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Climate signals in Palaeozoic land plants

Dianne Edwards

Department of Earth Sciences, University of Wales Cardiff, PO Box 914, Cardiff CF1 3YE, UK

The Palaeozoic is regarded as a period in which it is difficult to recognize climate signals in land plants because they have few or no close extant relatives. In addition early, predominantly axial, representatives lack the features, e.g. leaf laminae, secondary growth, used later as qualitative and quantitive measures of past climates. Exceptions are stomata, and the preliminary results of a case study of a single taxon present throughout the Devonian, and analysis of stomatal complex anatomy attempt to disentangle evolutionary, taxonomic, habitat and atmospheric effects on stomatal frequencies. Ordovician–Silurian vegetation is represented mainly by spores whose widespread global distribution on palaeocontinental reconstructions with inferred climates suggest that the producers were independent of major climate variables, probably employing the physiology and behavioural strategies of extant bryophytes, further characterized by small size. Growth-ring studies, first possible on Mid-Devonian plants, have proved most informative in elucidating the climate at high palaeolatitudes in Late Permian Gondwana. Changes in the composition of Carboniferous–Permian low-latitude wetland vegetation are discussed in relation to tectonic activity and glaciation, with most confidence placed on the conclusion that major extinctions at the Westphalian–Stephanian boundary in Euramerica resulted from increased seasonality created by changes in circulation patterns at low latitudes imposed by the decrease of glaciations in most parts of Gondwana.

Keywords: stomatal frequencies, early land plants, Carboniferous tropical vegetation, growth rings, Ordovician–Silurian cryptospores, Westphalian–Stephanian extinctions

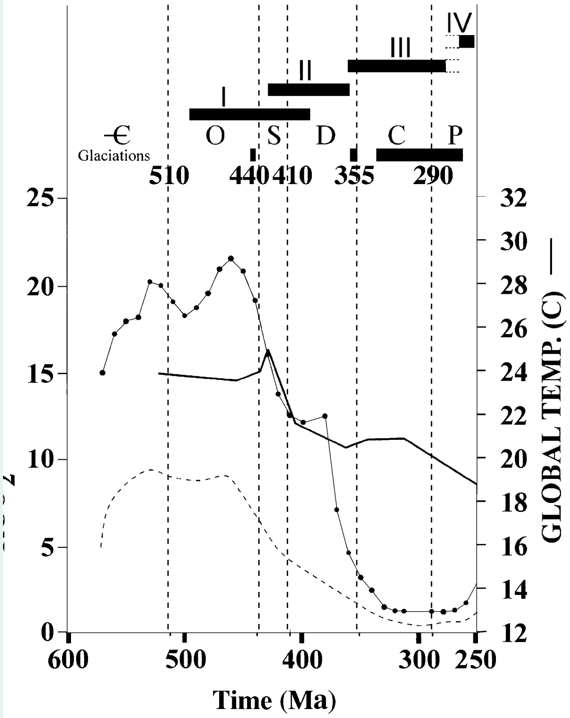
1. INTRODUCTION

The final 220 million years (Ma) of the Palaeozoic (*ca.* 470–250 Ma BP) saw the development and diversification of terrestrial ecosystems based on embryophytes. It was both a time of enormous evolutionary innovation, encompassing the appearance of all major groups of tracheophytes except the angiosperms, and a time of intense environmental change, to no small extent driven by the activities of the plants themselves (Berner 1992, 1994, 1997, this volume). Models suggest that early in the Palaeozoic (figure 1), CO_2 levels, and hence global temperatures, were higher than at any other time in the Palaeozoic (with the dampening proviso that solar luminosity was lower than at present: Berner 1994), but interrupted by a brief period of glaciation in the Late Ordovician (Brenchley *et al.* 1994; Worsley *et al.* 1994). Towards the end of the Palaeozoic, Earth became an 'ice-house' world with a period of major glaciation comparable only to the Pleistocene in the Phanerozoic. The Late Palaeozoic also saw episodes of major tectonic activity, and subsequent erosion associated with the Variscan orogeny, with consequences for regional topography, sedimentation patterns, precipitation and, possibly, atmospheric circulation patterns (Rowley *et al.* 1985). Such is the complexity of the palaeobotanical and physical background to the question posed in this paper.

Climate signals in land plants become increasingly faint as the past becomes more distant because the plants themselves are less familiar in appearance and more difficult to identify in terms of extant taxa. Thus, the 'nearest living relative' approach has little relevance for the Palaeozoic (Chaloner & Creber 1990; Chaloner & McElwain 1997). Interpretation of climate signals relying on the assumption that responses to environmental parameters in the past resulted in similar morphological and anatomical adaptations to those which occur today has achieved the greatest rewards in growth-ring studies and, more recently, stomatal frequencies (McElwain & Chaloner 1995; Beerling & Woodward 1997). Approaches involving leaf physiognomy based on angiosperm trees (e.g. Wolfe 1971, 1979) are generally not appropriate. While recognition of the tropical aspect of Carboniferous vegetation of the Euramerican province long before the advent of palaeocontinental reconstructions was partially based on large size of fronds as well as weakly developed, or absence of, growth rings (see summary in Schopf 1973; McElwain & Chaloner 1995), emphasis has now moved on to seeking causal relationships between changes in wetland communities in the Late Carboniferous and Early Permian and global climatic events (see summary in DiMichele & Phillips 1996*a*)

2. THE PALAEOBOTANICAL BACKGROUND

Four major phases of vegetation may be detected in the Palaeozoic (figure 1) subsequent to the first indications of land plants in the Llanvirn (Middle Ordovician) (Vavrdova 1988; Strother *et al.* 1996). Evidence for the earliest, Gray's Embryophytic: Evolutionary Level II (Gray 1993; I in figure 1), is predominantly from spores thought to have derived from plants at a bryophyte (possibly hepatic) level of organization, and hence showing behavioural and physiological adaptations to the



re 1. Phases in terrestrialization, modelled atmospheric on dioxide concentrations (based on Berner, references n), modelled global temperatures (Worsley *et al.* 1994) periods of glaciation in the Palaeozoic. The upper erature curve represents the 'best estimates' for various meters according to the GEOCARB II model. The lower epresents lowest crude error estimates based on modelling tivity analysis. I, pre-tracheophyte embryophytes (cryp- re producers); II, initital radiation of tracheophytes; III, eed plants and consolidation of four major clades; IV, ning of Mesophytic and dominance by gymnosperms.

strial environment (Gray 1984, 1985). Permanent ds and dyads plus their separated products (all cryp- ores *sensu* Richardson (1988)) persisted into the Lower onian, but the appearance in the Llandovery (Lower ian) of unequivocal trilete monads typical of those uced by the free-sporing vascular plants of the Devo- marked the start of the Eotracheophytic (Gray's utionary Level III). The first 'fertile megafossil ence' for the spore producers was in the Wenlock ddle Silurian) (Edwards *et al.* 1983), with indications roliferation of small-branching, leafless plants with inal sporangia in the Late Silurian and Early Devo- . Their affinities are with tracheophytes and pre- eophyte embryophytes, but the majority lack the cal anatomical evidence for conducting tissues. In entia, the end of the Lochkovian (Lower Devonian) a major radiation of these axial plants, with variation anching patterns, surface ornamentation and sporan- position, but retention of the basic 'switch habit', as as the appearance of the lycophytes (Edwards & es 1990). Gray (1993) used this to mark the base of Eutracheophytic Evolutionary Level IV. More ntly acquired information from outside Laurentia ests that the diversification might have started near nd of the Silurian (Edwards 1990). Successive radia- and competitive replacement occurred throughout the Lower and Middle Devonian (Edwards & Davies 1990; Berry & Fairon-Demaret 1998), resulting in the emergence of the progymnosperms in the Middle Devonian and of the sphenopsid and fern clades in the Upper Devonian (II in figure 1). At the cellular level, such plants had the full complement of anatomical features associated with homoiohydry, but apart from the lycophytes and some little-understood flabelliform structures, there were no large laminar leaves and their architecture bore little resemblance to that of modern ferns and horsetails.

The next phase in terrestrialization was marked by the appearance of ovule-bearing plants in the Famennian (III in figure 1). The subsequent radiation of the pteridosperms in the latest Devonian completed the establishment of the four major clades which were to dominate the vegetation throughout the Carboniferous. Each had a particular type of architecture (especially in relation to the tree habit), of life history and of reproductive biology, such that there was a 'strong phylogenetic overprint' on the various communities that were centred on physically distinct parts of the tropical lowlands (DiMichele & Hook 1992; DiMichele & Phillips 1996*b*). Broadly speaking, arborescent lycophytes occurred in the wettest swamps, seed plants dominated well-to-poorly drained clastic substrates, sphenopsids colonized regions characterized by major physical disturbance, and ferns were interstitial opportunists.

Such ecological partitioning in the tropical lowlands was disrupted by climate change beginning towards the end of the Carboniferous. In the globally drier periods that followed, seed plants, and particularly conifers, replaced arborescent free-sporing plants. This may be regarded as the start of the final vegetation phase of the Palaeozoic, indeed it is traditionally regarded as the beginning of the Mesophytic (Gothan & Weyland 1954; Gray 1993). However, as Knoll (1984) emphasized, the change was a gradual one, occurring at different times in different floristic regions, but it appears to be recorded most dramatically in the Mid-Permian of Laurentia (see also Kerp 1996).

3. ANATOMICAL FEATURES OF PALAEOZOIC PLANTS

(a) *Growth rings: 'trees as compulsive diarists'* (*Chaloner & Creber 1990*)

In this phrase, Chaloner & Creber (1990) nicely encapsulated the fact that secondary wood development results from the complex interaction between intrinsic and extrinsic controls on growth. Among the latter is climate, which influences seasonal activity and conditions affecting annual productivity (Creber & Chaloner 1984*a*). Growth-ring studies have produced a wealth of data on plant climates throughout the Phanerozoic, although detailed interpretation requires information on the whole plant not usually available in the fragments of twigs, branches, and trunks preserved in the Palaeozoic (e.g. Tomlinson & Craighead 1972; Creber & Chaloner 1984*a*; Ash 1985; Chapman 1994).

(i) *Devonian*

The oldest records of plants known to possess secondary wood are those of aneurophytalean progymnosperms in the Middle Devonian (Eifelian) of Germany (Schweitzer

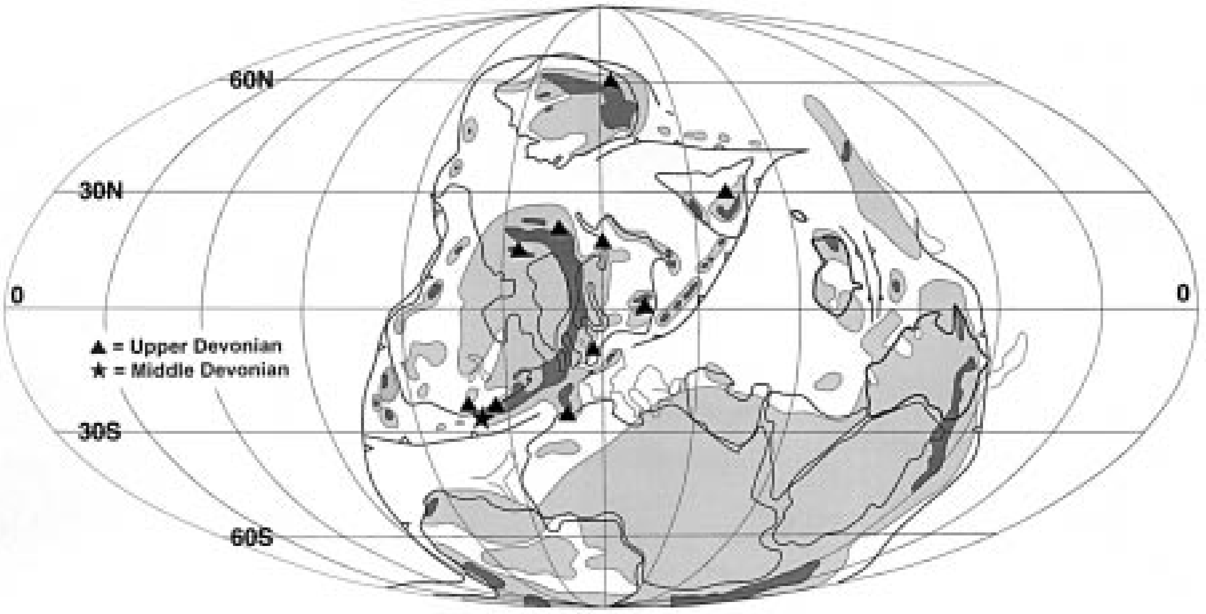
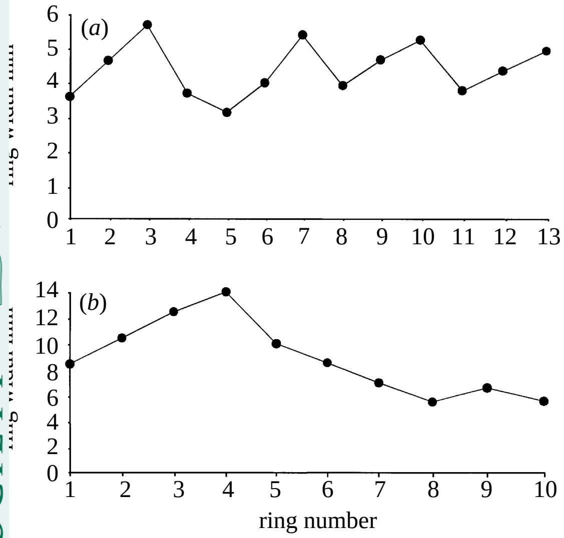


Figure 2. Distribution of *Callixylon* in the Upper Devonian with one Middle Devonian record of *Rellimia*. (Base map from Golonka *et al*. 1994.)

1974: *Rellimia*, Eifelian, Lindlar, Germany). Reconstructions of complete plants are not available but, in general habit, they were probably shrubs composed of leafless stems, the largest a few centimetres in diameter, with repeated branching patterns (described as N, N+1, N+2, etc.). Usually three- or four-lobed xylem was surrounded by relatively small amounts of secondary wood of coniferous aspect (Beck 1976), but evidence of periodicity in its growth and possible causes are conjectural. Dannenhoffer & Bonamo (1989) illustrated axes of Givetian (Upper Middle Devonian) *Rellimia thomsonii* from New York State with 2–3 growth layers (less than 22 mm wide) in N and N+1 axes, whose cells (*ca*. 30) show a gradual decrease in width with layers, 3–10 tracheids thick, interpreted as late wood. The secondary tissue is somewhat distorted and rings completely encircling the stem were not detected. They concluded that such growth rings reflected seasonal activity of the vascular cambium and that, although the New York localities were palaeogeographically located near the equator, these data plus sedimentological evidence (e.g. the presence of desiccation cracks in freshwater limestones; Kent 1985; Woodrow 1985) pointed to their being at higher tropical latitudes. Indeed, subsequently published reconstructions place them nearer 30° S (figure 2; Golonka *et al*. 1994). Dannenhoffer & Bonamo (1989) offered a similar climatic explanation for the often even fainter growth discontinuities in other aneurophytalean progymnosperms (e.g. Upper Devonian, *Triloboxylon*: Scheckler 1975; *Tetraxylopteris*: Matten & Banks 1967) including Eifelian *Aneurophyton* (Kräusel & Weyland 1929, 1935), although their existence had not been accepted by the original authors.

Far more attention has been paid to the Upper Devonian arborescent progymnosperm *Archaeopteris*, where isolated stems, composed almost entirely of secondary wood (*Callixylon*), may reach 1 m in diameter and 8.4 m in length (e.g. Chaloner & Creber 1973; Creber & Chaloner 1984*a,b*). Here the occurrences (plus a recently described Moroccan record; Galtier *et al*. 1996) are plotted on a more recent palaeocontinental reconstruction (figure 2; redrawn from Golonka *et al*. 1994). The majority of records show no discontinuities of growth. Exceptions include *Callixylon erianum* (Arnold 1929) and *C. newberry* from Indiana (Arnold 1947), described by Chaloner & Creber (1973) as having clear but subdued rings of variable width with very narrow zones, 2–3 cells wide, of late wood, but with no sharp distinction between successive growth periods. Lemoigne *et al*. (1983), in a revision of the type species *C. trifilievii* from the Donetz Basin, described occasional growth discontinuities which never completely encircled the stems and interpreted them as false rings, indicative of traumatic interruption of growth in plants inhabiting a non-seasonal, warm and humid environment. This conclusion was supported by Creber & Chaloner's quantitative analysis of *C. trifilievii* (based on cell numbers and radial tracheid diameters in individual growth rings) as being type 'O' (Creber & Chaloner 1984*b*), indicative of habitats where all the requirements for growth are constantly present. Discontinuities of growth may have been coincident with seasonal or traumatic shedding of leafy branches in *Archaeopteris*—the latter based on the frequent occurrences of foliage in large mats (Scheckler 1978). Scheckler interpreted *Archaeopteris* as a member of a low diversity gallery forest colonizing water-logged soils along streams or wetland flood plains, where temporary lowering of the water table might have interrupted growth. Replotting the data shows a wider latitudinal spread than earlier global distributions (e.g. a Siberian record of *C. trifilievii*; Lemoigne *et al*. 1983), although critical comparative data on wood from the highest southern latitudes, where *Archaeopteris* foliage does occur (e.g. South Africa), is absent. Further studies based on a recent report of *Archaeopteris*/*Callixylon* from the Aztec Formation, Antarctica, should prove particularly



re 3. Mean sensitivity data reproduced from Francis *et al.* 4) based on Late Permian wood from Antarctica. (*a*) J039: ring width, 4.40 mm; mean sensitivity, 0.227. (*b*) J024: ring width, 8.85 mm; mean sensitivity, 0.196.

inating (Retallack 1997). It therefore remains impos- to contribute to the debate as to whether *Archaeopteris*, ndeed the earlier progymnosperms, had not yet ved the capability to produce growth rings (Antevs), or whether existing records demonstrate an Upper nian equable climate.

Carboniferous

ne dearth of detailed quantitative studies on growth in Carboniferous woods, arguably the first period onstrating unequivocal global phytoprovincialism llips & Peppers 1984; Meyen 1987), reflects pre- pation with the wet tropics of Euramerica (for ws, see Chaloner & Creber 1973; Creber & Chaloner *b*) where they are usually faint and incomplete (in s) and more marked in roots (e.g. *Amyelon*), the latter ably related to local changes in water table (Phillips & ers 1984). Growth rings in cordaitalian wood from Upper Carboniferous of Siberia (Shilkina 1960) are pronounced and narrow, and are consistent with a palaeolatitude. The possibility of seasonal growth the equator in Lower Carboniferous times is ently being investigated by Falcon-Lang (1997). Preli- ary quantitative data on charcoal from Ireland and land indicate high rainfall of seasonal occurrence.

Permian

r the first time in the Palaeozoic, ring analysis ides a strong, if somewhat unexpected, signal on ate. Although low-latitude data are available (e.g. ern Europe; Frentzen 1931) that confirm a lack of nality, far more informative are those from Late dwanan high latitudes (i.e. greater than 70° S) (e.g. sel 1962; Maheshawari 1972; Jefferson & Taylor ; Francis *et al.* 1994), where growth rings are ounced, numerous, and wide, and occur in trunks ght to have borne the leaves assigned to *Glossopteris*. cis *et al.* (1993) provide a preliminary quantitative analysis of thin sections of silicified wood recovered from *in situ* stumps (less than 30 cm in diameter and 20 cm high) within coals and from mostly drifted larger branches and trunks (less than 1 m in diameter and 20 m long) in fluvial sediments from the late Early Permian Weller Coal Measures of Allan Hills, southern Victoria Land, Transantarctic Mountains. Their analysis demonstrated the following:

(i) that rings are very wide (3.21–14 mm; mean per tree = 3.75–4.00 mm in thin sections; 8.85 mm in rough-hand sections from larger specimens), such increments being comparable to those in present-day conifers growing under very favourable conditions at mid-latitudes (Creber & Chaloner 1984*a*);
(ii) that mean sensitivity (i.e. variation in width between adjacent rings averaged for the whole system; figure 3) is low (0.3, i.e. at the boundary between complacent and sensitive *sensu* Creber (1977));
(iii) that there is a large number of cells per ring (e.g. 114, 141, 194), leading to the prediction of a growing season of at least 48 days, based on Creber & Chaloner's observation that extant spruce produces up to 4 cells d^{-1} in good light (Creber & Chaloner 1984*b*);
(iv) well-defined ring boundaries, each comprising a wide zone of thin-walled early wood cells and a narrow zone of thick-walled, late-wood cells;
(v) cell diameters of 10–65 μm (mean = 30 μm);
(vi) that analysis of the radial diameters of cells across several rings plotted against the cumulative sum of deviation from mean radial diameters produces three of the types defined by Creber & Chaloner (1984*b*; figure 4), viz. type C or D, which indicate gradual changes in conditions during the growing season with a marked terminal cessation of growth *or* type B where the growing season was long, but there was the very abrupt cessation of growth typical of high-latitude fossil wood, attributed to decrease in light levels at the onset of the polar winter—the latter is considered most representative for the locality (figure 4); and
(vii) false rings were rare, as were rings caused by frost damage. Such data indicate that the trees flourished under favourable conditions throughout the growing season, with ample water, clement temperatures, enhanced by the extended daylight hours of the Antarctic summer, and conditions deteriorating only gradually as trees approached winter dormancy. Temperatures would have been increased by the low albedo of surfaces (little or no ice cover) and the greenhouse effect of the postulated high CO_2 concentrations (Francis *et al.* 1994).

Other less detailed numerical analyses from Late Permian Antarctic localities (e.g. Jefferson & Taylor 1983; Taylor & Taylor 1990) broadly support these conclusions on climate, although in the former, the growth rings (under 8 mm), while wide, were very variable in width, this being attributed to relatively low light during the growing season; and in the latter, the wide rings (greater than 11.38 mm, mean = 4.5 mm) show a late wood of only 1–3 cells. Further evidence for a (cool) temperate humid seasonal climate comes from diverse assemblages of

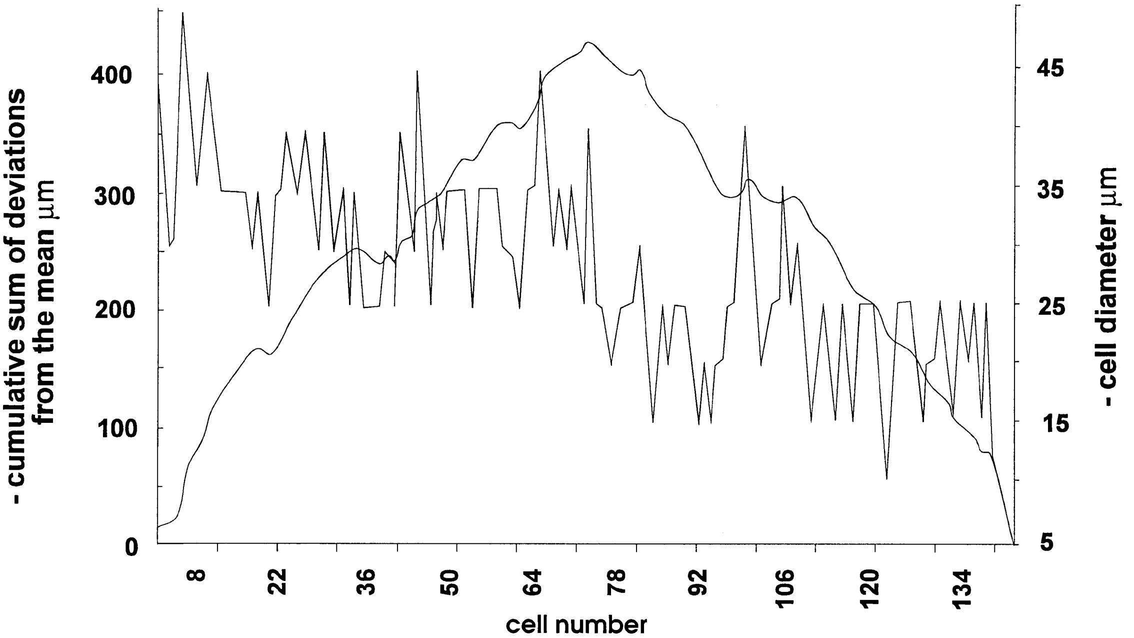


Figure 4. Plots from Permian Antarctic wood of radial diameter of cells across rings, and cumulative sum of deviations from the mean radial diameter. J039 ring type (From Francis *et al.* 1994.)

animals in the Late Permian of South Africa (Yemane 1993) and from sedimentation style which demonstrates that cyclic sedimentation was controlled by glacial melt. The latter contradicts the hypothesis that by post-Sakmarian Permian times, Antarctica was ice-free (Barrett 1991; Barrett *et al.* 1991; Francis *et al.* 1994). Conceptual and numerical modelling of Permian climates of the Pangaean supercontinent (see Parrish 1993) confirms a markedly seasonal climate at high latitudes with higher rainfall than in lower and middle latitudes where 'megamonsoons' are predicted. However, Kutzbach & Gallimore's (1989) model suggests winter temperatures of −40 °C in the continental interiors rising to 0 °C in summer, while Crowley *et al.* (1987) predict winter and summer temperatures of −30 °C and 5 °C, respectively. Such temperatures would hardly have allowed vigorous forest growth at those latitudes (Taylor & Taylor 1990), although the plants described here were probably growing in coastal swamps (Trusswell 1991) where temperatures would have been higher, and the modellers had not taken into account the ameliorating effects of the large inland bodies of water around which the animals lived (Yemane 1993). Such paradoxes indicate both the value of climate signals from Permian plants and the necessity to integrate biological data into computer models (Crowley 1994).

(b) *Cuticular features*

Recent work has concentrated on stomata (McElwain & Chaloner 1995; Edwards *et al.* 1996), but Kerp (1996) has emphasized the potential of additional features (e.g. thickness, ornamentation) of the cuticles of Permian conifers, hitherto most intensively studied as taxonomic characters, for responses to climate change at the end of the Palaeozoic glaciation and the emergence of Mesophytic vegetation.

(i) *Stomata: monitors of atmospheric* CO_2

The consistently inverse relationship between atmospheric CO_2 concentration and stomatal frequences, noted in experimental work on certain species and in analyses of fossil and subfossil leaves, has led to the hypothesis that change in atmospheric CO_2 is the most likely causal environmental factor in controlling stomatal densities (Woodward 1987; Beerling 1994, this volume). Here I concentrate on new, but preliminary data, on stomata in the earliest land plants (table 1) that McElwain & Chaloner (1995) have shown are present in the low frequencies that might be anticipated from the modelled exceedingly high CO_2 concentrations for the Mid-Palaeozoic (Berner 1994; Worsley *et al.* 1994; Mora *et al.* 1996).

Stomata are first recorded from the Upper Silurian (Pridoli) in presumed tracheophytes of axial organization bearing terminal sporangia, and, at least superficially, resemble extant stomata. More detailed anatomical studies from Early Devonian examples suggest similarities with the stomata of mosses and ferns. The lack of records from older Silurian axial and microphyllous megafossils probably relates to form of preservation. However, where detailed screening of large numbers of fragments of small coalified axes have been undertaken in Pridoli and Lochkovian strata, most lack stomata, and when present, they occur as isolated examples or in pairs. This produces very low densities. Higher frequencies with sometimes more regular stomatal distribution occur at the junction between the sporangium and the subtending axis and on the sporangium wall itself (Edwards *et al.* 1996). Data from excellently preserved Rhynie Chert plants are disappointing. Examples of paradermal sections are few, and it is both difficult and dangerous to isolate intact axes from the silicified matrix. Based on the drawings of Remy & Hass (1991), and some new information from Hass that, in total, would not survive statistical scrutiny, stomatal le 1. *Stomatal frequencies in Silurian (S) and Lower Devonian (LD) plants*

rcher	age	plant (*n*)	stomatal density (range) (mm^{-2})
lwain & Chaloner (1995)	Pragian	*Aglaophyton*	4.5
	Emsian	*Sawdonia ornata*	4.3
992)	Emsian	*Hsüa robusta*	5
blefield & Banks (1978)	?	*Drepanophycus spinaeformis*	<33
Edwards (1995, unpublished data)	Emsian	*Drepanophycus qujingensis* (26)	11.1 (3.1–20.2)
ırds (unpublished data)	Lochkovian	fragmentary unidentified sporangium	7.3
		fragmentary indeterminate Devonian axes (numerous)	2.5
	Pridoli	indeterminate Silurian axes (numerous)	0–2.3
ards & Hass (work in progress)	Pragian	*Aglaophyton*	1.0
ynie Chert plants		*Nothia* (3)	5.5 (3.1–8.8)
		Rhynia (2)	1.8 (1.6–2.0)
		Horneophyton (3)	3.1 (0.7–4.4)
		Asteroxylon indeterminate	10.4
		Asteroxylon (A) (4)	21.5 (16.0–27.7)
		Asteroxylon (B) (1)	31.5
		Langiophyton	0.4
		Lyonophyton	3.2

ıencies (table 1) are low except for the lycophyte *Aster-* ı where stomata occur on leaf bases and stems, but are ıtifiable only on the latter. Similarly higher frequencies recorded on the stems of the microphyllous Emsian *anophycus spinaeformis* (Gaspé: Canada), *D. qujingensis* ınan: China), and *Baragwanathia abitibiensis* (Ontario: ada) (table 2).

ıe record suggests that stomata evolved when CO_2 entrations (hence average global temperature) were ably at their highest in the Palaeozoic. Morphological, omical, sedimentological, and edaphic evidence from ian and Early Devonian axial fossils (a good ıple of the 'switch' habit (Edwards 1994)) suggests water stress was the major constraint to land coloniza- (see, also, Gray 1984). Particularly striking are the omatal adaptations in Rhynie plants which minimize ırea of evapotranspiration below the guard cells, the ın where most water loss occurs in extant plants. For ıple, in *Aglaophyton*, hypodermal cells extend below ınner periclinal walls of the guard cells, forming a ow canal lined by thickened walls below the pore ny & Hass 1996). Similar cradling produced by cuti- ion of epidermal cells has been demonstrated in fied axial fossils (Edwards & Axe 1992). Of those ts with comparatively high stomatal frequences, *Aster-* ı provides the earliest example of sunken stomata, *Drepanophycus qujingensis* has extensive cuticular enings associated with the guard cells (Li & ards 1995). Slightly sunken stomata are also seen in ian *Sawdonia ornata* (Chaloner *et al.* 1978) where ıencies are low (McElwain & Chaloner 1995).

ıus, in these exceedingly ancient examples of the ical dilemma between transpiration and photo- ıesis, it could be argued that high CO_2 concentration nitted' the minimizing of numbers of stomata, ough the latter may have had an important role in the ration of a transpiration stream (particularly to reproductive regions) and increased uptake of mineral nutrients in plants equipped only with rhizoids to absorb water. Indeed, the higher frequency of stomata in *Drepanophycus* and *Asteroxylon* might reflect their possession of rooting systems for more efficient exploitation of greater volumes of substrate, and hence more efficient replacement of water loss than their greater surface areas for photosynthesis, or as Edwards *et al.* (1996) recently suggested for *Drepanophycus*, their colonization of habitats with persistently high water tables.

In an attempt to demonstrate that early tracheophytes did indeed track the modelled reduction in CO_2 in the Devonian (Berner 1992, 1994, 1997; McElwain & Chaloner 1995; Chaloner & McElwain 1997), stomatal densities were calculated for the same species, *Drepanophycus spinaeformis* (identified by epidermal characters and gross morphology) from Lower, Middle and Upper Devonian localities in a limited geographical area. Preliminary results on preparations made by Stubblefield & Banks (1978), with kind permission from Professor Banks and Professor Niklas), from Emsian, Givetian and Frasnian localities from north-eastern North America indicate that *average* frequencies do increase as predicted, but more preparations are required for Lower and Upper Devonian localities to permit statistical analyses. The available fragments were small, perhaps accounting for the considerable variation between samples, while incomplete preservation prevented calculations of stomatal indices. The preliminary data also suggest an increase in size of pore and stomatal apparatus between Lower and Upper Devonian occurrences. Unfortunately, examples of taxa extending throughout the Devonian are rare: *Sawdonia ornata* (McElwain & Chaloner 1995: Lower Devonian, 4.3 mm^{-2}) is also recorded in the Frasnian and, provided that cuticles are recoverable, should allow further testing of the hypothesis.

A similar approach using cuticles of the pteridosperm *Neuropteris ovata*, recovered from Westphalian into

Table 2. *Preliminary results on stomatal frequencies in* Drepanophycus spinaeformis *based on preparations of Stubblefield & Banks (1978)*

locality	age	density (mm^{-2})	range	*n*	pore length
Gaspé, Canada	Emsian	16.6	(14.7–18.6)	2	27 µm
Brown Mt, NYS	Givetian	16.8	(15.3–19.1)	3	20 µm
Cairo, NYS	Givetian	17.0*	(10.8–30.4)*$^{+}$	14	27 µm
West Cave Mt, NYS	Frasnian	18.2	(12.5–23.6)	5	41 µm
Prattsville, NYS	Frasnian	23.5*	(19.7–26.7)	7	38 µm
Other lycophytes					
	Asteroxylon mackiei (Pragian)	= 16 − 32 mm^{-2}			
	D. qujingensis (Emsian)	= 3 − 20 mm^{-2}			

$^{+}$Majority 10.8 − 21.32 mm^{-2}, one= 30.42 mm^{-2}.
*Similar stomatal index.

Stephanian localities from eastern Canada (Cleal 1997; C. J. Cleal, R. James and E. L. Zodrow, unpublished abstract), shows a pronounced decrease in stomatal density in the very early Stephanian, coincident with the major changes in tropical wetland vegetation (see §5) and a decrease in the extent and occurrence of glaciations (figure 8: Frakes *et al*. 1992).

4. CLIMATE AND THE EARLIEST LAND PLANTS

The earliest direct evidence for embryophytes colonizing the land consists of spores, thought to derive from *land plants* because their resilient walls are assumed to have been composed of sporopollenin (their distribution in marine and fluvial facies making an acritarch origin unlikely), and from *embryophytes* because of their configuration (particularly tetrads) and possibly their ultrastructure. While spores themselves clearly do not possess a climate signal, their geographic distribution in the Ordovician and Early Silurian may provide some insights into the climates experienced by the pioneering colonizers (figure 5). The earliest records (dyads: Vavrdova 1988) occur on the palaeocontinent Gondwana (table 3): as do those later in the Llanvirn from Arabia (McClure 1988; Gray 1991; Strother *et al*. 1996). These show almost as much diversity as is ever later encountered (see legend to table 3). The exception is the ornamented envelope that first appears in the Caradoc (see references in Wellman 1996). The earliest records therefore come from high palaeolatitudes and, in a palaeontological context, in the cool Malvinokaffric Realm, but by Ashgill times they had spread into Laurentia (the North Atlantic realm). Indeed, Gray *et al*. (1992) considered that, based on British and North American records, the appearance of ornamentation was related to spread into warmer latitudes, a hypothesis that does not find support in the descriptions of sculptured envelopes in Gondwana by Richardson (1988) and Vavrdova (1982 *et seq*.).

Intuitively, and undoubtedly coloured by experience of the current atypical ice-house Earth, excessively cold temperatures, with concomitant harsh environmental conditions, and physical disturbance are associated with high latitudes. However, the time interval during which the producers flourished was one of very high postulated CO_2 concentrations (Berner 1992, 1994) and temperatures (Worsley *et al*. 1994) when poles might be anticipated to have been ice-free (figure 1). However, evidence for Gondwana glaciation from sediments is unequivocal. Analysis of the distribution of such deposits indicates ice-sheets in north and south Africa and the central Andes region from the Late Ordovician, and glacio-marine deposits further south in Brazil, Bolivia and northern Argentina (Caputo & Crowell 1985). However, the exact timing and duration of the glaciation remain contentious. Brenchley *et al*.'s (1994) estimation of a very short period of glaciation (0.5–1.0 Ma) in the Hirnantian based on bathymetric and isotopic data conflicts with Frakes *et al*.'s (1992) estimate of 35 Ma extending from the Caradoc into the Wenlock, which accommodates glaciation in the Early Silurian of

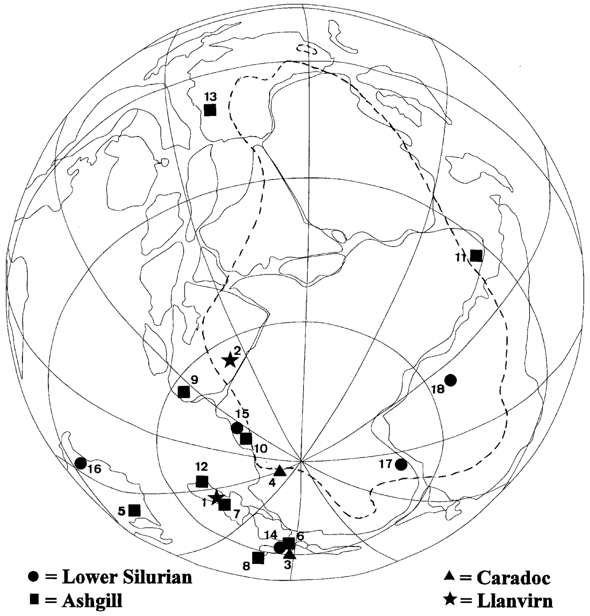


Figure 5. Distribution of spores on base map for late Ordovician (redrawn from Denham & Scotese 1987). This approach (see also figures 6 and 7) gives a general idea of the geographical distribution of localities, but cannot take into account the postulated and quite extensive 'polar wandering' during the time intervals. Numbers refer to table 3.

le 3. *Records of Ordovician and basal Silurian spore assemblages*

permanent tetrad indet; A, naked fused permanent tetrad; B, naked unfused permanent tetrad; C, permanent tetrad
osed within a laevigate envelope. D, permanent tetrad enclosed within a sculptured envelope; *Z*, permanent dyad
:; E, naked fused permanent dyad; F, naked unfused permanent dyad; G, permanent dyad enclosed within a laevi-
envelope; H, permanent dyad enclosed within a sculptured envelope; I, naked alete monad. J, alete monad enclosed
in a laevigate envelope; K, alete monad enclosed within a sculptured envelope; L, *Laevolancis*-type monad. *M*, *Ambi-*
ites? vavrdovii (?monads torn apart from tetrad). * Naked, no envelope; fused, no superficial line between monads;
sed, line present.)

	author	geographic area	*Y*	A	B	C	D	*Z*	E	F	G	H	I	J	K	L	*M*
lanvirn	Vavrdova 1984, 1990	Bohemia	×					×									?
	Corna 1970																
	McClure 1988	Saudi Arabia	×														
	Strother *et al.* 1996	Saudi Arabia		×	×	×			×	×	×					×	
aradoc	Richardson 1988	Southern Britain		×	×	×	×		×	×	×	×	×	×	×	×	
	Wellman 1996																
	Gray *et al.* 1982	Libya	×														×
shgill	Gray & Boucot 1972	Kentucky, USA		×		×	×										
	Gray *et al.* 1982																
	Gray 1985, 1988																
	Gray 1988	Tennessee, USA	×														
	Gray 1988	Georgia, USA	×														
	Strother 1991	Illinois, USA		×													
	Gray 1988	Ontario, Canada	×														
	Burgess 1991	southern Britain		×		×	×			×	×	×					
	Vavrdova 1982, 1984, 1988, 1989	Bohemia		×			×		×	×		×	×		×	×	×
	Reitz & Heuse 1994	Germany		×					×				×	×			
	Steemans *et al.* 1996	Turkey		×		×	×		×	×	×	×	×		×		×
	Richardson 1988	Libya		×			×		?	×		×			×		×
	Gray *et al.* 1986	South Africa	×														
Ashgill	Lakova *et al.* 1992	Bulgaria		×			×	×					×				
	Foster & Williams 1991	Australia	×														
huddanian	Burgess 1991	southern Britain			×	×	×		×	×	×	×			×		×
	Richardson 1988	Libya			×	×	×		×	×	×	×		×	×		×
	Miller & Eames 1982	New York State			×		×			×					×		
huddanian Aeronian	Johnson 1985	Pennsylvania			×		×		×	×	×	×	×	×	×		×
landovery	Bar & Riegel 1980	Ghana	×														
	Gray *et al.* 1985	Brazil	×					×									×

il (Grahn & Caputo 1992). Models suggest that else-
re there was a rapid amelioration of global
peratures (Worsley *et al.* 1994), resulting in a thermal
imum during the Silurian (Berner 1994).

ne Late Ordovician records from north Africa are
from an area known to have experienced glaciation
e Ashgill (Hirnantian). The Bohemian Ashgill occur-
es in the Lower Kosov Formation are particularly
mative in this respect because they are in rocks imme-
ly below glacio-marine deposits. Vavrdova (1988)
rded increase in numbers of cryptospores in the
ation (from 0.5–80% of palynomorphs in 20 m of
s) which she considered facies controlled and related
pid shallowing. Richardson (1996) tentatively corre-
this with decreasing temperature at the start of the
Ordovician and, because there were little differences
versity between Ashgill and earliest Llandovery cryptospore assemblages (see, also, Gray 1985), concluded that the climate changes had little or no effect on the cryptospore producers, with the plants rapidly re-invading previously glaciated areas, there being no direct evidence for glaciation in Bohemia or surrounding areas.

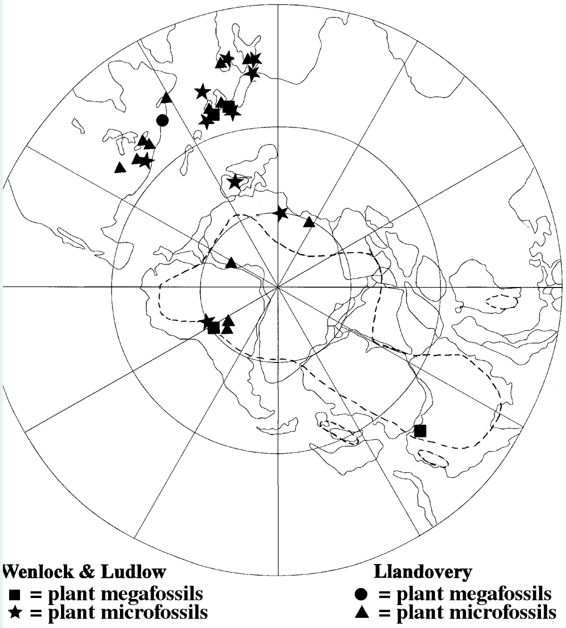
Such persistence is consistent with inferences, based on spore characteristics and absence of vegetative body fossils, that the plants possessed the behavioural and ecophysiological properties of bryophytes (Longton 1979; Proctor 1979; Scott 1982; Smith 1982). Gray (1985) in particular has advocated life styles similar to annual shuttle and fugutive species of semi-arid and arid deserts, both hot and cold, where survival relies on a variety of strategies, e.g. poikilohydry, anhydrobiosis, opportunism, telescoped life history (Bewley 1979; During 1979; Bischler & Jovet-Ast 1981; Gray 1984, 1985), while the widespread occurrences from the poles to the equator (Longton 1979) of extant mosses and to a lesser extent liverworts (e.g. Schuster 1984) today testify to their survival in a wide range of habitats and climate. Particularly relevant here are observations and experiments on polar bryophytes, where they are highly significant components of ecosystems in terms of cover and productivity, and colonize a wide range of microhabitats (Longton 1988). The limited height of bryophyte 'turfs' contributes to reduction of water stress by maintenance of higher humidity close to the ground in the boundary layer; nevertheless, such mats experience and tolerate far greater extremes of temperature than those measured by conventional meteorological means (Longton 1988).

Documentation of the diverse physiological attributes of polar bryophytes that allow colonization of severe environments is outside the scope of this paper, but as Longton (1988) observed, such attributes are also present in temperate species and even tropical ones. Indeed, distribution of bryophytes in the tropics is probably controlled more by competition, and thus a lack of suitable habitats, rather than by narrow tolerances. Endowing similar physiological versatility and behavioural strategies to the cryptospore producers would explain their widespread occurrences in the Ordovician and Silurian, when they are recorded at low latitudes. Then their local distribution was presumably mainly controlled by abiotic physical parameters, although competition from algal/cyanobacterial mats and possibly lichens cannot be discounted. Towards the end of the Silurian they would have suffered in competition from the increasingly tall tracheophytes that had the capacity to persist and flourish in the vegetative state even in water-stressed environments. The advent of tracheophytes is marked by the presence of trilete spores of *Ambitisporites*-type in dispersed assemblages. The earliest generally accepted record is from the Aeronian (Late Llandovery) of southern Britain (Burgess 1991). Trilete spores in assemblages from Greenland (Nøhr-Hansen & Koppelhus 1988) have been dismissed by Gray (1991), while more recently described examples from the Ashgill of Turkey may possibly represent monads torn apart from a permanent tetrad (Steemans *et al.* 1996; C. Wellman, personal communication). Trilete spores increased in numbers and diversity (spore ornaments first appeared in the Wenlock) throughout the Silurian, and from their advent show a wide latitudinal range (figures 6 and 7). The earliest megafossils of the plants known to have produced such spores later in the Silurian and Devonian occur in the Wenlock of Ireland (Edwards *et al.* 1983) and are widespread in low latitudes by the end of the Silurian. *Cooksonia* in the ?Ludlow/Pridoli of Bolivia is the first fertile record in high latitude (*ca.* 60° S) in Gondwana (Morel *et al.* 1995), while sterile axes occur in abundance at other horizons in the Kirusillas Formation, possibly extending down to the Wenlock (Toro *et al.* 1997). Thus, it seems likely that the earliest embryophytes of 'pteridophyte' aspect (direct anatomical evidence for homoiohydry being first recorded in the latest Silurian) were as geographically widespread as the cryptospore producers, and hence had similarly broad climate tolerances while adopting differing survival strategies. In this case there is more evidence from body fossils that they persisted in the vegetative state. Although nothing is known of the longevity of individual plants or the time taken to reach reproductive maturity (Gray 1985), morphological and anatomical characteristics (i.e. small size, high proportion of structural tissues, and axial architecture), rather than physiological ones probably contributed to their greater tolerance of abiotic/physical stress.

5. THE CARBONIFEROUS TROPICAL WETLANDS

Pioneering work on Carboniferous plants and climate centred on recognition of its tropical aspect (for recent summary see Chaloner & McElwain (1997)). This was superseded first by detailed reconstruction of communities associated with ecological partitioning within the low-lying tropical wetlands (e.g. Phillips & Peppers 1984), and more recently by attempts to relate changes in the composition of such communities to the global climate effects imposed by glaciations in the Southern Hemisphere (DiMichele & Phillips 1996*a*). They began in the Namurian, reached a maximum late in the Westphalian, at the end of which ice sheets began to wane in South America, but persisted in eastern Gondwana until the Kazanian (in Australia), a total period of *ca.* 60–70 Ma (Crowell & Frakes 1975; Frakes *et al.* 1992; Francis *et al.* 1994). Eustatic changes in sea level (Heckel 1989) would have impacted on tropical lowlands and, as Ziegler (1990) has emphasized, glacial and interglacial changes would have altered the position of the Intertropical Convergence Zone with implications for equatorial air flow and hence distribution and periodicity of rainfall. As the principal physical variables in the tropical mires and clastic wetlands relate to rainfall, runoff and evaporation, it might be anticipated that the major climatic oscillations of high latitudes would be reflected in vegetation in the low palaeotropics. An unparalleled record based on spores, compressions, and permineralizations (mainly coal balls) has produced an excellent database throughout Euramerica, such that we probably know more about the fate of tropical vegetation during the climate oscillations of the Late Palaeozoic Ice Age than that of the Pleistocene (DiMichele *et al.* 1996).

The community approach pioneered in Britain by Davies (1929), who recognized certain groupings of plants in the Welsh Coal Measures, was developed by Scott (1978). He interpreted similar groupings in terms of depositional environments, distinguishing the vegetation of the mires in swampy lowlands with persistently high groundwater table and rainfall from that associated with the rivers, lakes and deltas of the better drained flood plains (the wet clastic vegetation of DiMichele & Phillips (1996*b*)). Detailed information on the composition of the communities (table 4), their habitats, and ecological preferences, and the subsequent documentation of floristic change as recorded in a seminal series of papers by Phillips and associates, have allowed application of contemporary ecological philosophy and methodology to the Carboniferous as a prelude to interpreting causes of changes in community dynamics (DiMichele & Phillips 1996*b*). Within the mires of Euramerica they identified three major associations circumscribed by the architecture of dominant trees, their reproductive strategies, life histories, and the abundance and diversity of ground cover. From such data, plus associated mineral matter and fusain, and



e 6. Distribution of plant assemblages in the Silurian awn from Denham & Scotese 1987).

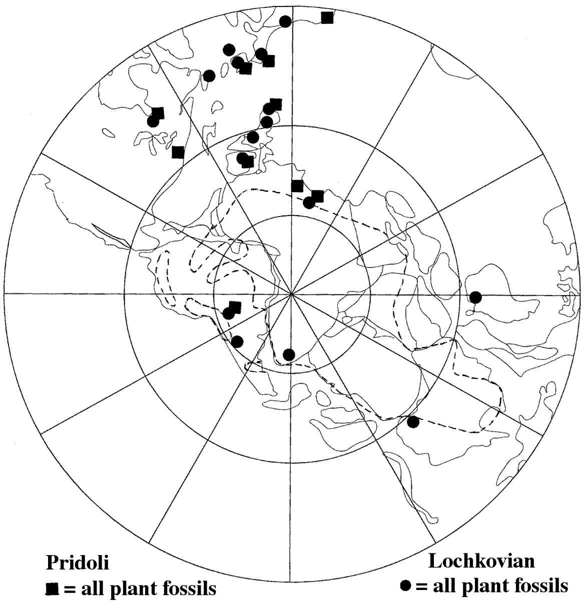


Figure 7. Distribution of plant assemblages in the Late Silurian–Early Devonian (redrawn from Denham & Scotese 1987).

proportions of roots and shoots, they inferred the ohabitats of the associations in terms of substrate ess, nutrient status, and physical disturbance (see 4; Phillips & Peppers 1984; Phillips *et al.* 1985; Phil- & DiMichele 1992; DiMichele & Phillips 1996*a*). With exception of marattialean ferns, these communities ined of broadly the same composition throughout –10 Ma of the Westphalian, but with species turnover comorphic' themes, i.e. species replacement by those similar growth architecture and life history, a conse- ce of the canalization between the major classes lished in the Late Devonian (see p. 2, DiMichele & ips 1996*b*).

ie lowland floodplains, with their far greater hetero- ity of microhabitats and concomitant diversity, were inated by communities of pteridosperms or sphenop- (in habitats characterized by physical disturbances) smaller numbers of lycopods, cordaites and ferns, again only marattialean ferns showed major changes ominance through time (e.g. Pfefferkorn & Thomson).

ie most detailed records, both temporal and spatial, from North America, but Phillips & Peppers (1984) rted similar vegetation patterns across the palaeocon- it from Oklahoma to the Ukraine with episodes of or less synchronous periods of change, at the West- ian A/B and the Westphalian–Stephanian boundary llips *et al.* 1974; Phillips & Peppers 1984). However, in pe, changes in the latter were time-transgressive from to east (e.g. recorded in the Early Stephanian in ia), with vegetation of typically Westphalian aspect sting in China until the Permian. These changes attributed to increased dryness, presumably resulting decreased rainfall and/or increased seasonality at the tor, and initially linked to tectonic activity as the sion of Euramerica with Gondwana produced raphic barriers and rain shadows (Phillips & Peppers 1984). However, the Westphalian–Stephanian boundary event, which resulted in major extinctions in tropical wetland vegetation, coincided with the termination of glaciation in most parts of Gondwana and inferred narrowing of the Intertropical Convergence Zone, and increased seasonality. Pfefferkorn & Thomson (1982) showed quantitatively that changes in dominance patterns involving the extinction of 50% of species (DiMichele & Phillips 1996*a*) occurred earlier in the floodplains (base of Westphalian D), attributing this to greater sensitivity of plants growing on well-drained soils to small changes in the water table.

The end Westphalian extinctions, which involved in total approximately two-thirds of mire species of North America, included 90% of the arborescent species and virtually all fern vines, although pteridosperm climbers survived (table 5). The greatest impact was suffered by the more highly physiologically and reproductively adapted edaphic specialists, with the less hydrophyllic taxa such as certain species of *Sigillaria* persisting locally in the Stephanian. Indeed in the Early Permian (Rotliegend) of Europe and North America, there remained only one tree-like lycopsid, *S. brardii*. This species was characterized by broad ecological tolerances but always grew in humid environments. The tree lycopod communities with their complex hierarchical dominance were replaced by those with less temporal and spatial complexity. Tree ferns, and to a lesser extent pteridosperms, were the opportunist survivors from groups narrowly distributed in the Westphalian. The commonest trees, viz. *Psaronius* species, were larger than Westphalian ones and probably longer-lived, and while fewer of the mire niches were colonized than earlier, marsh vegetation dominated by the lycopod *Chaloneria* (a 'pole' plant *ca.* 1 m high) flourished alongside the tree communities of ferns and, more rarely, pteridosperms and cordaites. The new wetland biome was quite distinct from that of the

Table 4. *Carboniferous mire vegetation data based on DiMichele & Phillips (1996a)*

mire vegetation	
assemblage 1	
dominant taxon:	*Lepidophloios hallii*: monocarpic (? aquacarpic) lycopsid
veg. characteristics:	*Low* biomass and *low* diversity in ground cover, vines, understorey *Psaronius*, if present very minor and decline if *Lepidophloios* > 70% biomass; low *Calamites*
habitat inference:	Extended periods of standing water—flooded peat surfaces/i.e. *wettest mires*
assemblage 2	
dominant taxa:	*Diaphorodendron scleroticum* or *Sigillaria* sp: polycarpic lycopsids
veg. characteristics:	Variable composition. *High* biomass but *low* diversity in ground cover. Understorey trees and shrubs. *Psaronius*, 5–15% biomass. Highest *Calamites*
habitat inference:	Wet peat, occasional flooding, minor physical disturbance and fire
assemblage 3	
dominant taxa:	*Paralycopodites brevifolius*: small polycarpic lycopsid. Medullosan pteridosperms (cordaites from Westphalian B)
veg. characteristics:	Highest diversity in ground cover, intermediate *Calamites*, abundant *Psaronius*
habitat inference:	High mineral content, fire prone (from abundant charcoal), transitional between peats and clastic wetland

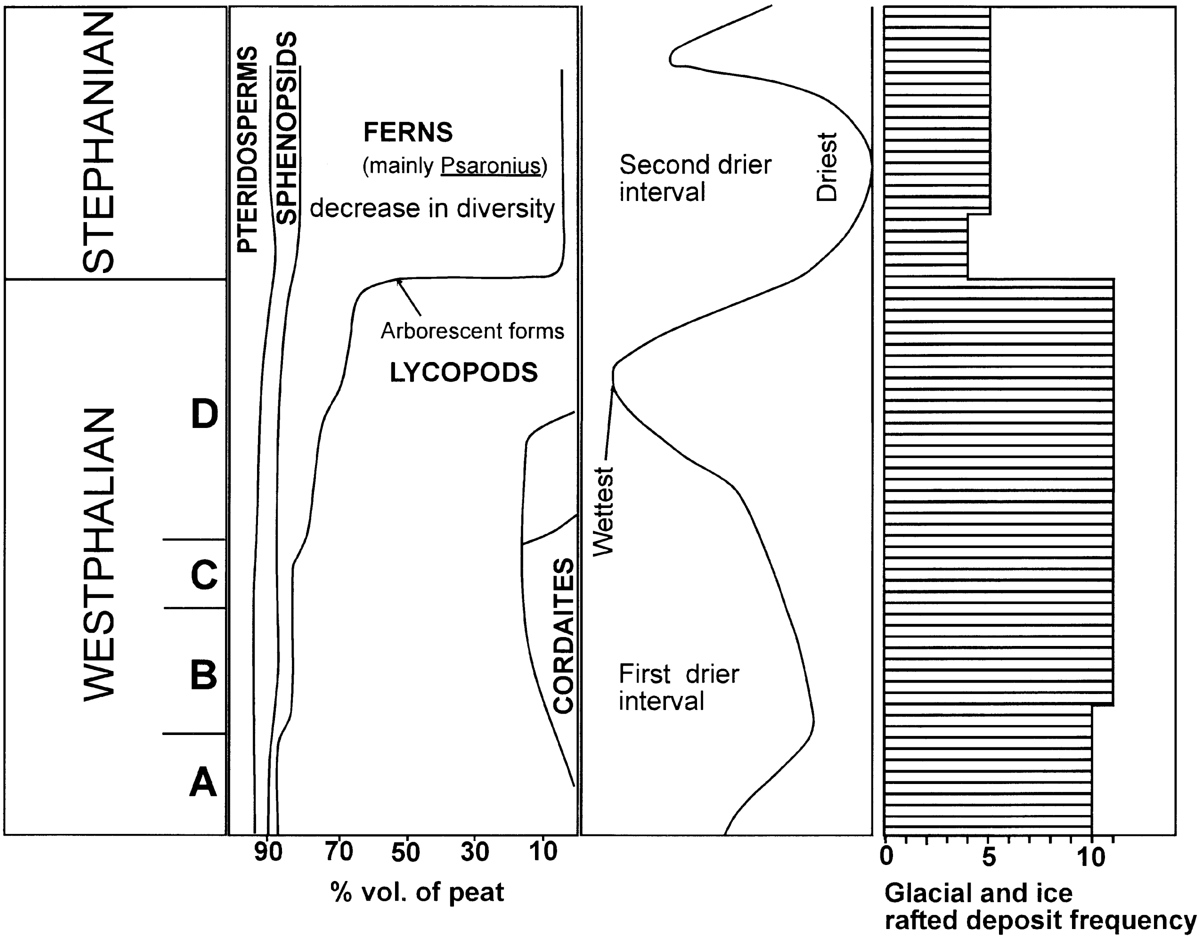
presumed drier hinterland, which was dominated by conifers and pteridosperms (DiMichele & Aronson 1992), many of which were also present in the Westphalian. However, in post-Carboniferous times many of the taxa, and particularly those with xeromorphic adaptations that originated in the 'moisture-limited' habitats of areas marginal to the lowlands, migrated into the lowlands when they became seasonally dry. Such plants subsequently formed the ancestral pool for the vegetation of the Mesozoic wetlands (DiMichele & Aronson 1992) and included members of the Cycadales, Ginkgoales and Coniferales. These would appear to be excellent examples of climate-driven change in vegetation—drying first eliminated wetland assemblages, which were then replaced by pre-adapted stocks from marginal lowlands (Knoll 1984); however, the incompleteness of the rock record and tectonic complications urge caution in accepting this simplistic casual relationship (Cleal 1991). There are very few continuous successions through the Westphalian–Stephanian transition, largely because the sediments were deposited in quite different settings. The Westphalian is known chiefly from paralic basins and the Stephanian, intermontane, thus complicating direct comparison of plant assemblages. In addition, erosion of the Variscan mountain chains resulting from the collision of the Gondwanan and Laurussian continental plates towards the end of the Westphalian, would have produced much coarser, more freely draining substrates in comparison with the swampy conditions in which peat had accumulated. Finally, the new mountain chains would have impacted on climate via changes in atmospheric circulation patterns and, particularly important for the wetland biomes, changes in atmospheric humidity (see p. 13 for Permian similarities).

The earliest drier phase at the Westphalian A/B boundary had major consequences for mire vegetation. A decline in the high level of lycopod dominance (except for an occasional marked increase of *Lepidophloios harcourtii*) was accompanied by a major expansion of cordaites, with pteridosperms and tree ferns all lacking the abundant aerating tissues of the wetland taxa as subdominants, and by an increase in herbaceous lycophytes (e.g. *Polysporia*), suggestive of development of marshlands. The ferns, in particular, are considered able to have exploited the climatic fluctuations consistent with an erratic monsoonal circulation with the *Lepidophloios* marking intervals in flooding. Further indications of drying come from the low shoot to root ratio in coal balls, and the abundant fusain indicative of wild fires.

Apart from these drying phases (figure 8), the persistence of vegetation composition and landscapes in the tropical lowlands for most of the Westphalian may seem inconsistent with the existence of repeated high-latitude glacial cycles of an ice age, and leads to the possibility that there were no repercussions for tropical vegetation (DiMichele *et al.* 1996). However, peat formation was not continuous. A period of cyclothems (limestones ± clastics–peat) in the coal measures was roughly consistent with the glaciations in Gondwana, and allows the hypothesis that repeated flooding relating to interglacials could be glacially driven (Heckel 1989), although it is clearly difficult to distinguish between such eustatic changes in sea level and local sedimentation dynamics. Late Carboniferous (Westphalian–Stephanian) coal basins of north-

Table 5. *Extinction, survivorship and origin of species based on coal-ball data*[1] *(from DiMichele & Phillips 1996a), spore-pollen data*[2] *(from Peppers 1985) and clastic compressions*[3] *(from Gillespie & Pfefferkorn 1979)*

	Late Westphalian		W/S	Early Stephanian	
	total	extinction	Persistence	total	origination
trees[1]	30	26 (86.7%)	4 (13.3%)	17	13 (76.5%)
ground cover[1] vines and shrubs	18	6 (33.3%)	12 (66.6%)	25	13 (52%)
spore/pollen[2]	43	19 (44.2%)	24 (55.8%)	26	2 (7.7%)
compressions[3]	18	9 (50%)	9 (50%)	10	1 (10%)



re 8. Percentage volume of plants forming peat (column 2), wetness–dryness curve (column 3), and number of records of al deposits (column 4) during the Upper Carboniferous, assembled from Phillips *et al.* (1985) and Frakes *et al.* (1992).

Central Europe developed initially (probably in urian times) as equatorial wetland paralic basins g the southern margin of Laurussia in front of the ıward-propagating Variscan fold belt. The early es of deformation and nappe emplacement involved e suturing of Gondwana and Laurussia led to lithoric flexuring and the production of a foredeep, acting more or less continuous shallow foreland basin north ie advancing orogen. Pre-Westphalian D sedimenta- was largely from the foreland, but increasingly the centres were in-filled by clastic material derived the orogenic wedge, first dividing the original more ısive region into smaller, isolated, shallowing upward ssor basins. DiMichele *et al.* (1996) thus chose to late Desmoinesian sediments (Late Westphalian D uivalent to maximum glaciation in the North and h Hemispheres; Frakes *et al.* 1992) in the Illinois ı, whose physical setting suggested that climate and evel fluctuations produced a major impact on sedi- ary pattern. Here successive coal seams were rated by intervals of *ca.* 100 000 years of fresh water marine clastics and limestones, with evidence for sition close to the shore rather than on floodplains. showed that species persisted in communities exhig the same dominance, diversity, and architecture for stimated average period of 1.0–1.5 Ma, recolonizing areas when conditions for peat formation returned. Comparisons with events in the Tertiary and Pleistocene produced three possible explanations for such persistence in the face of environmental change: (i) vegetation was repeatedly disrupted and then reassembled in similar habitats, but with assemblages in drier lowland areas between peat-forming episodes being quite different; (ii) vegetation was able to migrate regionally into other basins protected from the effects of climate changes; and (iii) vegetation persisted intact in isolated refugia outside the lowland preservational areas.

DiMichele & Phillips (1996*b*) favoured a combination of explanations (ii) and (iii), noting that the species persistence of this relatively short time (1–1.5 Ma) contrasted with the situation for the entire Westphalian when over ten million years the structural aspects of communities remained the same, but there was almost complete species turnover, albeit involving ‘ecomorphic replacement by close relatives’ (p. 89, DiMichele & Phillips 1996*b*).

6. THE PERMIAN TRANSITION

Continued northward drift of Pangaea involved Stephanian–Lower Permian wrench faulting, which produced a number of intramontane basins across the former hinterland and caused fragmentation of the wetland zone.

Changes in topography and drainage again drastically reduced the number of habitats available to the mire plants (particularly the arborescent lycopods that comprise the most conservative of communities), and associated changes in sedimentation patterns produced new edaphic conditions, e.g. an increase in the production of sandy soils. Red bed fluvial/alluvial plain sediments became extensively developed in some regions (Kerp 1996). In addition, the newly formed mountain chains may have altered atmospheric circulation patterns (Rowley *et al*. 1985) and, from observed changes in major vegetation types from wetland communities to the mesophytes and xerophytes earlier associated with the uplands, atmospheric humidity. Considering the plant record during this interval, in Europe at least, interpretation of data from the Upper Stephanian and Lower Permian is frustrated by imprecise correlation between small basins, stratigraphic hiatuses, and facies biases of certain taxa. During the Stephanian however, the conifers became more abundant and callipterid pteridosperms diversified. These trends continued into the Rotliegend (Lower Permian) with increasing numbers of plants adapted to drier conditions, although peat-forming communities still persisted and dominate concepts of Lower Rotliegend vegetation (e.g. Barthel 1976).

In contrast, in the Late Permian Zechstein, meso- and xerophilous vegetation types dominated, marked by a proliferation of gymnosperms (particularly conifers and to a lesser extent pteridosperms), with adaptations typical of a warm and dry climate. Such differences in assemblage have led to the concept of a Palaeophytic–Mesophytic boundary within the Permian (e.g. Gothan & Weyland 1954) and one which might be related to the cessation of glaciations in Gondwana (IV in figure 1). However, as Kerp (1996) has observed, such a boundary is based more on incomplete knowledge rather than on hard facts. Radiometric and palaeomagnetic dating suggests that for the Permian in most of Europe, only the lowermost and very uppermost parts are present, and where there is believed to have been more continuous sedimentation (e.g. the Fore-Urals) a gradual development of floras is seen. Indeed, more recent research has also demonstrated similarities in walchiaceans and callipterids between Lower and Upper Permian assemblages (see references in Kerp 1996).

7. CONCLUSIONS

From the above, it becomes obvious that at the present time there are very few quantitative signals of climate in individual plants that we are capable of exploiting, with growth rings supplying the best evidence to date. Stomatal frequencies have been shown to have potential in tracing fluctuations in atmospheric CO_2, although interpretation of the data for the earliest land plants is clouded by their many anatomical adaptations to increase water use efficiency in their pioneering attempts to colonize the subaerial environment. Their archetypal switch habit provides little scope for morphological adaptations. In considering vegetation rather than individual plants, the Carboniferous tropical lowland studies provide an excellent example of how detailed descriptions of communities and their ecological preferences, even where there are no close extant relatives, can be used in disentangling causal relationships for changes at the regional level, while similar approaches for the Permian are in their infancy. Interpretation would be greatly facilitated by detailed integrated information on climate itself from geological data (e.g. Boucot & Gray 1982) and from computer modelling (e.g. Valdes 1993), which is proving so rewarding for the Mesozoic and later.

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REFERENCES

Antevs, E. 1953 Tree rings and seasons in past geological eras. *Tree Rings Bull.* **20**, 17–19.

Arnold, C. A. 1929 On the radial pitting in *Callixylon*. *Am. J. Bot.* **16**, 391–393.

Arnold, C. A. 1947 *An introduction to paleobotany.* New York: McGraw-Hill.

Ash, J. 1985 Growth rings and longevity of *Agathis vitiensis* (Seemann) Benth. & Hook. f. ex Drake in Fiji. *Australian J. Bot.* **33**, 81–88.

Bär, P. & Riegel, W. 1980 Mikrofloren des höchsten Ordovizium bis tiefen Silurs aus der Unteren Sekondi-Serie von Ghana (Westafrika) und ihre Beziehung zu den Itaim-Schichten des Maranhao-Beckens in NE-Brasilien. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **160**, 42–60.

Barrett, P. J. 1991 The Devonian to Jurassic Beacon Supergroup of the Transantarctic Mountains and correlatives in other parts of Antarctica. In *The geology of Antarctica* (ed. R. Tingey), pp. 120–152. Oxford: Clarendon Press.

Barrett, P. J., Smith, N. D. & Woolfe, K. J. 1991 Early Permain glaciation in Antarctica—evidence from Allen Hills (extended abstract). *Sixth International Symposium on Antarctic Earth Sciences, Tokyo, Japan*, pp. 34–37.

Barthel, M. 1976 Die Rotliegendflora Sachsens. *Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden* **24**, 1–190.

Beck, C. B. 1976 Current status of the Progymnospermopsida. *Rev. Palaeo. Palynol.* **21**, 5–23.

Beerling, D. J. 1994 Modelling palaeophotosysthesis: Late Cretaceous to present. *Phil. Trans. R. Soc. Lond.* B **346**, 421–432.

Beerling, D. J. & Woodward, F. I. 1997 Changes in land plant function over the Phanerozoic: reconstructions based on the fossil record. *Bot. J. Linn. Soc.* **124**, 137–158.

Berner, R. A. 1992 Weathering, plants, and the long-term carbon cycle. *Geochim. Cosmochim. Acta* **56**, 3225–3231.

Berner, R. A. 1994 GEOCARBII: a revised model of atmospheric CO_2 over Phanerozoic time. *Am. J. Sci.* **294**, 56–91.

Berner, R. A. 1997 The rise of plants and their effect on weathering and atmospheric CO_2. *Science* **276**, 544–546.

Berry, C. M. & Fairon-Demaret, M. 1998 The Middle Devonian flora revisited. (Submitted.)

Bewley, J. D. 1979 Physiological aspects of desiccation tolerance. *A. Rev. Plant Physiol.* **30**, 195–238.

Bischler, H. & Jovet-Ast, S. 1981 The biological significance of morphological characters in Marchantiales (Hepaticae). *The Bryologist* **84**, 208–215.

Boucot, A. J. & Gray, J. 1982 Paleozoic data of climatological significance and their use for interpreting Silurian–Devonian climate. In *Climate in Earth history. Studies in geophysics*, pp. 189–198. Washington, DC: National Academy Press.

hley, P. J., Marshall, J. D., Carden, G. A. F., Robertson, D. R., Long, D. G. F., Meidla, T., Hints, L. & Anderson, T. F. 4 Bathymetric and isotopic evidence for a short-lived Late dovician glaciation in a greenhouse period. *Geology* **22**, 295– 8.

ess, N. D. 1991 Silurian cryptospores and miospores from the e Llandovery area, south-west Wales. *Palaeontology* **34**, 575– 9.

to, M. V. & Crowell, J. C. 1985 Migration of glacial centers ross Gondwana during the Paleozoic Era. *Bull. Geol. Soc. Am.* , 1020–1036.

oner, W. G. & Creber, G. T. 1973 Growth rings in fossil ods as evidence of past climates. In *Implications of continental ft to the earth sciences. 1.* (ed. D. H. Tarling & S. K. Runcorn), 425–437. London and New York: Academic Press.

oner, W. G. & Creber, G. T. 1990 Do fossil plants give a matic signal? *J. Geol. Soc. Lond.* **147**, 343–350.

oner, W. G. & McElwain, J. 1997 The fossil plant record and bal climatic change. *Rev. Palaeo. Palynol.* **95**, 73–82.

oner, W. G., Hill, A. & Rogerson, E. C. W. 1978 Early vonian plant fossils from a southern England borehole. *aeontology* **21**, 693–707.

man, J. L. 1994 Distinguishing internal developmental aracteristics from external palaeoenvironmental effects in sil wood. *Rev. Palaeo. Palynol.* **81**, 19–32.

, C. J. 1991 *Plant fossils in geological investigation*. Chichester, : Ellis Horwood.

a, O. 1970 Plant remains in the Ordovician of the Bohemian assif. *Geologica Carpathica* **21**, 183–186.

er, G. T. 1977 Tree-rings: a natural data storage system. *Bot. . Cambridge Phil. Soc.* **50**, 349–383.

er, G. T. & Chaloner, W. G. 1984*a* Influence of environ-ntal factors on the wood structure of living and fossil trees. *. Rev.* **50**, 357–448.

er, G. T. & Chaloner, W. G. 1984*b* Climatic indications from wth rings in fossil woods. In *Fossils and climate* (ed. P. enchley), pp. 49–74. Chichester, UK: Wiley.

ell, J. C. & Frakes, L. A. 1975 The Late Palaeozoic glaciation. *Gondwana geology* (ed. K. S. W. Campbell), pp. 313–331. nberra: Australian National University Press.

ley, T. J. 1994 Pangean climates. In *Pangea: paleoclimate, onics, and sedimentation during accretion, zenith and breakup of a ercontinent* (ed. G. D. Klein), pp. 25–39. Boulder, CO: ological Society of America, Special Paper no. 288.

ley, T. J., Mengel, J. G. & Short, D. A. 1987 ndwanaland's seasonal cycle. *Nature* **329**, 803–807.

enhoffer, J. M. & Bonamo, P. M. 1989 *Rellimia thomsonii* m the Givetian of New York: secondary growth in three ders of branching. *Am. J. Bot.* **76**, 1312–1325.

es, D. 1929 Correlation and palaeontology of the coal measures East Glamorganshire. *Phil. Trans. R. Soc. Lond.* B **217**, 91–153.

am, C. R. & Scotese, C. R. 1987 Terra Mobilis$^{\mathrm{TM}}$: a plate tonics program for the Macintosh. Austin, TX: Earth in otion Technologies.

ichele, W. A. & Aronson, R. B. 1992 The Pennsylvanian– rmian vegetational transition: a terrestrial analogue to the shore–offshore hypothesis. *Evolution* **46**, 807–824.

ichele, W. A. & Hook, R. W. 1992 Paleozoic terrestrial osystems. In *Terrestrial ecosystems through time* (ed. A. K. hrensmeyer, J. D. Damuth, W. D. DiMichele, R. Potts, H.- Sues & S. L. Wing), pp. 205–325. Chicago and London: iversity of Chicago Press.

ichele, W. A. & Phillips, T. L. 1996*a* Climate change, plant inctions and vegetational recovery during the Middle–Late nsylvanian transition: the case of tropical peat-forming vironments in North America. In *Biotic recovery from mass inction events* (ed. M. B. Hart), pp. 201–221. London: ological Society Special Publication no. 102.

DiMichele, W. A. & Phillips, T. L. 1996*b* Clades, ecological amplitudes, and ecomorphs: phylogenetic effects and persistence of primitive plant communities in the Pennsylvanian-age tropical wetlands. *Palaeo. Palaeo. Palaeo.* **127**, 83–105.

DiMichele, W. A., Pfefferkorn, H. W. & Phillips, T. L. 1996 Persistence of Late Carboniferous tropical vegetation during glacially driven climatic and sea-level fluctuations. *Palaeo. Palaeo. Palaeo.* **125**, 105–128.

During, H. J. 1979 Life strategies of bryophytes: a preliminary review. *Lindbergia* **5**, 2–18.

Edwards, D. 1990 Constraints on Silurian and Early Devonian phytogeographic analysis based on megafossils. In *Palaeozoic palaeogeography and biogeography* (ed. W. S. McKerrow & C. R. Scotese), pp. 233–242. London: Geological Society, Memoir no. 12.

Edwards, D. 1994 Towards an understanding of pattern and process in the growth of early vascular plants. In *Shape and form in plants and fungi* (ed. D. S. Ingram & A. Hudson), pp. 39–59. Linnean Society Symposium Series no. 16. London: Academic Press.

Edwards, D. & Axe, L. 1992 Stomata and mechanics of stomatal functioning in some early land plants. *Courier Forschungsinstitut Senckenberg* **147**, 59–73.

Edwards, D. & Davies, M. S. 1990 Interpretations of early land plant radiations: 'facile adaptationist guesswork' or reasoned speculation? In *Major evolutionary radiations* (ed. P. D. Taylor & G. P. Larwood), pp. 351–376. The Systematics Association Special Volume no. 42. Oxford: Clarendon Press.

Edwards, D., Abbott, G. D. & Raven, J. A. 1996 Cuticles of early land plants: a palaeoecophysiological evaluation. In *Plant cuticles—an integrated functional approach* (ed. G. Kerstiens), pp. 1–31. Oxford: BIOS Scientific Publishers.

Edwards, D., Feehan, J. & Smith, D. G. 1983 A Late Wenlock flora from Co. Tipperary, Ireland. *Bot. J. Linn. Soc.* **86**, 19–36.

Falcon-Lang, H. 1997 A Lower Carboniferous palaeo-monsoon: charcoal as a palaeoclimatic tool. Abstracts of the Fire and the Palaeonvironment Symposium, University of Sheffield, pp. 47–48.

Foster, C. B. & Williams, G. E. 1991 Late Ordovician–Early Silurian age for the Mallowa Salt of the Carribudy Group, Canning Basin, Western Australia, based on occurrences of *Tetrahedraletes medinensis* Strother and Traverse 1979. *Australian J. Earth Sci.* **38**, 223–228.

Frakes, L. A., Francis, J. E. & Syktus, J. L. 1992 *Climate models of the Phanerozoic*. Cambridge University Press.

Francis, J. E., Woolfe, K. J., Arnott, M. J. & Barrett, P. J. 1994 Permian climates of the southern margins of Pangea: evidence from fossil wood in Antarctica. In *Pangea: global environments and resources*, pp. 275–282. Canadian Sociey of Petroleum Geologists, Memoir no. 17.

Francis, J. E., Woolfe, K. J., Barrett, P. J. & Arnott, M. J. 1993 Permian fossil forests of Allan Hills, Antarctica. *Special Pap. Palaeontology* **49**, 75–83.

Frentzen, K. 1931 Die palaeographische Bedeutung des Auftretens von Zuwachszonen (Jahresingen) bei Holzern der Sammelgattung *Dadoxylon Endl.* aus dem Carbon und dem Rotliegenden des Oberrheingebeites. *Zentralblatt für Mineralogie, Geologie und Paläontologie*, **1931B**, 617–624.

Galtier, J., Paris, F. & El Aouad-Debbaj, Z. 1996 La présence de *Callixylon* dans le Dévonien supérieur du Maroc et sa signification paléogéographique. *Compte Rendu de l'Académie des Sciences, Paris* **322**(2a), 893–900.

Gillespie, W. M. & Pfefferkorn, H. W. 1979 Distribution of commonly occurring plant megafossils in the proposed Pennsylvanian System Stratotype. In *Proposed Pennsylvanian System Stratotype, Virginian and West Virginia. 9th International Congress of Carboniferous Stratigraphical Geology* (ed. K. J. England), pp. 87–96. Guidebook Fieldtrip volume 1.

Golonka, J., Ross, M. I. & Scotese, C. R. 1994 Phanerozoic paleogeographic and paleoclimatic modelling maps. In *Pangea: global environments and resources*, pp. 1–47. Canadian Society of Petroleum Geologists, Memoir no. 17.

Gothan, W. & Weyland, H. 1954 *Lehrbuch der paläobotanik*. Berlin: Akademie.

Grahn, Y. & Caputo, M. V. 1992 Early Silurian glaciations in Brazil. *Palaeo. Palaeo. Palaeo.* **99**, 9–15.

Gray, J. 1984 Ordovician–Silurian land plants: the interdependence of ecology and evolution. In *Autecology of Silurian organisms* (ed. M. G. Bassett & J. D. Lawson), pp. 281–295. *Special Papers in Palaeontology* no. 32.

Gray, J. 1985 The microfossil record of early land plants: advances in understanding of early terrestrialization, 1970–1984. *Phil. Trans. R. Soc. Lond.* B **309**, 167–195.

Gray, J. 1988 Land plant spores and the Ordovician–Silurian boundary. *Bull. Br. Museum Nat. Hist. (Geology)* **43**, 351–358.

Gray, J. 1991 *Tetrahedraletes, Nodospora*, and the 'cross' tetrad: an accretion of myth. In *Pollen and spores, patterns of diversification* (ed. S. Blackmore & S. Barnes), pp. 49–87. The Systematics Association Special Volume no. 44. Oxford: Clarendon Press.

Gray, J. 1993 Major Paleozoic land plant evolutionary bio-events. *Palaeo. Palaeo. Palaeo.* **104**, 153–169.

Gray, J. & Boucot, A. J. 1972 Palynological evidence bearing on the Ordovician–Silurian paraconformity in Ohio. *Bull. Geol. Soc. Am.* **83**, 1299–1314.

Gray, J., Massa, D. & Boucot, A. J. 1982 Caradocian land plant microfossils from Libya. *Geology* **10**, 197–201.

Gray, J., Theron, J. N. & Boucot, A. J. 1986 Age of the Cedarberg Formation, South Africa and early land plant evolution. *Geol. Mag.* **123**, 445–454.

Gray, J., Boucot, A. J., Grahn, Y. & Himes, G. 1992 A new record of early Silurian land plant spores from the Paraná Basin, Paraguay (Malvinokaffric Realm). *Geol. Mag.* **129**, 741–752.

Gray, J., Colbath, G. K., de Faria, A., Boucot, A. J. & Rohr, D. M. 1985 Silurian-age fossils from the Paleozoic Paraná Basin, southern Brazil. *Geology* **13**, 521–525.

Heckel, P. H. 1989 Updated Middle–Upper Pennsylvanian eustatic sea level curve for mid-continent North America and preliminary biostratigraphic characterization. *Eleventh International Congress of Carboniferous Stratigraphy and Geology, C.R.* **4**, 160–185.

Jefferson, T. J. & Taylor, T. N. 1983 Permian and Triassic wood from the Transantarctic Mountains: paleoenvironmental indicators. *Antarctic J. US 1983 review*, pp. 55–57.

Johnson, N. G. 1985 Early Silurian palynomorphs from the Tuscarora Formation in central Pennsylvania and their paleobotanical and geological significance. *Rev. Palaeobot. Palynol.* **45**, 307–360.

Kent, D. V. 1985 Paleocontinental setting for the Catskill Delta. In *The Catskill Delta* (ed. D. L. Woodrow & W. D. Sevon), pp. 9–13. Boulder, CO: Geological Society of America, Special Paper no. 201.

Kerp, H. 1996 Post-Variscan Late Palaeozoic Northern Hemisphere gymnosperms: the onset to the Mesozoic. *Rev. Palaeobot. Palynol.* **90**, 263–285.

Knoll, A. H. 1984 Patterns of extinction in the fossil record of vascular plants. In *Extinctions* (ed. M. Nitecki), pp. 21–68. University of Chicago Press.

Kräusel, R. 1962 Antarctic fossil wood. In *Fossil floras of Antarctica* (ed. E. P. Plumstead). Transantarctic Expedition 1955–1958, Scientific Report **9**, 133–154.

Kräusel, R. & Weyland, H. 1929 Beiträge zur Kenntnis dur Devonflora, 3. *Abhandlung der Senckenbergischen Naturforschenden Gesellschaft* **41**, 315–360.

Kräusel, R. & Weyland, H. 1935 Neue Pflanzenfunde im Rheinischen Unterdevon. *Palaeontographica* B **80**, 171–190.

Kutzbach, J. E. & Gallimore, R. G. 1989 Pangaean climates: megamonsoons of the megacontinent. *J. Geophys. Res.* **94**, 3341–3357.

Lakova, I., Gocev, P. M. & Yanev, S. 1992 Palynostratigraphy and geological setting of the Lower Palaeozoic allochthon of the Dervent Heights, S.E. Bulgaria. *Geol. Balcanica* **22**, 71–88.

Lemoigne, Y., Iurina, A. & Snigirevskaya, N. 1983 Revision du genre *Callixylon* Zalessky 1911 (*Archaeopteris*) du Dévonien. *Palaeontographica* B **186**, 81–120.

Li, C.-S. 1992 *Hsüa robusta*, an Early Devonian plant from Yunnan Province, China and its bearing on some structures of early land plants. *Rev. Palaeobot. Palynol.* **71**, 121–147.

Li, C.-S. & Edwards, D. 1995 A re-investigation of Halle's *Drepanophycus spinaeformis* Göpp. from the Lower Devonian of Yunnan Province, southern China. *Bot. J. Linn. Soc.* **118**, 163–192.

Longton, R. E. 1979 Climatic adaptation of bryophytes in relation to systematics. 511–531. In *Bryophyte systematics* (ed. G. C. S. Clarke & J. G. Duckett). The Systematics Association Special Volume no. 14. London: Academic Press.

Longton, R. E. 1988 *The biology of polar bryophytes and lichens*. Cambridge University Press.

Maheshwari, H. K. 1972 Permian wood from Antarctica and revision of some Lower Gondwana wood taxa. *Palaeontographica* B **138**, 1–43.

Matten, L. C. & Banks, H. P. 1967 Relationship between the Devonian progymnosperm genera *Sphenoxylon* and *Tetraxylopteris*. *Bull. Torrey Bot. Club* **94**, 321–333.

McClure, H. A. 1988 The Ordovician–Silurian boundary in Saudi Arabia. *Bull. Br. Mus. (Nat. Hist.), Geol. Ser.* **43**, 155–163.

McElwain, J. & Chaloner, W. G. 1995 Stomatal density and index of fossil plants track atmospheric carbon dioxide in the Palaeozoic. *Ann. Bot.* **76**, 389–395.

Meyen, S. V. 1987 *Fundamentals of palaeobotany.* London and New York: Chapman & Hall.

Miller, M. A. & Eames, L. E. 1982 Palynomorphs from the Silurian Medina Group (Lower Llandovery) of the Niagara Gorge, Lewiston, New York, USA. *Palynology* **6**, 221–254.

Mora, C. I., Driese, S. G. & Colarusso, L. A. 1996 Middle-to-Late Paleozoic atmospheric CO_2 levels from soil carbonate and organic matter. *Science* **271**, 1105–1107.

Morel, E., Edwards, D. & Iñigez Rodriguez, M. 1995 The first record of *Cooksonia* from South America in Silurian rocks of Bolivia. *Geol. Mag.* **132**, 449–452.

Nøhr-Hansen, H. & Koppelhus, E. B. 1988 Ordovician spores with trilete rays from Washington-Land, North Greenland. *Rev. Palaeobot. Palynol.* **56**, 305–311.

Parrish, J. T. 1993 Climate of the supercontinent Pangea. *J. Geol.* **101**, 215–233.

Peppers, R. A. 1985 Comparison of miospore assemblages in the Pennsylvanian System of the Illinois Basin with those in the Upper Carboniferous of Western Europe. *Comptes Rendus 9th International Congress of Carboniferous Stratigraphical Geology* **2**, 483–502.

Pfefferkorn, H. W. & Thomson, M. C. 1982 Changes in dominance patterns in upper Carboniferous plant–fossil assemblages. *Geology* **10**, 641–644.

Phillips, T. L. & DiMichele, W. A. 1992 Comparative ecology and life history biology of arborescent lycopsids in Late Carboniferous swamps in Euramerica. *Ann. Missouri Bot. Gdn* **79**, 560–588.

Phillips, T. L. & Peppers, R. A. 1984 Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrence. *Int. J. Coal Geol.* **3**, 205–255.

Phillips, T. L., Peppers, R. A. & DiMichele, W. A. 1985 Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: environmental inferences. *Int. J. Coal Geol.* **5**, 43–109.

ps, T. L., Peppers, R. A., Avcin, M. J. & Laughnan, P. F. 74 Fossil plants and coal: patterns of change in nsylvanian coal swamps of the Illinois Basin. *Science* **184**, 57–1369.

or, M. C. F. 1979 Structure and eco-physiological adaptation ryophytes. In *Bryophyte systematics* (ed. G. C. S. Clarke & J. G. ckett), pp. 479–509. The Systematics Association Special lume no. 14. London: Academic Press.

, E. & Heuse, T. 1994 Palynofazies im Oberordovizium des xsothuringikums. *Neues Jahrbuch für Geologie und Paläntologie, natshefte* **6**, 348–360.

, W. & Hass, H. 1991 *Langiophyton mackiei* nov. gen., nov. c., ein Gametophyt mit Archegoniophoren aus dem Chert Rhynie (Unterdevon, Schottland). *Argumenta Palaeobot.* **8**, –117.

, W. & Hass, H. 1996 New information on gametophytes d sporophytes of *Aglaophyton major* and inferences about ssible environmental adaptations. *Rev. Palaeobot. Palynol.* **90**, –193.

lack, G. J. 1997 Early forest soils and their role in Devonian bal change. *Science* **276**, 583–585.

ardson, J. B. 1988 Late Ordovician and Early Silurian cryp- pores and miospores from northeast Libya. In *Subsurface ynostratigraphy of northeast Libya* (ed. A. El-Arnauti, B. Ownes B. Thusu), pp. 89–109. Benghazi, Libya: Garyounis iversity Press.

ardson, J. B. 1996 Lower and Middle Palaeozoic records of restrial palynomorphs. In *Palynology: principles and applica- s. 2. Applications* (ed. J. Jansonius & D. C. McGregor), pp. 5–574. American Association of Stratigraphic Palynologists ndation. Salt Lake City, Utah: Publishers Press.

ey, D. B., Raymond, A., Parrish, J. T., Lottes, A. L., tese, C. R. & Ziegler, A. M. 1985 Carboniferous leogeographic, phytogeographic and paleoclimatic recon- uctions. *Int. J. Coal Geol.* **5**, 17–42.

kler, S. E. 1975 A fertile axis of *Triloboxylon ashlandicum*, a gymnosperm from the Upper Devonian of New York. *Am. Bot.* **62**, 923–934.

kler, S. E. 1978 Ontogeny of progymnosperms. II. Shoots Upper Devonian Archaeopteridales. *Can. J. Bot.* **56**, 3136– 0.

f, J. M. 1973 Coal, climate and global tectonics. In *blications of continental drift to the earth sciences. 1.* (ed. D. H. rling & S. K. Runcorn), pp. 609–622. London: Academic ess.

ster, R. M. 1984 *New manual of bryology.* Hattori Botanical boratory, Nichinan.

eitzer, H.-J. 1974 Zur mitteldevonischen Flora von Lindlar heinland). *Bonner Paläobotanische Mitteilungen* **1**, 1–9.

, A. C. 1978 Sedimentological and ecological control of stphalian B plant assemblages from West Yorkshire. *Proc. ks. Geol. Soc.* **41**, 461–508.

, G. A. M. 1982 Desert bryophytes. In *Bryophyte ecology* (ed. A. . Smith), pp. 105–122. London: Chapman & Hall.

ina, I. A. 1960 Cordaitalean wood—*Taxopitys arctica* sp. nov. m the Upper Carboniferous of eastern Siberia. *aeontologicheskii Zhurnal* **3**, 123–126. (In Russian.)

, A. J. E. (ed.) 1982 *Bryophyte ecology.* London: Chapman & ll.

nans, P., Le Herisse, A. & Bozdogan, N. 1996 Ordovician d Silurian cryptospores and miospores from southeastern rkey. *Rev. Palaeobot. Palynol.* **93**, 35–76.

her, P. K. 1991 A classification schema for the cryptospores. *ynology* **15**, 219–236.

her, P. K., Al-Hajri, S. & Traverse, A. 1996 New evidence land plants from the lower Middle Ordovician of Saudi abia. *Geology* **24**, 55–58.

Stubblefield, S. & Banks, H. P. 1978 The cuticle of *Drepanophycus spinaeformis*, a long-ranging Devonian lycopod from New York and eastern Canada. *Am. J. Bot.* **65**, 110–118.

Taylor, E. L. & Taylor, T. N. 1990 Structurally preserved Permian and Triassic floras from Antarctica. In *Antarctic paleobiology, its role in the reconstruction of Gondwana* (ed. T. N. Taylor & E. L. Taylor), pp. 149–163. New York: Springer.

Tomlinson, P. B. & Craighead, F. C. Sr 1972 Growth ring studies on the native trees of sub-tropical Florida. In *Research trends in plant anatomy: K. A. Chowdhury memorial volume* (ed. A. K. M. Ghouse & M. Yunus), pp. 39–51. New Delhi: McGraw-Hill.

Toro, M., Chamon, O., Salguero, R. & Vargas, C. 1997 Las plantas de la formación Kirusillas (Silurico) en la region de la Angostura Departamento de Cochabamba. *Memorias del XII Congreso Geologico de Bolivia*, 523–529.

Trusswell, E. M. 1991 Antarctica: a history of terestrial vegetation. In *The geology of Antarctica* (ed. R. Tingey), pp. 499–537. Oxford: Clarendon Press.

Valdes, P. J. 1993 Atmospheric general circulation models of the Jurassic. In *Palaeoclimates and their modelling* (ed. J. R. L. Allen, B. J. Hoskins, B. W. Sellwood, R. A. Spicer & P. J. Valdes), pp. 109–118. London: Chapman & Hall.

Vavrdova, M. 1982 Recycled acritarchs in the uppermost Ordovician of Bohemia. *Casopis pro Mineralogii a Geologii* **27**, 337–345.

Vavrdova, M. 1984 Some plant microfossils of possible terrestrial origin from the Ordovician of Central Bohemia. *Vestnik Ustredniho Ustavu Geologickeho* **59**, 165–170.

Vavrdova, M. 1988 Further acritarchs and terrestrial plant remains from the Late Ordovician at Hlásná Treban (Czechoslovakia). *Casopis pro Mineralogii a Geologii* **33**, 1–10.

Vavrdova, M. 1989 New acritatchs and miospores from the late Ordovician of Hlásná Treban, Czechoslovakia. *Casopis pro Mineralogii a Geologii* **34**, 403–420.

Vavrdova, M. 1990 Coenobial acritarchs and other palynomorphs from the Arenig–Llanvirn boundary, Prague Basin. *Vestnik Ustredniho Ustava Geologickeho* **65**, 237–242.

Wellman, C. H. 1996 Cryptospores from the type area of the Caradoc Series in southern Britain. *Special Pap. Palaeo.* **55**, pp. 103–136.

Wolfe, J. A. 1971 Tertiary climatic fluctuations and methods of analysis of tertiary floras. *Palaeo. Palaeo. Palaeo.* **9**, 27–57.

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. *US Geol. Surv. Profess. Pap.* **1106**, 1–37.

Woodrow, D. L. 1985 Paleogeography, paleoclimate and sedimentary processes of the Late Devonian Catskill Delta. In *The Catskill Delta* (ed. D. L. Woodrow & W. D. Sevon), pp. 51–63. Geological Society of America Special Paper, 201. Boulder, CO.

Woodward, F. I. 1987 Stomatal numbers are sensitive to increases in CO_2 from pre-industrial levels. *Nature* **327**, 617–618.

Worsley, T. R., Moore, T. L., Fraticelli, C. M. & Scotese, C. R. 1994 Phanerozoic CO_2 levels and global temperatures inferred from changing paleogeography. In *Pangea: paleoclimate, tectonics, and sedimentation during accretion, zenith and breakup of a supercontinent* (ed. G. D. Klein), pp. 57–73. Geological Society of America Special Paper no. 288. Boulder, CO.

Yemane, K. 1993 Contribution of Late Permian palaeogeography in maintaining a temperate climate in Gondwana. *Nature* **361**, 51–54.

Ziegler, A. M. 1990 Phytogeographic patterns and continental configurations during the Permian period. In *Palaeozoic biogeography and palaeogeography* (ed. W. S. McKerrow & C. R. Scotese), pp. 363–379. London: The Geological Society Memoir no. 12.

Discussion

A. C. SCOTT (*Department of Geology, Royal Holloway, University of London, UK*). You talked about the general lack of growth rings in Devonian woods, but their clear presence in Permian Glossopterid woods from Antarctica, and commented on the possibility that the lack of rings in the older woods may either relate to their latitudinal position, or the plants' being unable to produce rings. Growth rings in Lower Carboniferous wood can be seen in charcoal fragments from the equatorial Lower Carboniferous and can be useful, therefore, in not only yielding data on seasonality but also on fires and fire ecology, a climate-related feature. (Scott *et al*. 1996; Falcon-Lang 1997).

Scott, A. C., Meyer-Berthaud, B., Galtier, J., Rex, G. M., Brindley, S. & Clayton, G. 1986 Studies on a new Lower Carboniferous flora from Kingswood near Pettycur, Scotland: preliminary report. *Rev. Palaeobot. Palynol*. **48**, 161–180.