covariant, fickle and unpredictable.

Conclusions

The application of leaf physiognomy to the reconstruction of past climates – especially leaf margin analysis and its multivariate cousin, CLAMP – has revolutionized our understanding of Late Cretaceous and Cenozoic climates (fig. 1). Today’s climate modelers of past ‘hothouse earths’ – times in the geological past, such as the Eocene when global climates were substantially warmer than the present – rely on quantitative estimates from paleobotany and other disciplines to test their GCMs (e.g., SHELLITO et al. 2003). Quantitative analyses over short stratigraphic intervals are permitting assessment of the impacts of short-term climate change on vegetation (e.g., WILF 2000, WING et al. 2000, WILF et al. 2003). The roots of this revolution ultimately rest with BAILEY and SINNOTT (1915, 1916) and others (e.g., CHANEY 1924, CHANEY & SANBORN 1933, MACGINNIE 1969). However, it was the seminal works of Wolfe (1971, 1978, 1979) and DILCHER (1973, ROTH & DILCHER 1978, DOLPH & DILCHER 1979, 1980a, 1980b) that set us on this path. WOLFE (1971, 1978, 1979) in particular set the stage for quantitative analyses of temperature and other environmental variables placed in geochronostratigraphic context, and set against the emerging marine isotopic record (e.g., WOLFE & HOPKINS 1967, WOLFE & POORE 1982, WILF et al. 2003), through his determination of the east Asian leaf margin analysis calibration (fig. 2). It has been argued here that DOLPH and DILCHER’s papers on Indiana and Costa Rica helped spur on the development of a multivariate approach – CLAMP – that employed 31 leaf traits and multiple climate and atmospheric variables. ROTH and DILCHER’s (1978) recommendation that foliar physiognomic analysis take into account the taphonomic biases characteristic of different depositional environments and climates has only been adopted to a minor degree (e.g., BURNHAM 1989, GREENWOOD 1991, 1992, 2005a, WOLFE 1995).

Over the past 15–18 years there has been a renaissance in the application of leaf physiognomy to understanding Cretaceous and Cenozoic climate change (e.g., WING & GREENWOOD 1993, GREENWOOD & WING 1995, HERMAN & SPICER 1996, WILF 2000, WING et al. 2000, JACOBS 2002, KENNEDY et al. 2002, KENNEDY 2003, GREENWOOD et al. 2003a, 2003b, 2005, WILF et al. 2003, JACOBS & HERENDEEN 2004), primary investigations of leaf physiognomy and climate (e.g., KOVACH & SPICER 1995, STRANKS & ENGLAND 1997, WIEMANN et al. 1998 2001, WILF et al. 1998, JACOBS 1999, GREGORY-WODZICKI 2000, KOWALSKI 2002, GREENWOOD et al. 2004, ROYER et al. 2005, TRAISER et al. 2005), and the testing and refinement of its accuracy and precision – including taphonomic concerns (e.g., BURNHAM 1989, WILF 1997, BURNHAM et al. 2001, 2005, KOWALSKI & DILCHER 2003, GREENWOOD 1991, 1992, 2005a). None of these endeavors were perfect in their execution and application, and they continue to be refined and criticized. But where would we be without them? More than likely still using vegetation types as proxies for broadly defined climates.

Acknowledgements

Original research reported here was funded by grants from the Australian Research Council (ARC), the Smithsonian Institution and NSERC (Canada). My costs for attending the ‘Advances in paleobotany’ conference in Gainesville and writing the paper were provided by a NSERC Discovery Grant. I thank Robyn BURNHAM, David CHRISTOPHEL, David DILCHER, David FERGUSON, Bob SPICER, David STEART, Peter WILF, Scott WING and Jack WOLFE for their advice and fellowship during my explorations of leaf physiognomy and taphonomy, and also my students and other colleagues for sharing their enthusiasm and ideas. Robin SMITH and Jim BASINGER provided comments on a draft of the paper. I would also like to thank Steve MANCHESTER for suggesting I contribute this topic, and David JARZEN, David FERGUSON and an anonymous reviewer for their suggestions on how to improve the paper.

References

- BAILEY, I. W. & SINNOTT, E. W. (1915): A botanical index of Cretaceous and Tertiary climates. — *Science*, **41**: 831–834.
- BAILEY, I. W. & SINNOTT, E. W. (1916): The climatic distribution of certain kinds of angiosperm leaves. — *American Journal of Botany*, **3**: 24–39.
- BERGGREN, W. A., KENT, D. V., SWISHER III, C. C. & AUBRY, M.-P. (1995): A revised Cenozoic geochronology and chronostratigraphy. — In: BERGGREN, W. A., KENT, D. V., AUBRY, M.-P. & HARDENBOL, J. (Eds.): *Geochronology, Time Scales and Global Stratigraphic Correlation*, SEPM Special Publication, **54**: 129–202. Tulsa, Oklahoma (Society for Sedimentary Geology).
- BURNHAM, R. J. (1989): Relationships between standing vegetation and leaf litter in a paratropical forest: implications for palaeobotany. — *Review of Palaeobotany and Palynology*, **58**: 5–32.
- BURNHAM, R. J., ELLIS, B. & JOHNSON, K. R. (2005): Modern tropical forest taphonomy: does high biodiversity affect paleoclimatic interpretations? — *Palaeos*, **20**: 440–452.
- BURNHAM, R. J., WING, S. L. & PARKER, G. C. (1992): The reflection of deciduous forest communities in leaf litter: implications for autochthonous litter assemblages from the fossil record. — *Paleobiology*, **18**: 30–49.
- BURNHAM, R. J., PITMAN, N. C. A., JOHNSON, K. R. & WILF, P. (2001): Habitat-related error in estimating temperatures from leaf margins in a humid tropical forest. — *American Journal of Botany*, **88**: 1096–1102.
- CHANAY, R. W. (1924): Quantitative studies of the Bridge Creek flora. — *American Journal of Science* 5th series, **7**: 127–145.
- CHANAY, R. W. & SANBORN, E. I. (1933): The Goshen flora of west-central Oregon. — *Carnegie Institution of Washington Contributions to Paleontology*, **43**: 1–103.
- DILCHER, D. L. (1973): A Paleoclimatic Interpretation of the Eocene Floras of Southeastern North America. — In: GRAHAM, A. (Ed.): *Vegetation and Vegetational History of Northern Latin America*. — 39–59; Amsterdam (Elsevier Publ. Co.).
- DOLPH, G. (1979): Variation in leaf margin with respect to climate in Costa Rica. — *Bulletin of the Torrey Botanical Club*, **106**: 104–109.
- DOLPH, G. & DILCHER, D. L. (1979): Foliar physiognomy as an aid in determining paleoclimate. — *Palaeontographica, Abteilung B*, **170**: 151–172.
- DOLPH, G. E. & DILCHER, D. L. (1980a): Variation in leaf size with respect to climate in the Western Hemisphere. — *Bulletin of the Torrey Botanical Club*, **107**: 157–162.
- DOLPH, G. E. & DILCHER, D. L. (1980b): Variation on leaf size with respect to climate in Costa Rica. — *Biotropica*, **12**: 91–99.
- FERGUSON, D. K. (1985): The origin of leaf assemblages – new light on an old problem. — *Review of Palaeobotany and Palynology*, **46**: 117–188.
- GREENWOOD, D. R. (1991): The Taphonomy of Plant Macrofossils. — In: DONOVAN, S. K. (Ed.): *The Processes of Fossilization*. — 141–169; London (Belhaven Press).
- GREENWOOD, D. R. (1992): Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary palaeoclimates. — *Review of Palaeobotany and Palynology*, **71**: 142–196.
- GREENWOOD, D. R. (2005a): Leaf margin analysis: taphonomic constraints. — *Palaeos*, **20**: 499–506.
- GREENWOOD, D. R. (2005b): Leaf form and the reconstruction of past climates. — *New Phytologist*, **166**: 355–357.
- GREENWOOD, D. R. & WING, S. L. (1995): Eocene continental climates and latitudinal temperature gradients. — *Geology*, **23**: 1044–1048.
- GREENWOOD, D. R., CHRISTOPHEL, D. C. & SCARR, M. (2003 b): Leaf stomatal frequency in the Australian tropical rainforest tree, *Neolitsea dealbata* (Lauraceae) as a proxy measure of pCO_2 . — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **196**: 375–393.
- GREENWOOD, D. R., ARCHIBALD, S. B., MATHEWES, R. W. & MOSS, P. T. (2005): Fossil biotas from the Okanagan Highlands, southern British Columbia and northeastern Washington State: climates and ecosystems across an Eocene landscape. — *Canadian Journal of Earth Sciences*, **42**: 167–185.
- GREENWOOD, D. R., WILF, P., WING, S. L. & CHRISTOPHEL, D. C. (2004): Paleotemperature estimates using leaf margin analysis: Is Australia different? — *Palaeos*, **19**: 129–142.
- GREENWOOD, D. R., MOSS P. T., ROWETT, A. I., VADALA, A. J. & KEEFE, R. L. (2003a): Plant communities and climate change in southeastern Australia during the early Paleogene. — In: WING, S. L., GINGERICH, P. D., SCHMITZ, B. & THOMAS, E. (Eds.): *Causes and Consequences of Globally Warm Climates in the Early Paleogene*. Special Paper, **369**: 365–380; Boulder, Colorado (Geological Society of America).

- GREGORY, K. M. (1994): Palaeoclimate and palaeoelevation of the 35 Ma Florissant flora, Front Range, Colorado. — *Palaeoclimates*, **1**: 23–57.
- GREGORY, K. & CHASE, C. G. (1992): Tectonic significance of paleobotanically estimated climate and altitude of the late Eocene erosion surface, Colorado. — *Geology*, **20**: 581–585.
- GREGORY, K. M. & McINTOSH, W. C. (1996): Paleoclimate and paleoelevation of the Oligocene Pitch-Pinnacle flora, Sawatch Range, Colorado. — *Geological Society of America Bulletin*, **108**: 545–561.
- GREGORY-WODZICKI, K. M. (2000): Relationship between leaf morphology and climate, Bolivia: Implications for estimating paleoclimate from fossil floras. — *Paleobiology*, **26**: 668–688.
- HERMAN A. B. & SPICER, R. A. (1996): Palaeobotanical evidence for a warm Cretaceous Arctic Ocean. — *Nature*, **380**: 330–333.
- HERMAN, A. B. & SPICER, R. A. (1997): New quantitative paleoclimate data for the Late Cretaceous Arctic: Evidence for a warm polar ocean. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **128**: 227–251.
- HOLDRIDGE, L. R. (1967): Life zone ecology. — 1–206; San Jose, Costa Rica (Tropical Science Center).
- HUFF, P. M., WILF, P. & AZUMAH, E. J. (2003): Digital future for paleoclimate estimation from fossil leaves? Preliminary results. — *Palaios*, **18**: 266–274.
- JACOBS, B. F. (1999): Estimation of rainfall variables from leaf characters in tropical Africa. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **145**: 231–250.
- JACOBS, B. F. (2002): Estimation of low-latitude paleoclimates using fossil angiosperm leaves: Examples from the Miocene Tugen Hills, Kenya. — *Paleobiology*, **28**: 399–421.
- JACOBS, B. F. & DEINO, A. L. (1996): Test of climate–leaf physiognomy regression models, their application to two Miocene floras from Kenya, and 40Ar/39Ar dating of the Late Miocene Kaputu site. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **123**: 259–271.
- JACOBS, B. F. & HERENDEEN, P. S. (2004): Eocene dry climate and woodland vegetation in tropical Africa reconstructed from fossil leaves from northern Tanzania. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **213**: 115–123.
- JOHNSON, K. R. & ELLIS, B. (2002): A tropical rainforest in Colorado 1.4 million years after the Cretaceous-Tertiary Boundary. — *Science*, **296**: 2379–2383.
- KENNEDY, E. M. (2003): Late Cretaceous and Paleocene terrestrial climates of New Zealand: leaf fossil evidence from South Island assemblages. — *New Zealand Journal of Geology and Geophysics*, **46**(2): 295–306.
- KENNEDY, E. M., SPICER, R. A. & REES, P. M. (2002): Quantitative palaeoclimate estimates from Late Cretaceous and Paleocene leaf floras in the northwest of the South Island, New Zealand. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **184**(3–4): 321–345.
- KOVACH, W. L. & SPICER, R. A. (1995): Canonical Correspondence Analysis of leaf physiognomy: a contribution to the development of a new palaeoclimatological tool. — *Palaeoclimates*, **1**: 125–138.
- KOWALSKI, E. A. (2002): Mean annual temperature estimation based on leaf morphology: A test from tropical South America. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **188**: 141–165.
- KOWALSKI, E. A. & DILCHER, D. L. (2003): Warmer paleotemperatures for terrestrial ecosystems. — *Proceedings of the National Academy of Sciences*, **100**: 167–170.
- MACGINNIE, H. D. (1953): Fossil plants of the Florissant beds, Colorado. — Carnegie Institution of Washington Publication, **599**: 1–198.
- MACGINNIE, H. D. (1969): The Eocene Green River flora of northwestern Colorado and northeastern Utah. — University of California Publications in Geological Science, **83**: 1–140.
- PAGANI, M., ZACHOS, J. C., FREEMAN, K. H., TIPPLE, B. & BOHATY, S. (2005): Marked decline in atmospheric carbon dioxide concentrations during the Paleogene. — *Science*, **308**: 600–603.
- RANDOM HOUSE. (2000): Random House Webster College Dictionary. — 1–1600; New York, NY (Random House Reference).
- ROTH, J. L. & DILCHER, D. L. (1978): Some considerations in leaf size and leaf margin analysis of fossil leaves. — *Courier Forschungsinstitut Senckenberg*, **30**: 165–171.
- ROYER, D. L. (2001): Stomatal density and stomatal index as indicators of paleoatmospheric CO₂ concentration. *Review of Palaeontology and Palynology*, **114**: 1–28.
- ROYER, D. L., WILF, P., JANESKO, D. A., KOWALSKI, E. A. & DILCHER, D. L. (2005): Correlations of climate and plant ecology to leaf size and shape: potential proxies for the fossil record. — *American Journal of Botany*, **92**(7): 1141–1151.
- SEWALL, J. O., SLOAN, L. C., HUBER, M. & WING, S. L. (2000): Climate sensitivity to changes in land surface characteristics. — *Global and Planetary Change*, **26**: 445–465.
- SHELLITO, C. J., SLOAN, L. C. & HUBER, M. (2003): Climate model sensitivity to atmospheric CO₂ levels in the Early–Middle Paleogene. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **193**: 113–123.
- SLOAN, L. C. & BARRON, E. J. (1990): ‘Equable’ climates during Earth history? — *Geology*, **18**: 489–492.
- SLOAN, L. C. & BARRON, E. J. (1992): A comparison of Eocene climate model results to quantified paleoclimatic interpretations. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **93**: 183–202.
- SOANES, C. & STEVENSON, A. (2004): Concise Oxford English Dictionary. Eleventh Edition. — 1–1728; Oxford, UK (Oxford University Press).
- SPICER, R. A. (1981): The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berkshire, England. — United States Geological Survey Professional Paper, **1143**: 1–77.
- SPICER, R. A. (1989): The formation and interpretation of plant fossil assemblages. — *Advances in Botanical Research*, **16**: 95–191.
- SPICER, R. A., HERMAN, A. B. & KENNEDY, E. M. (2005): The sensitivity of CLAMP to taphonomic loss of foliar physiognomic characters. — *Palaios*, **20**(5): 429–438.
- STEART, D. C., BOON, P. I. & GREENWOOD, D. R. (2006): Overland transport of leaves in two forest types in southern Victoria, Australia and its implications for palaeobotanical studies. — *Proceedings of the Royal Society of Victoria*, **118**(1): 65–74.
- STEART, D. C., BOON, P. I., GREENWOOD, D. R. & DIAMOND, N. T. (2002): Transport of leaf litter in upland streams of *Eucalyptus* and *Nothofagus* forests in south-eastern Australia. — *Archiv für Hydrobiologie*, **156**: 43–61.
- STEART, D. C., GREENWOOD, D. R. & BOON, P. I. (2005): Paleoecological implications of differential biomass and litter production in canopy trees in Australian *Nothofagus* and *Eucalyptus* forests. — *Palaios*, **20**(5): 452–462.
- STRANKS, L. & ENGLAND, P. (1997): The use of a resemblance function in the measurement of climatic parameters from the physiognomy of woody dicotyledons. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **131**: 15–28.
- TRAISER, C., KLOTZ, S., UHL, D. & MOSBRUGGER, V. (2005): Environmental signals from leaves – A physiognomic analysis of European vegetation. — *New Phytologist*, **166**: 465–484.
- UPCHURCH, G. R. & WOLFE, J. A. (1987): Mid-Cretaceous to Early Tertiary vegetation and climate: Evidence from fossil leaves and woods. — In: FRIIS, E. M., CHALONER, W. G. & CRANE, P. R. (Eds.): *The Origins of Angiosperms and their Biological Consequences*. — 75–106; Cambridge (Cambridge University Press).
- UPCHURCH, G. R. & WOLFE, J. A. (1993): Cretaceous vegetation of the western interior and adjacent regions of North America. — In: CALDWELL, W. G. E. & KAUFMAN, E. G. (Eds.): *Evolution of the Western Interior Basin. Special Paper*, **39**: 243–281; Ottawa (Geological Association of Canada).
- WIEMANN, M. C., DILCHER, D. L. & MANCHESTER, S. R. (2001): Estimation of mean annual temperature from leaf and wood physiognomy. — *Forest Science*, **47**(2): 141–149.

- WIEMANN, M. C., MANCHESTER, S. R., DILCHER, D. L., HINOJOSA, L. F. & WHEELER, E. A. (1998): Estimation of temperature and precipitation from morphological characters of dicotyledonous leaves. — *American Journal of Botany*, **85**: 1796–1802.
- WILF, P. (1997): When are leaves good thermometers? A new case for Leaf Margin Analysis. — *Paleobiology*, **23**: 373–390.
- WILF, P. (2000): Late Paleocene–early Eocene climate changes in southwestern Wyoming: paleobotanical analysis. — *Geological Society of America Bulletin*, **112**(2): 292–307.
- WILF, P., JOHNSON, K. R. & HUBER, B. T. (2003): Correlated terrestrial and marine evidence for global climate changes before mass extinction at the Cretaceous–Paleogene boundary. — *Proceedings of the National Academy of Sciences*, **100**: 599–604.
- WILF, P., WING, S. L., GREENWOOD, D. R. & GREENWOOD, C. L. (1998): Using fossil leaves as paleoprecipitation indicators. An Eocene example. — *Geology*, **26**: 203–206.
- WING, S. L. & GREENWOOD, D. R. (1993): Fossils and fossil climates: the case for equable Eocene continental interiors. — *Philosophical Transactions of the Royal Society, London series B*, **341**: 243–252.
- WING, S. L., BAO, H. & KOCH, P. L. (2000): An early Eocene cool period? Evidence for continental cooling during the warmest part of the Cenozoic: — In: HUBER, B. T., MACCLEOD, K. & WING, S. L. (Eds.): *Warm Climates in Earth History*. — 197–237; Cambridge (Cambridge University Press).
- WOLFE, J. A. (1971): Tertiary climatic fluctuations and methods of analysis of Tertiary floras. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **9**: 27–57.
- WOLFE, J. A. (1978): A paleobotanical interpretation of Tertiary climates in the Northern Hemisphere. — *American Science*, **66**: 694–703.
- WOLFE, J. A. (1979): Temperature parameters of Humid to Mesic Forests of Eastern Asia and relation to forests of other regions of the Northern Hemisphere and Australasia. — *United States Geological Survey Professional Paper*, **1106**: 1–37.
- WOLFE, J. A. (1987a): An overview of the origins of the modern vegetation and flora of the Northern Rocky Mountains. — *Annals of the Missouri Botanical Garden*, **74**(4): 785–803.
- WOLFE, J. A. (1987b): Late Cretaceous-Cenozoic history of deciduousness and the terminal Cretaceous event. — *Paleobiology*, **13**(2): 215–226.
- WOLFE, J. A. (1990): Palaeobotanical evidence for a marked temperature increase following the Cretaceous/Tertiary boundary. — *Nature*, **343**: 153–156.
- WOLFE, J. A. (1993): A method of obtaining climatic parameters from leaf assemblages. — *U.S. Geological Survey Bulletin*, **2040**: 1–73.
- WOLFE, J. A. (1994): An analysis of Neogene climates in Beringia. — *Palaeogeography, Palaeoclimatology, Palaeoecology*, **108**: 207–216.
- WOLFE, J. A. (1995): Paleoclimatic estimates from Tertiary leaf assemblages. — *Annual Review of Earth and Planetary Sciences*, **23**: 119–142.
- WOLFE, J. A. (2001): Response By Jack A. Wolfe. For The Paleontological Society Medal, October 2000. — *Journal of Paleontology*, **75**: 920–921.
- WOLFE, J. A. & HOPKINS, D. M. (1967): Climatic changes recorded by Tertiary land floras in northwestern North America. — In: KOTORAWA HATAI (Ed.): *Tertiary Correlations and Climatic Changes in the Pacific*. — 67–76; Sendai, Japan (Sasaki Printing and Publishing Co. Ltd.).
- WOLFE, J. A. & POORE, R. Z. (1982): Tertiary marine and non-marine climatic trends. — In: BERGER, W. H. & CROWELL, J. C. (Eds.): *Climate in Earth History*. — 154–158; Washington, DC (National Academy of Sciences).
- WOLFE, J. A., SCHORN, H. E., FOREST, C. E. & MOLNAR, P. (1997): Paleobotanical evidence for high altitudes in Nevada during the Miocene. — *Science*, **276**: 1672–1675.
- ZACHOS, J. C., PAGANI, M., SLOAN, L., THOMAS, E. & BILLUPS, K. (2001): Trends, rhythms, and aberrations in global climate 65 Ma to present. — *Science*, **292**: 686–693.

Manuscript submitted 2006–08–12
Manuscript accepted 2007–02–21