Frontiers in Palaeobotany: Plant fossils and their role in predicting future climate change

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ABSTRACT

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Palaeobotany has a long history of providing insights into past climates. As the issue of climate change becomes of global concern it is essential that the predictive capabilities of numerical climate models become more precise, accurate and robust with regard to how fundamental aspects of the Earth system might react to future atmospheric compositions, vegetation and ocean dynamics. The only way of testing model capabilities for conditions that depart from those of the present is to retrodict the past, particularly for times when greenhouse gas loadings were as they are now, and as they are likely to be over the next few centuries. This means successfully modelling pre-Quaternary climates. For model validation over land surfaces the most useful proxies in terms of quantification of a range of climate variables are fossil plants. The characteristics of palaeobotanical climate proxies for "deep time" are reviewed and examined. Both nearest living relative and physiognomic techniques are then applied to the Vilui Basin, Russia which represents an ancient (Late Cretaceous) continental interior where models display an inability to replicate conditions revealed by the proxies, and exhibit an inherent conservatism that is likely to underestimate the degree of future change experienced by such regions.

Key-words—Palaeobotanical climate proxies, NLR, Plant physiognomy, Climate modelling, Continental interiors, Climate model uncertainty.

पुरावनस्पतिविज्ञान में सीमाएं : पादप जीवाश्म तथा भविष्य के जलवायु परिवर्तन पूर्वानुमान में इनकी भूमिका

राबर्ट ए. स्पाइसर

सारांश

पुरावनस्पतिविज्ञान में विगत जलवायुओं में अंतर्दृष्टि प्रदान करने का लंबा इतिहास है। जैसे ही जलवायु परिवर्तन का वैश्विक सरोकार हो जाता है यह जरूरी है कि पृथ्वी तंत्र के मूलभूत पहलू भविष्य के वातावरणीय संघटनों, वनस्पति व महासागर गतिविज्ञान कैसे प्रतिक्रिया कर सकती है का सम्यक ध्यान रखते हुए सांख्यिकीय जलवायु मॉडल ज्यादा सुस्पष्ट, शुद्ध एवं संतुलित हो जाते हैं। स्थितियों के लिए मॉडल क्षमताओं को परीक्षित करने का एक ही तरीका है कि विगत के पश्चानुमान से वर्तमान का पता चलता है विशेषतः उस समय जब पौधाधर गैस भार इतना था जितना कि अब है तथा आगामी कुछ शताब्दियों में इसके बढ़ने की उम्मीद है। इसका तात्पर्य है सफलतापूर्वक चतुर्थमहाकल्प-पूर्व जलवायु प्रतिरुपण। स्थल पृष्ठीयों पर प्रतिरूप प्रमाणिकता हेतु जलवायु की श्रेणी में परिवर्तन के संदर्भ में सर्वाधिक उपयोगी प्रतिपत्र अंदाजे में जीवाश्म पेड़-पौधे हैं। 'गहन समय' हेतु पुरावनस्पतिक जलवायु के लक्षण पुनरीक्षित एवं परीक्षित किए गए हैं। दोनों नजदीकी जीवित सापेक्ष एवं रूपात्मक तकनीकें जो उस समय विलुई द्रोणी, रूस में अनुप्रयुक्त की गईं थीं जो प्राचीन (अंतिम चाकमय) अंतः महाद्वीपीय रूपायित करती हैं जबकि प्रतिपत्रियों द्वारा उजागर दोहराई गई स्थितियां असमर्थता दर्शाती हैं तथा अंतर्निहित रूढ़िवाद प्रदर्श करते हैं जो कि ऐसे प्रदेशों द्वारा अनुभव किए गए भविष्य परिवर्तन की मात्रा का अल्पानुमान हो सकता है।

मुख्य शब्द – पुरावानस्पतिक जलवायु प्रतिपत्रियाँ, एन.एल.आर., पादप रूपात्मकविज्ञान, जलवायु प्रतिरुपण, अंतःमहाद्वीपीय, जलवायु अनिश्चितता।

Changing Scenario in Palaeobotany
and Allied Subjects
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INTRODUCTION

WHILE at Cambridge in 1892 Albert Charles Seward submitted an essay for the Sedgewick Prize entitled "Fossil Plants as Tests of Climate". This of course was at a time long before the reality of current global climate warming had become a concern and global mean surface temperatures (GMSTs) were 0.2 °C ± 0.1 °C below the 1951-1980 mean (GISS/ NASA, 2005) (Fig. 1). However, the anthropogenic causes and processes underlying the present warming were already embedded in the Earth system and, apart from a brief interval around 1910, the GMST has been higher ever since.

Palaeobotanists are a group of scientists who have known, perhaps longer than any other, that the climate of the Earth is never constant. The earliest recorded instance of fossil plants being used to determine past climate is that of Shen Kuo who in 1086 used what he thought was fossil bamboo to speculate on the ancient climate of China (Deng, 1976).

Unfortunately Shen Kuo misidentified the specimen, it was a fossil sphenophyte, but the principle of using plant fossils as palaeoclimatic indicators has been shown subsequently to be sound. Seward's essay and numerous palaeobotanical papers subsequent to it have sought to improve and quantify palaeobotanical tools for charting the patterns of climate change throughout the time that green plants have occupied the land.

From Shen Kuo's first faltering steps palaeobotanists have been at the forefront of charting climate change, exploiting the fact that plants are spatially fixed entities that process the atmosphere, and therefore have to possess adaptations to their local environment that allow them to function efficiently and out-compete other plants. Competition between individuals, coupled with selection, ensures that plant form reflects the climate and edaphic conditions in which they grow. This reflection occurs either at the level of individual plant parts (e.g. leaves and wood) or as characteristics that morphologically define species. This encoding of climatic information in plant form ensures that plant fossils provide an invaluable means of determining not only the patterns and rates of past climate change and vegetation responses to it but, coupled with modelling techniques, also inform future climate change.

Climate change is a natural part of Earth system processes. This is demonstrable from the geological record and what we know about variations in the Earth's orbit and changes in solar energy flux over time. What is different now is that the present change is recognised by almost all climate scientists, and many political leaders, as being uniquely attributable to the activities of a single species – *Homo sapiens* (IPCC 4th Assessment, 2007). Moreover, the primary cause of that change, a sustained rise in greenhouse gases in the atmosphere over the last 300 years, is unprecedented in Earth history as far as we can tell. In pre-industrial times at around 1750 the atmospheric level of CO_2 was 280 ppmv. Now it is 380 ppmv. Taken together with other greenhouse gases recognised by the Kyoto Protocol (CO_2, methane, nitrous oxide, PFCs, HFCs and SF6) the greenhouse gas CO_2 equivalent is 430 ppmv. This is rising at a rate of 2.3 ppmv per year (Stern, 2007) and we
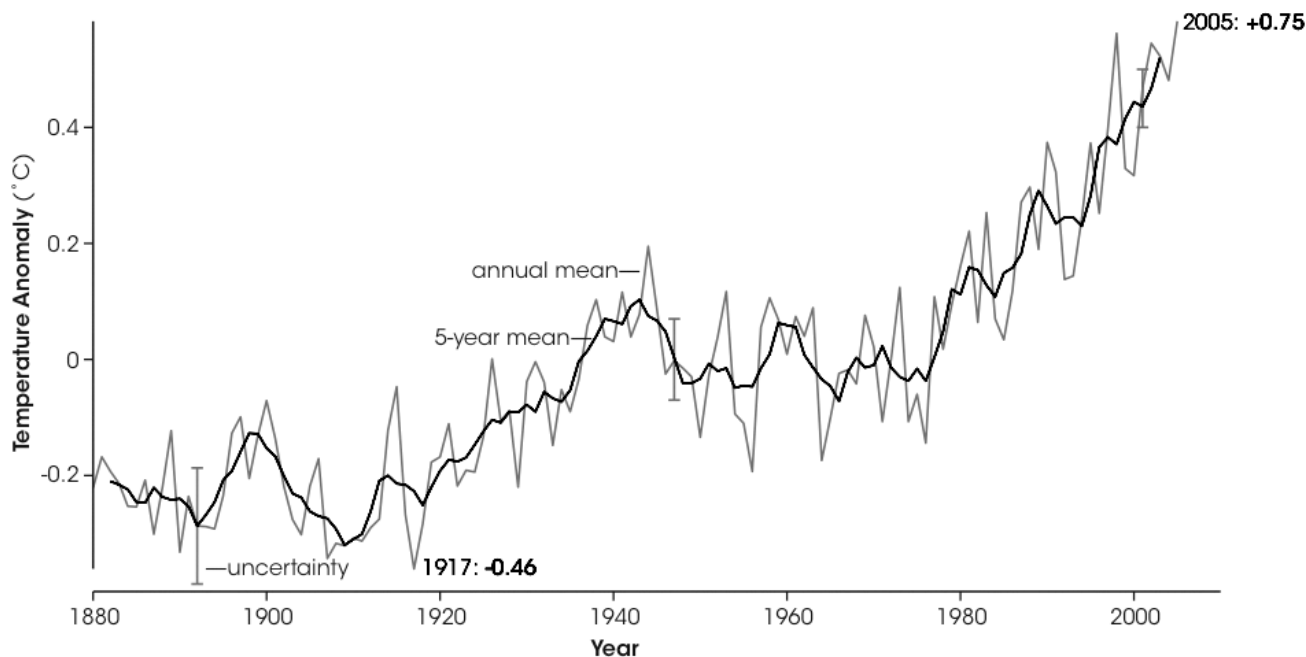

Fig. 1—Summary global mean surface temperature observations between 1880 and 2005 relative to the 1951-1980 mean. Error bars are estimated 2σ (95% confidence) uncertainty (GISS/NASA, 2005).

will soon have atmospheric greenhouse gas loadings higher than anything seen in the last million years. We are heading for an environment more similar to that of the Mesozoic than the Quaternary. Never before has palaeobotany's unique insight into quantifying past greenhouse climates over land surfaces, and illuminating the workings of the carbon cycle on short and long timescales, been so relevant to society.

PLANT FOSSIL CLIMATE PROXIES

Scepticism regarding the validity of global compilations of direct observations and proxy data to obtain the GMST, in particular that comprising what has become known as the "hockey stick" graph (Mann *et al.,* 1998), led the US Congress to commission a report from the National Research Council to examine the uncertainties inherent in such compilations for the last 2000 years. The committee reported in 2006 (National Research Council, 2006) and concluded that while overall it agreed with the findings and use of proxies (tree rings, corals, ocean and lake sediments, cave deposits, ice cores, boreholes, glaciers, and documentary evidence) back to around 900 AD, it also stated "very little confidence can be assigned to statements concerning the hemispheric mean or global mean surface temperature prior to about A.D. 900 because of sparse data coverage and because the uncertainties associated with proxy data and the methods used to analyze and combine them are larger than during more recent time periods." However, it went on to state "…the committee finds that efforts to reconstruct temperature histories for broad geographic regions using multiproxy methods are an important contribution to climate research and that these large-scale surface temperature reconstructions contain meaningful climatic signals." As atmospheric concentrations of greenhouse gases rise to those last seen further and further back in time, the relevance of data more recent than 1 Ka becomes more and more limited. In fact rising greenhouse gas concentrations now demand that proxies applicable to "deep time" (> 1Ma), being more relevant than ever, are made more precise, accurate and robust. The study of palaeobotany has demonstrated that plant fossils are key proxies for past climate over land and therefore, because of the importance of climate change to us all, has a relevance to society never before seen in the history of the subject.

Plant palaeoclimate proxies may be divided into two types:

1. Those based on environmental tolerances of assumed living relatives (nearest living relative approach, and

2. Those that are based on aspects of plant architecture constrained by environmental conditions (physiognomic approaches).

Each has specific advantages and disadvantages that will now be reviewed in turn.

Nearest Living Relative Techniques

Nearest living relative techniques (NLR) have had the longest use in palaeobotany and the principle is the same as

that employed by Shen Kuo (Deng, 1976). Unfortunately this early application of the method fell foul of the technique's greatest source of potential error, i.e. misidentification, in that it identified the extinct sphenophyte *Neocalamites* to bamboo. NLR techniques can be applied to all plant organs assignable to modern taxa (including non-angiosperms), but are most useful for those plant organs lacking known morphological adaptations to the physical environment (e.g. seeds and pollen). Of these pollen is by far the most abundant and widespread and so is particularly useful as a palaeoclimate proxy. However, all NLR techniques are restricted to timescales where evolutionary change at the species level is unlikely. In most cases this means <1-5Ma.

The underlying assumption of NLR techniques that there has been little change in environmental tolerance within a lineage over time, is hardly likely to be true for older material. Errors due to evolutionary change may be minimized, however, by using large numbers of taxa. In these cases those taxa that exhibit environmental tolerances seemingly inconsistent with those of the majority may be excluded. Where there is consistency and the environmental tolerances show the greatest overlap, there is likely to be most confidence in the environmental relationship. This is the basis of Co-existence Analysis (CoA) of Mosbrugger and Utescher, (1997), the European Leaf Physiognomic Approach (ELPA) (Traiser, 2004; Traiser *et al.,* 2005) and Overlapping Distribution Analysis (ODA) (Yang *et al.,* 2007). All NLR techniques rely on correct identification of the nearest living relative, ideally to the species level, and for calibration it is assumed that the nearest living relative occupies the entire geographic area over which the climate to which it is adapted is experienced. This complete range occupancy may not, of course, occur leading to potential errors in palaeoclimate determination. The exact point in time where NLR methodology becomes inappropriate is difficult to define and will be dependant on biogeographic history. This lack of certainty over when NLR techniques become unreliable, and the undoubted increasingly large (but unquantifiable) errors further back in time the NLR is applied, presents problems.

Physiognomic Techniques

The temporal limits on the applicability of NLR techniques do not exist with physiognomic techniques. Climatic signals are encoded in plant architecture as a developmental and growth response to the environment, honed by selection favouring a maximization of functional efficiency. No single architectural feature of a leaf, or whole plant, determines adaptive success (Lande & Arnold, 1983), no single feature can be expected to correlate with a single climatic variable, and numerous interacting traits influence fitness (Ackerly *et al.,* 2000). Because physiognomic adaptations are grounded in the time-stable physical laws governing, for example, fluid flow in vascular systems, diffusion processes through stomata, radiation absorbtion and emission from leaves, boundary layer

processes over plant surfaces and structural mechanics, they remain uniform through time. The degree to which individual plant organs reflect climate does depend on biogeographic history of the lineage to which they belong, but as with CoA and ODA the most reliable results are obtained by examining the physiognomy of *populations* of plant fossils.

Physiognomic environmental adaptation is achieved within the context of the capabilities imparted by the genome and is the product of long-term natural selection. Non-adapted physiognomies fail to survive and over time there is a degree of convergence largely independent of taxonomy. Of course in reality environmental conditions are always in a state of flux, as is inter-plant competition. Adaptation is a dynamic process. Because of this, congruence between any aspect of physiognomy and an inherently dynamic environment can never be perfect. However, uncertainties are minimized by examining signals across a number of plant characteristics within populations of taxa.

Wood anatomy—Wood in trunks and branches serves two primary functions; fluid conduction and mechanical support. Unsurprisingly, these functions are reflected in wood structure with spring (early) wood cells having large cross sectional area and thin walls that facilitate fluid conductance during leaf expansion and spring growth, but offer limited mechanical strength. By way of contrast, autumnal (late) wood cells have small cross sectional areas produced when demand for fluids conduction is low, but thickened cell walls provide strength. Variations in such cell characteristics as a tree grows provide an almost daily record of conditions throughout the period of growth and are the basis of tree ring studies. Strongly developed rings mark the degree of seasonality, but so called false rings formed within the growing season record temporary variations in growth conditions. For deep time studies these are difficult to calibrate in terms of a single climate parameter, such as temperature, because cell growth is a response to a number of environmental variables including drought, waterlogging of the root system, temperatures outside the optimum for that species and even insect attack (e.g. Fritts, 1976).

Stomatal analysis—Stomatal index (SI; the number of stomata divided by the sum of the numbers of stomatal and epidermal cells) and stomatal density (SD; the number of stomata per unit leaf area) are often used as proxy indicators of past atmospheric CO_2 concentrations (e.g. Woodward, 1987; Van Der Burgh *et al.,* 1993; Royer, 2001). However, environmental factors other than CO_2 such as irradiance and wind stress (Whitehead, 1965; Whitehead & Luti, 1962) are known to affect stomatal number, size and distribution. The observed SI and SD will depend upon several environmental constraints each related to stomatal function – the concentrations of CO_2 in the atmosphere, the diffusion gradient

through the stoma of CO_2 and water vapour as a function of stomatal architecture, wind speed and photosynthetic activity, and the genome. Stomatal characteristics are highly species dependant (Garbutt *et al.,* 1990), a fact recognized when using stomatal characteristics in palaeoaltimetry (McElwain, 2004), and some taxa are not CO_2 sensitive at all (Reid *et al.,* 2003; Raven & Ramsden, 1989). This strong variation between species in terms of reliably reflecting atmospheric CO_2 concentrations raises serious concerns as to appropriate calibrations for deep timed studies using extinct taxa. Those plants that do demonstrate an inverse relationship between pCO_2 and SD or SI (mostly woody C_3 taxa) do so in the context of other atmospheric properties that may or may not be related to CO_2 concentrations. These properties include diffusion gradients as a function of photosynthetic activity (which in turn is temperature dependant) and, in the case of plants at high altitudes, changes in atmospheric pressure (Gale, 1972a, b; Smith & Geller, 1979; Smith & Knapp, 1990; Terashima *et al.,* 1995; Johnson *et al.,* 2005). As with wood, stomatal characteristics cannot be related to a single environmental parameter such as pCO_2, but represent a compromise solution to maximising efficiency in the face of often-antithetic constraints. The strong species dependency of stomatal response to pCO_2 imposes limits on the applicability of the technique to deep time studies, although this has not prevented some useful work being carried out using long lived taxa such as *Ginkgo* (Beerling & Royer, 2002; Retallack, 2001) and even by the use of so called "nearest living equivalents" (McElwain, 1998) – plants that have no genetic relationship but only have architectural similarity.

Foliar physiognomic techniques—There are two foliar physiognomic techniques in common usage. The first of these is simple Leaf Margin Analysis (LMA) first introduced by Bailey and Sinnott (1915; 1916) and more recently revisited by Wolfe (1979), Wing and Greenwood (1993) and Wilf (1997). LMA relies on the correlation that exists between the proportion of toothed versus non-toothed (entire) woody dicot leaves in a given patch of stable (non-pioneer) vegetation and the mean annual temperature (MAT). In humid to mesic vegetation the relationship is essentially a straight line, the slope and intercept of which differs between the northern and southern hemispheres.

MAT errors can be calculated by Wilf's (1997) sample error equation:

where $c = 30.6$ and is the slope of the MAT vs. leaf margin regression, r is the total species number, and p $(0<p<1)$ is the fraction of r species that have entire margins (Wilf, 1997). In sub-humid and arid environments the relationship is complicated by small leaf size leading to tooth loss and margin adaptations to deter browsing. In sub-humid and arid settings

LMA is unreliable but other aspects of leaf physiognomy can indicate palaeoprecipitation (Wilf *et al.,* 1998, 1999)

The relationship between margin form and temperature has no simple explanation. It is likely to relate to the generation of turbulence and thinning of the boundary layer, gas exchange, water relations, transpiration and photosynthesis, particularly early in the growing season (e.g. Mauseth, 1988; Schuepp, 1993; Royer & Wilf, 2006). More than one factor is likely to influence the adaptive morphology of any leaf architectural characteristic (Spicer *et al.,* 2005), so correlating margin form with just MAT is over simplistic. However, the advantage of LMA is that it is straight forward to compute. The disadvantage is that it only returns one climate variable: the mean annual temperature (MAT). More advanced multivariate physiognomic analyses return far more information on past climate.

CLAMP—An evolutionary development of LMA introduced by Wolfe (1993) is the so-called Climate-Leaf Analysis Multivariate Program (CLAMP). As its name suggests CLAMP extends LMA beyond its underlying simplistic assumption that a single leaf character (in this case the geometry of the leaf margin) is correlated with a single climate variable (the MAT). CLAMP is the most comprehensive foliar physiognomic technique currently available, and with the present calibration datasets (PHYSG3AR and PHYSG3BR) it is capable of yielding values for up to thirteen palaeoclimate variables, although eleven are most commonly returned (see the CLAMP website cited in the references for details).

Inevitably the multivariate nature of the technique means that the computational simplicity of univariate methods such as LMA is lost, but this cost is more than outweighed by the precision obtained across an array of temperature related parameters. Moreover, the use of a multiplicity of leaf characters ordinated in the context of a multiplicity of climate parameters, more properly reflects the complex interplay between both foliar characters and climate parameters and the nexus of correlations that exist between them all. For example the distribution of leaf characters in multidimensional space can be directly mapped on to the distribution of calibration sites and climate vectors, and the degree to which vectors are co-aligned reflects the degree of correlation between climate parameters as recorded by foliar physiognomy. These parameters include the length of the growing season and enthalpy (a property of the atmosphere useful in determining palaeoaltitudes; Forest *et al.,* 1995; Wolfe *et al.,* 1998; Spicer *et al.,* 2003). The CLAMP technique is founded on the assumption that physiognomy is determined by the physical laws related to fluid flow, diffusion, and irradiance/heat balance, and that consequently constraints over plant architecture are largely invariant over time. Like LMA, CLAMP is only calibrated for woody dicots. For any given situation there will

be an optimum leaf architecture that satisfies the prevailing constructional and environmental constraints whilst returning maximum efficiency, particularly with respect to photosynthetic productivity.

In CLAMP, 31 foliar physiognomic character states are used including aspects of lobing, margin geometry, apex and base shape, lamina size and shape. At each modern vegetation stand used to calibrate CLAMP the full morphological range of leaves of at least 20 taxa of woody dicots, including shrubs and lianas, are numerically scored for the 31 character states using defined protocols. This data array is analysed together with a similar one composed of climate parameters observed at each calibration stand site. Where possible thirty-year (or greater) climate averages are used recorded within 1 km of, and at the same altitude as, the stand site. Typically eleven climate variables (MAT; warm month mean temperature, WMMT; cold month mean temperature, CMMT; length of the growing season, LGS; mean growing season precipitation, MGSP; mean monthly growing season precipitation, MMGSP; precipitation during the three wettest months, 3-WET; precipitation during the three driest months, 3-DRY; specific humidity, SH; relative humidity, RH; and Enthalpy) are correlated with the foliar physiognomic data. This is done using canonical correspondence analysis (ter Braak, 1986) in the form of CANOCO v. 4 (see the CLAMP website for details). This particular multivariate statistical engine is used because it is robust to incomplete data (important when dealing with fossil material where some character states may be missing), makes no assumptions about the Gaussian distribution of variables, and does not assume that the variables, either foliar or climatic, are independent of one another (which they obviously are not).

Fossil leaves are scored for the same 31 foliar character states as for those living leaf forms making up the calibration data sets. Like the modern leaves the full morphological range of foliar form within a morphotype (fossil species) should be scored. The fossil data, lacking any accompanying climate data, are introduced into the analysis and behave as passive samples, i.e. their inclusion does not change the structure of the multidimensional physiognomic space defined by the modern calibration samples. The relationship between modern leaf physiognomy and modern climate data determines the positions of vectors (one for each climate variable) running through physiognomic space. These vectors are calibrated from the observed climate.

The position of the fossil assemblage in physiognomic space is determined only by the aggregate score of its foliar characteristics and, when projected normally on to the calibrated vector, yields the palaeoclimate prediction. In practice 2nd order polynomial regressions are plotted between the climate vector score (as defined by co-ordinates in the first (greatest) four axes of variation), and the matching observed climate variable. The standard deviation of the

residuals about this line is used as a measure of the uncertainty of the climate estimates.

The calibration data sets currently in use comprise either 173 sites from predominantly North America and Japan and include sites where some significant cold is experienced (data set PHYSG3AR), or 144 sites derived from within this dataset where cold sites are excluded (PHYSG3BR). As such these data sets are not relevant to tropical vegetation or sites in the southern hemisphere. Exceptions to this are cited in Kennedy *et al.,* (2002).

Because CLAMP is designed to yield quantitative climate information from the leaves of woody dicots its use in deep time is restricted to deposits younger than around 100 Ma. This is when angiosperms first become ecologically significant, at least in environments likely to be represented in the fossil record, and there is a realistic chance of assemblages containing the minimum of 20 morphotypes necessary to obtain climatic estimates with small uncertainties (e.g. MAT uncertainties less than ± 2°C (2σ)). This does not mean, however, that non-angiosperms do not carry a climatic signal.

Climate Signals from non-Angiosperm Foliar Physiognomy—Compilations of Jurassic and Early Cretaceous taxon lists, initially from China and Russia (Spicer *et al.,* 1994) and more recently globally (Rees *et al.,* 2000), reveal distribution patterns that show beyond doubt that non-angiosperm plant physiognomies reflect climate. When conifer, fern, sphenophyte, cycadophyte, pteridosperm and ginkgophyte genera are ordinated using multivariate analysis structure or groupings emerge that reflect their foliar physiognomies. They may be grouped based on morphological categories or "morphocats" such as microphyllous or megaphyllous forms and they display distribution patterns that reflect both latitude gradients and the distributions of climatically sensitive sediments such as coals, sand seas, evaporates etc.. This allowed Rees *et al.,* (2000) to recognise five main biomes in the Jurassic: seasonally dry (summerwet or subtropical), desert, seasonally dry (winterwet), warm temperate and cool temperate. Tropical everwet vegetation was, if present at all, highly restricted. The boundaries of these biomes remained at near-constant palaeolatitudes while the continents moved through them (south, in the case of Asia, and north, in the case of North America) demonstrating that no significant broad scale patterns of climate change occurred throughout the Jurassic.

That is not to say that change did not take place at all or that plants were insensitive to such change. In the mudrocks of the Yorkshire coast, northeast England, three regularly spaced negative carbon isotopic excursions each of -2 to -3 per mil in the early Toarcian (approximately 183 Ma) are interpreted to have been the result of astronomically forced climate changes that triggered three rapid clathrate dissociation (Kemp *et al.,* 2005). The methane released, and the subsequent oxidation product CO_2, was sufficient to cause global warming pulses of between 8 - 10 °C each lasting around a few 100 Ka before the CO_2 was absorbed by natural systems, mostly photosynthetic organisms. Such short-term warmings are reflected in the plant fossil record in central Siberia, (Ilyina, 1985; Vachrameev, 1991), Denmark (Wade-Murphy *et al.,* 2006) and China (Yang *et al.,* 2006) demonstrating the sensitivity of plant fossils for detecting short-term as well as long-term climate change even before the advent of the flowering plants and their well calibrated foliar physiognomy. Of particular note here is that in all cases it was the apparently anomalous occurrence of remains of the extinct Mesozoic thermophillic conifer family, the Cheirolepidiaceae, which records the warming.

Some members of the Cheirolepidiaceae such as *Frenelopsis* and *Pseudofrenelopsis* display remarkable physiognomic adaptations to drought (i.e. they have well developed xeromorphic characters) with guard cells deeply sunken in a pit overarched by papillae that conceivably might have sealed the stomatal pit when in a flaccid state. At the very least the guard cells would have been bathed in air with a higher water-vapour content than in the free atmosphere. As well as having thick cuticles and highly reduced adpressed leaves, *Frenelopsis* and *Pseudofrenelopsis* had small hairs fringing their leaf margins and thin cuticles between the leaf and stem. This may have been an adaptation that nucleated water from the atmosphere and when droplets had formed on the hairs water ran down between the leaf and stem and could be absorbed (Spicer, 1989). Such well developed xeromorphic adaptations offer strong and unmistakeable climate signals, but as global compilations show (Rees *et al.,* 2000) other plants inhabiting the pre-angiosperm world had just as specific climatic tolerances but are harder to decode in terms of climate. More detailed analysis, coupled with greater precision in dating and isotopic studies, offer considerable scope for understanding short-term climate variations in greenhouse worlds.

DATA/MODEL COMPARISONS

Rees *et al.* (2000) in their Jurassic study noted that in general there was good agreement between the results of general circulation (climate) models (GCMs) and the climate determined from biome/sediment distributions. The match was not perfect, however, with major discrepancies occurring at high latitudes where the models predicted cold temperate conditions far beyond the tolerance limits indicated by the plants. Such a data/model mismatch is not confined to the Jurassic. Whenever models have been used to simulate past greenhouse climates they have failed to reproduce the climate characteristics suggested by the geological data in two key areas: at high latitudes and in continental interiors. So pronounced is this failure that it has become known as the "continental interior paradox (Valdes, 2000). This tendency of

the models to fail in these areas is particularly worrying because it is precisely in these areas that the greatest rate of observable change is taking place today. Here I will focus on the issue of continental interiors.

Future changes in the climates of continental interiors are of particular interest because these will significantly impact, for example, agricultural productivity. To help understand how well the models reproduce past climate in these regions detailed quantitative comparisons are required between geological data and model simulations. The Late Cretaceous was a time of pronounced greenhouse warmth and yet the availability of woody dicot leaves also offers the potential for quantitative climate data over land using CLAMP. The largest Late Cretaceous land mass not flooded by epicontinental seaways was in northeastern Asia, and in the area today known as the Vilui Basin (Fig. 2) abundant sediments bearing well preserved plant fossils offer a detailed insight into the Cretaceous vegetation and climate of the region.
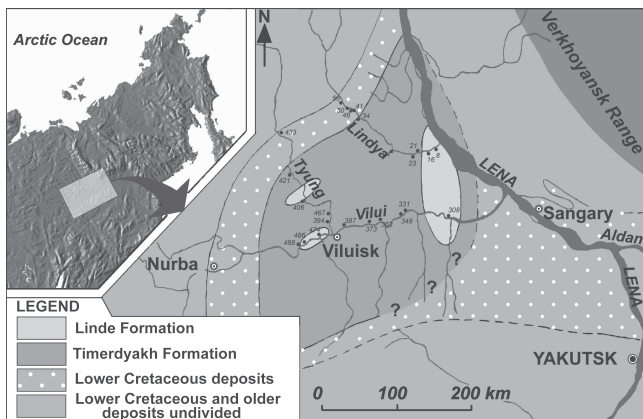

Fig. 2—Map of the Vilui Basin, Russia.

Early Cretaceous sediments exposed in the peripheral parts of the basin encompass stream channel sandstones interbedded with floodplain fines, autochthonous coals and stacked paleosols. Middle to Late Cretaceous successions of the Timerdyakh Formation in the center of the Vilui Basin, show strong reworking of floodplain deposits. River channel deposits contain abundant mud and peat balls, slumped fossil tree bases, drift wood and log jams. Rare immature paleosols with leaf mats, rooting, destratification and slickensides represent sites where ancient vegetation grew. Analyses with respect to clay mineralogy in Early Cretaceous mudstones and detrital mud balls show subequal kaolinite and smectite contents, while in the middle to Late Cretaceous (the Timerdyakh and overlying Linde formations) kaolinite dominates, sometimes together with illite, but without any notable smectite content. This suggests increasingly humid weathering conditions from the middle Cretaceous and onwards (Sellwood & Price, 1994).

The Timerdyakh Formation pollen and spore content reveals a high floral diversity with ferns and angiosperms being most strongly represented. Of over 170 taxa, 61 are spores (at least 33 represent ferns), 14 are gymnosperm pollen, 10 are monocot pollen (including two probable palm species), and approximately 90 are dicot pollen. Not more than 10% of the assemblage shows evidence of reworking from pre middle Cretaceous rocks and forms such as *Azonia calvata* (Samoilovitch) Wiggins suggest some samples are of latest Campanian /earliest Maastrichtian age. Both *Aquilapollenites* forms and representatives of the *Normapolles* group are present. The remarkable diversity of palynomorphs, together with presence of thermophilic taxa representing the Mastixiaceae, Araliaceae, Arecaceae and Cercidiphyllaceae, indicates warm and humid atmospheric conditions throughout the period of deposition of the Timerdyakh Formation (latest Albian to Maastrichtian). This is consistent with the climatic conditions suggested by clay mineralogy.

CLAMP analysis of leaves from clay partings in the lower part of the Timerdyakh Formation (77 well preserved specimens representing 25 morphotypes and all assigned to a Cenomanian age) placed them within the physiognomic space occupied by modern temperate vegetation, unlike test samples from the modern Vilui Basin vegetation that plot in isolation (Fig. 3). This shows that modern foliar physiognomic adaptations to today's extreme annual temperature range are not possessed by the Cretaceous fossils. The CLAMP analysis yielded a mean annual temperature (MAT) of 13.1 ± 3.5 °C (2σ), a warm month mean (WMMT) of 21.1 ± 3.6 °C, and a cold month mean temperature (CMMT) of 5.8 ± 5.1 °C. These CLAMP data suggest at least parts of the Cretaceous continental interior of Asia was remarkably equable with winter temperatures well above freezing for all but the coldest days, and a warm summer. This is in marked contrast with the wide annual temperature ranges seen in continental interiors today (Spicer *et al.,* 2004), and with the results from variously configured climate models. (DeConto *et al.,* 2000; Sloan *et al.,* 2001).

Results from numerous different Cretaceous simulations, using different boundary conditions such as palaeogeography, vegetation cover, atmospheric composition and using a variety of sea surface temperatures (SSTs), all yield temperature values substantially different from those derived from CLAMP and qualitative estimates from palynological analysis or clay mineralogy (Fig. 4). Although the uncertainty in both CLAMP and GCM model results are large, the extent of the mismatch greatly exceeds the errors in the methods. This test is clearly showing that currently configured models do not reproduce the Cretaceous Asian continental interior greenhouse climate as currently interpreted from a variety of congruent geological and biological data. This model-data mismatch is also seen in models of the Eocene (Sloan & Barron, 1990; DeConto *et al.,* 2000; Sloan *et al.,* 2001; Sloan & Barron, 1992) and the Jurassic (Rees *et al.,* 2000) and suggests that model-data discrepancies

cannot be simply explained by incorrect boundary conditions. Assuming the congruence of both geological and biological proxies reflects reality, the model predictions may be a result of other incorrectly specified boundary conditions, or intrinsic inadequacies of the models (e.g. inappropriate parameterisation of sub-grid scale processes such as clouds).

In regard to assessing the extent to which our interpretation of the proxies might be in error, CLAMP-derived climate estimates from coastal regions match climate model simulations well (Herman & Spicer, 1997), and suggests that calibration of the terrestrial climate proxies is comparable with those from the marine realm (particularly oxygen isotope data)
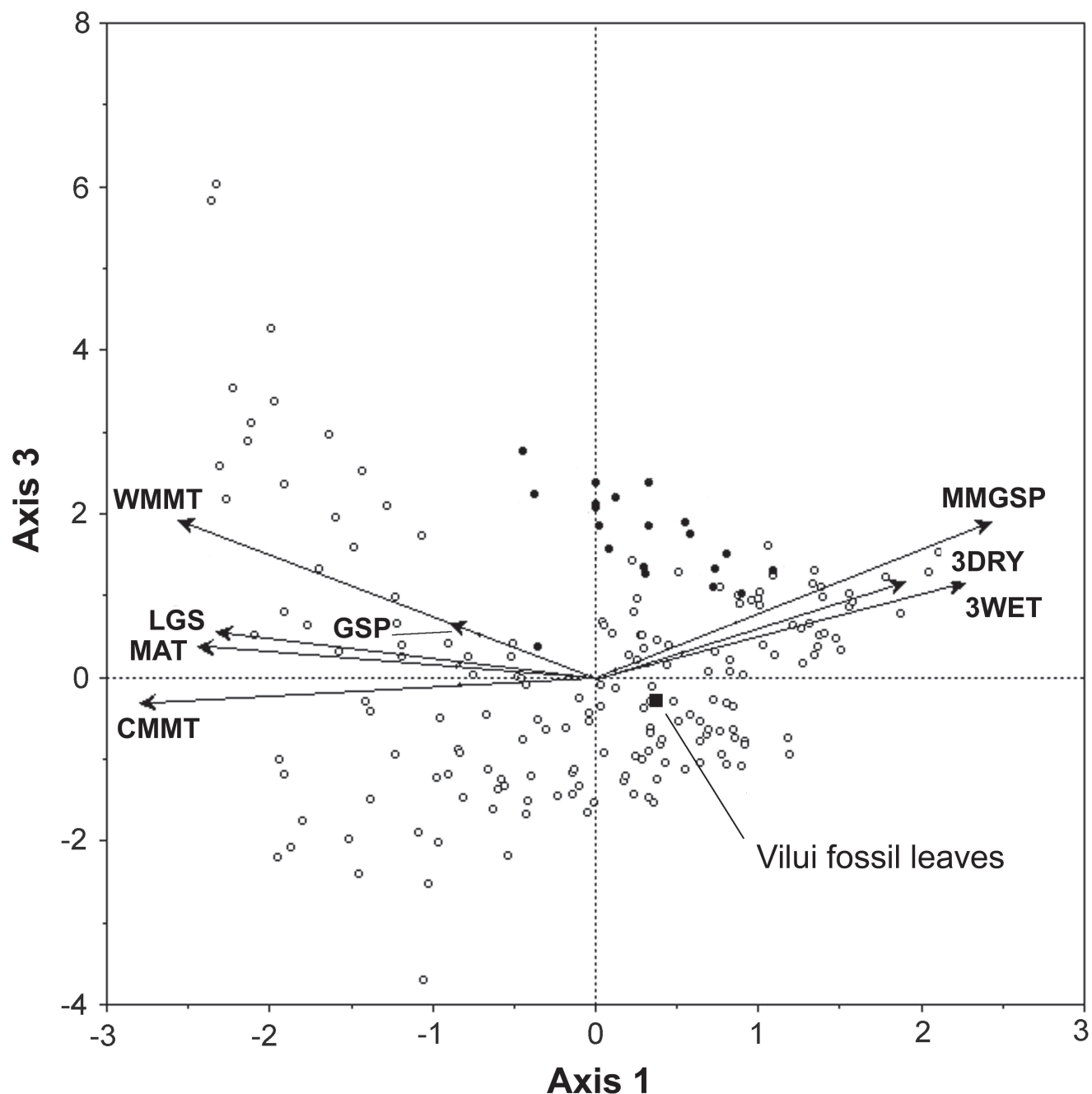
Fig. 3—Axis 1/Axis 3 CLAMP analysis of the PHYSG3AR data set (open circles) with modern Siberian samples (solid circles) added as passive samples. The position of the Late Cretaceous Vilui Basin fossil leaf assemblage is shown as a solid square and plots away from the modern indicated a foliar physiognomy quite distinct from that seen today in Siberia and more similar that displayed by warm to cool temperate vegetation. (Modified from Spicer *et al.,* 2004).

	MAT (°C)	WMMT (°C)	CMMT (°C)
CLAMP ± uncertainty (2σ)	13.1 ± 3.5	21.1 ± 3.6	5.8 ± 5.1
Models:			
Maastrichtian (n = 41)	1.41 ± 6.88	29.55 ± 9.58	-24.21 ± 9.76
Turonian (n = 16)	1.81 ± 6.06	28.92 ± 7.94	-22.76 ± 8.64
Cenomanian (n = 4)	-1.98 ± 3.66	25.57 ± 2.96	-24.75 ± 5.74

Fig. 4—Summary of differences between CLAMP-derived palaeotemperatures for the continental interior Late Cretaceous Vilui Basin, Russia, and model predictions for the same location. All uncertainties are ± 2 standard deviations about mean values.

employed to inform model ocean temperatures (Kennedy *et al.,* 2002). Moreover, when CLAMP analysis is used to estimate palaeoaltitude (Spicer *et al.,* 2003) the results are identical (within uncertainty bounds) to estimates derived from oxygen isotopes (Currie *et al.,* 2005).

One possible source of error in CLAMP applications in deep time is that in some way leaf physiognomy might be susceptible to changes in pCO_2 levels. This is not an unreasonable assertion given that $pCO2$ affects stomatal characteristics and water relations. However, the agreement of CLAMP derived MAT and enthalpy determinations with those obtained by oxygen isotope analysis argues that if there is an effect it is small compared to inherent uncertainties as a function of the statistical analysis, taphonomy and the quality and appropriateness of the calibration/training data sets. Moreover experimental data points to CLAMP being immune to CO_2 effects (Gregory, 1996).

The systematic mismatch between the models and the data, in which the models appear to impose a modern thermal regime (i.e. a large mean annual range and a low mean annual temperature) on greenhouse climate continental interiors, may mean that models could underestimate the magnitude of future climate change in such regions. It is clearly important that we determine why the model-data mismatch exists.

Defining the boundary conditions for models for "deep time" simulations is not straightforward. Describing the land/sea distributions, ocean bathymetry and topography, is actually one of the easier aspects of the past to determine. Less certain and potentially more important is the composition of the atmosphere, particularly the concentration of CO_2. Fig. 5 illustrates the best estimates we have of past CO_2 concentrations both from the point of view of proxies and modelling (Berner, 1991, 1998, 1999, 2006; Berner & Kothavala, 2001; Petsch & Berner, 1998). Even this combined approach yields little precision. For example CO_2 levels for the Cenomanian based on palaeosol proxies range between that of the present to 12 x present. The GEOCARB model yields values of 2 x present to 6 x present. One element in obtaining these values is an estimate of weathering which in turn is a function of palaeovegetation type; something that requires detailed but comprehensive palaeobotanical research.

INTEGRATING THE PAST AND THE FUTURE

Despite their limited spatial distribution for any given time slice, palaeobotanical proxies clearly play an important role in helping define past environmental conditions for comparison with model simulations, and in the case of stomatal measurements may help inform our understanding of ancient atmospheric conditions. However, with deep time boundary conditions poorly defined, modelling the past successfully can be problematic. In these situations, to determine whether models are capable of simulating reliably greenhouse climates that are significantly different to those of the present, requires numerous model runs, each with slightly different configurations of boundary conditions. Each run can then be examined to see which particular boundary condition configurations yield results that best match the proxy data.

Model success, however, is not simply a function of correctly defining boundary conditions. Inability to reproduce reality may be the result of errors intrinsic to the model itself. A widely recognised source of intrinsic model error is inappropriate sub grid-scale parameterisation schemes. When predicting the future or retrodicting the past, numerous Earth system processes such as weathering, ice dynamics or even growth of vegetation, operate over timescales measured in centuries or millennia and to integrate over such intervals coarse spatial grids and simplifications (parameterisations) are
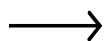
Fig. 5—Summary plot of model-derived CO_2 concentrations for the Phanerozoic and CO_2 values estimated from a variety of proxies. For past greenhouse climates such as those of the Mesozoic there are large uncertainties in both model and proxy estimates. Modified from Skelton (2003), after Crowley & Berner (2001).
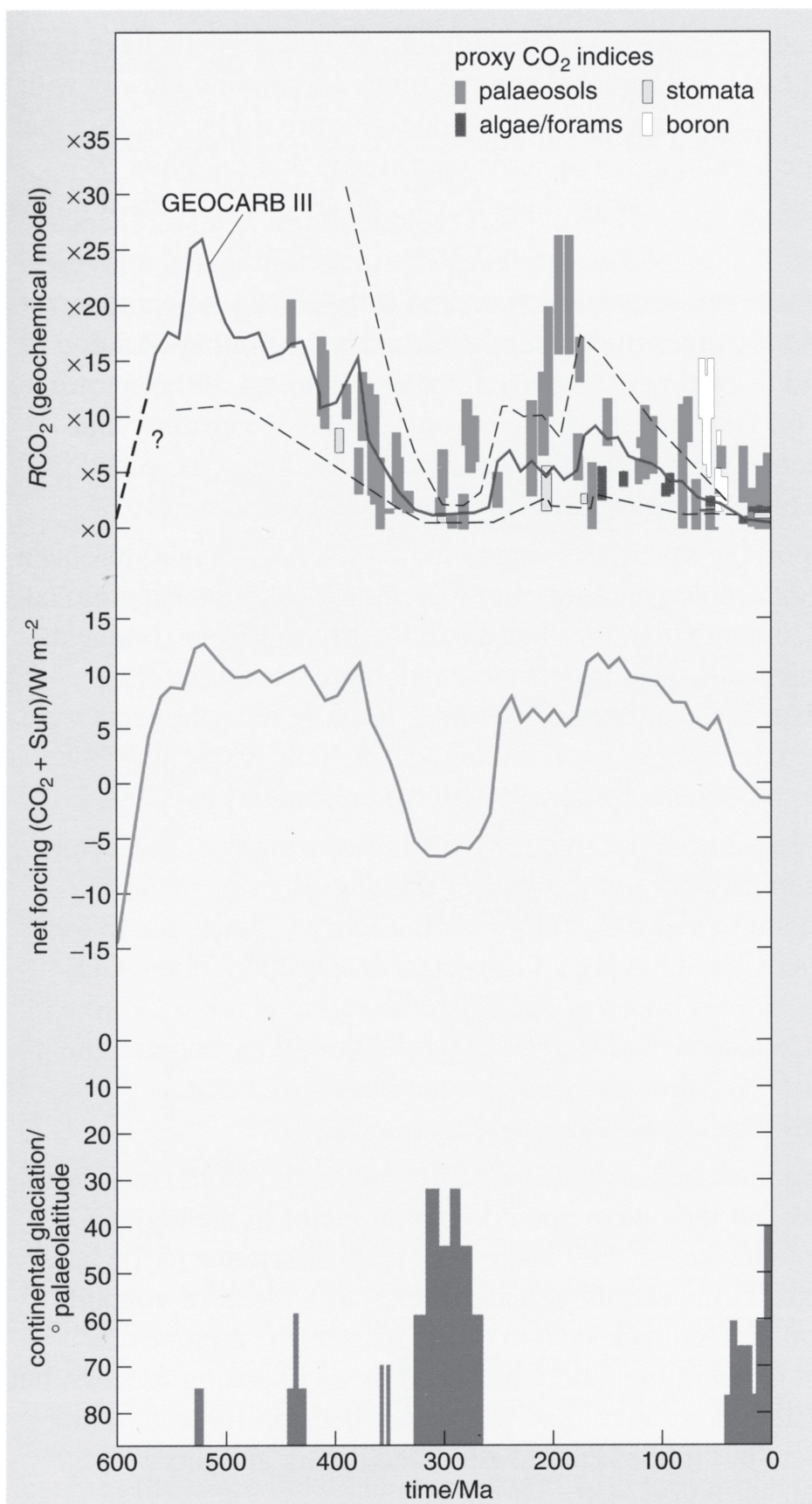
Fig. 5

necessary to facilitate computation. Even for the present day integrations, model decades are required for spin up and to average weather processes into climate.

However, this does introduce parameterisations that go beyond those used for the present. Exploring parameter space in models configured to simulate present or near future conditions is an important and ongoing process involving small numbers of model versions (McAvaney *et al.,* 2001) to grand ensembles e.g. climate*prediction*.net (Stainforth *et al.,* 2005), but to date comprehensive explorations of parameter space for models attempting to reproduce past greenhouse conditions have not been undertaken.

FUTURE DEVELOPMENTS

At the present time reasons for the model/data mismatch remain unclear. It is possible that there may be a systematic error in the palaeobotanical proxies although the congruence displayed with non-biological proxies such as oxygen isotopes and clay mineralogy suggests this if such an error esists, it is likely to be small. Nevertheless, palaeobotanical proxies do need to be improved. CLAMP and those methods based on the Co-existance Approach are all susceptible to biogeographic history effects, and in all cases the calibration data sets that underpin them need to be enhanced so that area-specific sets can be applied to obtain the highest precision and accuracy. Particular attention needs to be paid to tropical and sub-tropical climates and all climate/vegetation zones in the Southern hemisphere. Sometimes CLAMP appears to yield cooler results than CoA-based approaches (Uhl *et al.,* 2003, 2006, 2007) due, possibly, to the fact that leaf physiognomy reflects the local microclimate rather than the regional average (Burnham *et al.,* 2001; Kowalski & Dilcher 2003). Undoubtedly this regional climate signal is better reflected by the species composition of regional vegetation at the heart of the CoA. family of techniques. Clearly taphonomic factors affecting the fossil assemblage composition need to be understood when undertaking a palaeoclimate analysis whatever method is applied. If CLAMP does routinely underestimate regional temperatures then the correlation of CLAMP-derived MATs and enthalpy values with oxygen isotope data is an interesting one that demands further investigation.

As CLAMP calibration/training sets become more comprehensive so the structure of physiognomic space becomes more complex rendering climate variable derivations from straight line vectors more problematic. With the current training sets it is obvious that no vectors pass through large areas of physiognmic space suggesting that commonly used climate measurements do not exlain all aspects of foliar architecture. Edaphic factors are also likely to influence leaf form but this has yet to be explored.

As the structure of physiognomic space becomes more complex it seems appropriate to move away from the use of linear vectors and return to the nearest neighbour approach pioneered by Stranks and England (1997). Here sites would still be plotted in multidimensional physiognomic space but instead of using CANOCO to define that structure correspondence analysis would be used (Hill, 1973, 1979) and a weighted mean of the observed environmental factors associated with the *n* nearest calibration sites to a fossil sample would be used to derive palaeoclimate information. There are several weighting schemes that could be used and the number of nearest neighbours might vary depending on the density of samples or the proximity to the margins of physiognomic space. Again this is an area of research that remains to be explored.

Tackling the issue of model uncertainty is more problematic in that there are an extremely large number of parameterisations and boundary conditions to examine. The use of public participation and grid computing *sensu* climate*prediction*.net (Stainforth *et al.,* 2005) using "grand ensembles" is the only realistic way of exploring both parameter and boundary condition space when there are so many unknowns, particularly as regards atmospheric composition. Stomatal analysis could prove useful in constraining pCO_2 but issues such as wind effects, how leaves detect free air pCO_2 when exposed to high soil respiration pCO_2 in shady and humid sub-canopy space, and calibrating the sensitivity of extinct species need to be resolved first.

Clearly palaeobotany has much to offer to the climate change community, and society in general, over an above its traditional contributions to biostratigraphy, plant phylogeny, and the chemistry/composition of fossil fuels. Unfortunately, large parts of the climate change research community, politicians, the media and the public at large remain unaware of the importance of global vegetation present or past. Nevertheless, if his precient essay on the relationship between fossil plants and climate is anything to go by Professor Seward would be fascinated and enthusiastic about the role palaeobotany has to play in determing the future of our world.

REFERENCES

Ackerly DD, Dudley SA, Sultan SE, Schmitt J, Coleman JS, Linder CR, Sandquist DR, Geber MA, Evans AS, Dawson TE & Lechowicz MJ 2000. The evolution of plant ecophysiological traits: recent advances and future directions. Bioscience 50: 979-995.

Bailey I & Sinnott E 1915. A botanical index of Cretaceous and Tertiary climates. Science 41: 831-834.

Bailey I & Sinnott E 1916. The climatic distribution of certain types of angiosperm leaves, American Journal of Botany 3: 24-39.

Beerling DJ & Royer DL 2002. Fossil Plants as Indicators of the Phanerozoic Global Carbon Cycle. Annual Reviews of Earth and Planetary Science Letters 30: 527-556.

Berner RA 1991. A model for atmospheric CO_2 over Phanerozoic time. American Journal of Science 291: 339-376.

Berner RA 1998. The carbon cycle and CO_2 over Phanerozoic time: the role of land plants. Philosophical Transactions of the Royal Society of London Series B 353: 75-81.

Berner RA 1999. A new look at the long-term carbon cycle. GSA Today 9: 1-6.

Berner RA 2006. GEOCARBSULF. A combined model for Phanerozoic atmospheric O_2 and CO_2. Geochimica et Cosmochimica Acta 70: 5653-5664.

Berner RA & Kothavala Z 2001. GEOCARB III: a revised model of atmospheric CO_2 over Phanerozoic time. American Journal of Science 301: 182-204.

Burnham RJ, Pitman NCA, Johnson KR & Wilf P 2001. Habitat-related error in estimating temperatures from leaf margins in a humid tropical forest. American Journal of Botany 88: 1096-1102.

CLAMP website: http://tabitha.open.ac.uk/spicer/CLAMP/Clampset1.html

Crowely TJ & Berner RA 2001. CO_2 and climate change. Science 292: 870-872.

Currie BS, Rowley DB & Tabor NJ 2005. Middle Miocene paleoaltimetry of southern Tibet: Implications for the role of Mantle Thickening and delamination in the Himalayan orogen. Geology 33: 181-184.

DeConto RM, Brady EC, Bergengren J & Hay HH 2000. Late Cretaceous climate, vegetation, and ocean interactions. Cambridge University Press, Cambridge, p. 275-296.

Deng LH 1976. A review of the 'bamboo shoot' fossils at Yenzhou recorded in 'Dream Pool Essays' with notes on Shen Juo's contribution to the development of palaeontology. Acta Palaeobotanica Sinica 15: 1-16.

Forest CE, Molnar P & Emanuel KA 1995. Palaeoaltimetry from energy conservation principles. Nature 374: 347-350.

Fritts HC 1976. Tree rings and climate. Academic Press, New York 567 p.

Gale J 1972a. Availability of carbon dioxide at high altitudes: Theoretical considerations. Ecology 53: 494-497.

Gale J 1972b. Elevation and transpiration: Some theoretical considerations with special reference to mediterranean-type climate. Journal of Applied Ecology: 691-701.

Garbutt K, Williams WE & Bazzaz FA 1990. Analysis of differential response of five annuals to elevated CO_2 during growth. Ecology 71: 1185-1194.

GISS/NASA 2005. http://data.giss.nasa.gov/gistemp/2005/

Gregory KM 1996. Are palaeoclimate estimates biased by foliar physiognomic responses to increased atmospheric CO_2? Palaeogeography, Palaeoclimatology, Palaeoecology 124: 39-51.

Herman AB & Spicer RA 1997. New quantitative palaeoclimate data for the Late Cretaceous Arctic: evidence for a warm polar ocean. Palaeogeography, Palaeoclimatology, Palaeoecology 128: 227-251.

Hill MO 1973. Reciprocal averaging-an eigenvector method of ordination. Journal of Ecology 61: 237-249.

Hill MO 1979. Correspondence Analysis – A neglected multivariate method. Applied Statistics 23: 340-354.

Ilyina VI 1985. Jurassic Palynology of Siberia. Nauka, Moscow 237p. [In Russian].

IPCC 4th Assessment 2007. http://ipcc-wg1.ucar.edu/wg1/wg1-report.html

Johnson DM, Smith WK & Silman MR 2005. Climate-independent paleoaltimetry using stomatal density in fossil leaves as a proxy for CO_2 partial pressure: COMMENT. Geology: Online Forum pp. e82.

Kemp DB, Coe AL, Cohen AS & Schwark L 2005. Astronomical pacing of methane release in the Early Jurassic Period. Nature 437: 396-399.

Kennedy EM, Spicer RA & Rees PM 2002. Quantitative paleoclimate estimates from Late Cretaceous and Paleocene leaf floras in the northwest of the South Island, New Zealand. Palaeogeography, Palaeoclimatology, Palaeoecology 184: 321-345.

Kowalski EA & Dilcher DL 2003. Warmer paleotemperatures for terrestrial ecosystems. Proceedings of National Academy Sciences USA 100: 167-170.

Lande R & Arnold SJ 1983. The measurement of selection on correlated characters. Evolution 36: 1210-1226.

Mann ME, Bradley RS & Hughes MK 1998. Global-scale temperature patterns and climate forcing over the past six centuries. Nature 392: 779-787.

Mauseth JD 1988. Plant anatomy. Benjamin/Cummings, Menlo Park, CA.

McAvaney BJ, Covey C, Joussaume S, Kattsov V, Kitoh A, Ogana W, Pitma A, Weaver A, Wood R & Zhao ZC 2001. Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge: 317-336 p.

McElwain JC 1998. Do fossil plants signal paleoatmospheric CO_2 concentration in the geological past? Royal society of London Philosophical Transactions B 353: 83-96.

McElwain JC 2004. Climate-independent paleoaltimetry using stomatal density in fossil leaves as a proxy for CO_2 partial pressure. Geology 32: 1017-1020.

Mosbrugger V & Utescher T 1997. The coexistence approach - a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. Palaeogeography, Palaeoclimatology, Palaeoecology 134: 61-86.

National Research Council 2006. Surface temperature reconstructions for the last 2000 years. Committee on Surface Temperature Reconstructions for the Last 2,000 years, Board on Atmospheric Sciences and Climate, Division of Earth and Life Studies, National Research Council, The National Academies Press, Washington, DC. 160 pp.

Petsch ST & Berner RA 1998. Coupling the geochemical cycles of C, P, Fe, and S: the effect on atmospheric O_2 and the isotopic records of carbon and sulphur. American Journal of Science 298: 246-262.

Raven JA & Ramsden HJ 1989. Similarity of stomatal index in the C4 plant *Salsola kali* L. in material collected in 1843 and 1987: relevance to changes in atmospheric CO_2 content. Transactions of the Botanical Society of Edinburgh 45: 223-233.

Rees PM, Ziegler AM & Valdes PJ 2000. Jurassic phytogeography and climates: New data and model comparisons. *In* : Huber BT, Macleod KG & Wing SL (Editors)—Warm Climates in Earth History : 297-318. Cambridge: Cambridge University Press.

Reid CD, Maherali H, Johnson HB, Smith SD, Wullschleger SD & Jackson RB 2003. On the relationship between stomatal characters and atmospheric CO_2. Geophysical Research Letters 30 No. 19, 1983, doi: 10.1029/2003GL017775.

Retallack GJ 2001. A 300 million year record of atmospheric carbon dioxide from fossil plant cuticles. Nature 411: 287-290.

Royer DL 2001. Stomatal density and stomatal index as indicators of paleoatmospheric CO_2 concentration. Review of Palaeobotany & Palynology 114: 1-28.

Royer DL & Wilf P 2006. Why do toothed leaves correlate with cold climates? Gas-exchange at leaf margins provides new insights into a

classic paleotemperature proxy. International Journal of Plant Sciences 167: 11-18.

Schuepp PH 1993. Leaf boundary layers. New Phytologist 125: 477-507.

Sellwood BW & Price GD 1994. Sedimentary facies as indicators of Mesozoic Climate, Chapman and Hall, London, 1994, 17-26 pp.

Skelton 2003 (Editor). The Cretaceous World. The Open University. Cambridge University Press.

Sloan LC & Barron EJ 1990. ''Equable'' climates during Earth history? Geology18: 489-492.

Sloan LC & Barron EJ 1992. A comparison of Eocene climate model results to quantified paleoclimatic interpretations. Palaeogeography, Palaeoclimatology, Palaeoecology 93: 183-202.

Sloan LC, Huber M, Crowley T, Sewall JO & Baum S 2001. Effect of sea surface temperature configuration on model simulations of a equable climate in the Early Eocene. Palaeogeography, Palaeoclimatology, Palaeoecology 167: 321-335.

Smith WK & Geller G 1979. Plant transpiration at high elevations: Theory, field measurement, and comparisons with desert plants. Oecologia 41: 109-122.

Smith WK & Knapp AK 1990. Ecophysiology of high elevation forests. In: Osmond CB, Pitelka LF & Hidy GM (Editors)—Plant Biology of the Basin and Range: 87-142. Springer-Verlag, New York.

Spicer RA 1989. Physiological Characteristics of Land Plants in Relation to Environment through time. Transactions of the Royal Society of Edinburgh, Earth Sciences 80: 321-329.

Spicer RA, Harris NBW Widdowson, Herman AB, Guo S, Valdes PJ, Wolfe JA & Kelley SP 2003. Constant elevation of southern Tibet over the past 15 million years. Nature 421: 622-624.

Spicer RA, Herman AB & Kennedy EM 2004. The Foliar Physiognomic Record of Climatic Conditions During Dormancy: CLAMP and the Cold Month Mean Temperature. Journal of Geology 112: 685-702.

Spicer RA, Herman AB & Kennedy EM 2005. The sensitivity of CLAMP to taphonomic loss of foliar physiognomic characters. Palaios 20: 429-438.

Spicer RA, Rees PM & Chapman JL 1994. Cretaceous Phytogeography and Climate Signals. In: Allen JRL, Hoskins BJ, Sellwood BW, Spicer RA & Valdes PJ (Editors)—Palaeoclimates and their modelling: 69-78. Chapman and Hall, London.

Stainforth DA, Aina T, Christensen C, Collins M, Faull N, Frame DJ, Kettleborough JA, Knight S, Murphy JM, Piani C, Sexton D, Smith LA, Spicer RA, Thorpe AJ & Allen MR 2005. Uncertainty in predictions of the climate response to rising levels of greenhouse gases. Nature 433: 403-406.

Stern NH 2007. The Economics of Climate Change: the Stern Review. Cambridge University Press, Cambridge, 692 p.

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.

Terashima I, Masuzawa T, Ohba H & Yokoi Y 1995. Is photosynthesis suppressed at higher elevation due to low CO_2 pressure? Ecology 76: 2663-2668.

ter Braak CJF 1986. Canonical Correspondence Analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67: 1167-1179.

Traiser C 2004. Blattphysiognomie als Indikator für Umweltparameter: Eine Analyse rezenter und fossiler Floren. Dissertation, Tübingen University, 113pp.

Traiser C, Klotz S, Uhl D & Mosbrugger V 2005. Environmental signals from leaves—A physiognomic analysis of European vegetation. New Phytologist 166: 465-484.

Uhl D, Mosbrugger D, Bruch A & Utescher T 2003. Reconstructing palaeotemperatures using leaf floras- case studies for a comparison of leaf margin analysis and the coexistence approach. Review of Palaeobotany & Palynology 126: 49-64.

Uhl D, Bruch A, Traiser C & Klotz S 2006. Palaeoclimate estimates for the Middle Miocene Schrotzburg flora (S-Germany)—A multi-method approach. International Journal of Earth Sciences 95: 1071-1085.

Uhl D, Klotz S, Traiser C, Thiel C, Utescher T, Kowalski E & Dilcher DL 2007. Cenozoic paleotemperatures and leaf physiognomy - A European perspective. Palaeogeography, Palaeoclimatology, Palaeoecology 248: 24-31.

Vakhrameev VA 1991. Jurassic and Cretaceous floras and climates of the Earth. Cambridge University Press, Cambridge, 318p.

Valdes PJ 2000. Warm climate forcing mechanisms. In: Huber BT, Macleod KG & Wing SL (Editors)—Warm Climates in Earth History: 3-20. Cambridge University Press, Cambridge.

Van Der Burgh J, Visscher J, Dilcher DL & Kuerschner WM 1993. Paleoatmospheric Signatures in Neogene Fossil Leaves. Science 260: 1788-1790.

Wade-Murphy J, Kuerschner WM & Hesselbo SP 2006. Early Toarcian vegetation History from the Korsodde Section of Bornholm (Denmark) and its Possible Impact on Terrestrial Carbon Isotope Records. 7th European Palaeobotany Palynology Conference Program and Abstracts, Prague: 153-164.

Whitehead F 1965. The effect of wind on plant growth and soil moisture relations: A reply to the re-assessment by Humphries and Roberts. New Phytologist 64: 319-322.

Whitehead FH & Luti R 1962. Experimental studies of the effect on wind on plant growth and anatomy. I. Zea mays. New Phytologist 61: 56-58.

Wilf P 1997. When are leaves good thermometers? A new case for Leaf Margin Analysis. Paleobiology 23: 373-390.

Wilf P, Wing SL, Greenwood DR & Greenwood CL 1998. Using fossil leaves as paleoprecipitation indicators: an Eocene example. Geology 26: 203-206.

Wilf P, Wing SL, Greenwood DR & Greenwood CL 1999. Using fossil leaves as paleoprecipitation indicators: an Eocene example, Reply. Geology 27 p. 92.

Wing SL & Greenwood DR 1993. Fossils and fossil climate: The case for equable continental interiors in the Eocene. Philosophical Transactions of the Royal Society of London, Series B 341: 243-252.

Wolfe JA 1979. Temperature Parameters of Humid to Mesic Forests of Eastern Asia and their Relation to Forests of Other Areas of the Northern Hemisphere and Australasia. U.S. Geological Survey Professional Paper 1106.

Wolfe JA 1993. A method of obtaining climatic parameters from leaf assemblages. United States Geological Survey Bulletin 2040: 1-73.

Wolfe JA, Forest CE & Molnar P 1998. Paleobotanical evidence of Eocene and Oligocene paleoaltitudes in midlatitude western North America. Geological Society of America Bulletin 110: 664-678.

Woodward FI 1987. Stomatal numbers are sensitive to increases in CO_2 from pre-industrial levels. Nature: 617-619.

Yang J, Wang YF, Spicer RA, Mosbrugger V, Li CS & Sun QG 2007. Climatic reconstruction at the Miocene Shanwang Basin, China, using Leaf Margin Analysis, CLAMP, Coexistence Approach and Overlapping Distribution Analysis. American Journal of Botany 94: 599-608.

Yang XJ, Deng SH & Li WB 2006. A New Cheirolepidiaceous conifer from the early Jurassic of the Junggar basin, Northern Xinjiang and its Paleoclimatic Implication. 7th European Palaeobotany Palynology Conference Program and Abstracts, Prague: 159-160.