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The Early Carboniferous (Courceyan–Arundian) monsoonal climate of the British Isles: evidence from growth rings in fossil woods

H. J. FALCON-LANG*

Department of Geology, Royal Holloway, University of London, Egham, Surrey TW20 0EX UK

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Abstract – The British Isles lay at a palaeolatitude of 4° S during the Early Carboniferous (Courceyan–Arundian) period. This paper examines fossil gymnosperm wood from ten localities in western Ireland and southern Scotland in order to analyse palaeoclimate. Fifty-two percent of the 77 fossil wood specimens studied exhibit growth rings that possess subtle, discontinuous ring boundaries and ring increments of narrow but variable width. These growth rings are qualitatively and quantitatively analysed, and are shown to bear a close similarity to growth rings in modern araucarian conifer woods; these araucarian growth rings are formed in response to tropical rainfall seasonality linked to monsoonal circulation. The findings of this study therefore support earlier palaeoclimatic interpretations, based on sedimentological evidence, which suggest that the British Isles experienced a monsoonal climate during the Early Carboniferous (Courceyan–Arundian) period.

1. Introduction

During the Early Carboniferous (Courceyan–Arundian, 343–354 Ma), the British Isles lay on the southeastern margins of the Laurussian continent at a palaeolatitude of 4° S (Scotese & McKerrow, 1990). Despite its proximity to the equator, sedimentological evidence, in particular playa-lake deposits (Leeder, 1992), schizohaline lagoonal facies (Leeder, 1974; Wright, 1981) and vertic palaeosols (Wright, 1990; Wright, Vanstone & Robinson, 1991; Vanstone, 1991), suggests that palaeoclimate possessed a distinct seasonality in annual rainfall, perhaps linked to monsoonal circulation. This interpretation is partly supported by the results of non-parametric climate modelling (Golonka, Ross & Scotese, 1994); these data placed the British Isles on the margins of the humid and seasonal tropics during the Early Carboniferous (Viséan) period. Direct evidence for rainfall seasonality at this time, however, is lacking.

Growth rings in fossil woods provide the most sensitive geological data for assessing palaeoclimatic seasonality (Chaloner & Creber, 1988). They are particularly useful because they lend themselves to a quantitative approach, allowing for detailed comparison of modern and ancient climates and environments (e.g., Creber & Chaloner, 1984; Francis, 1984). Anatomically preserved fossil woods are very common in the Lower Carboniferous rocks of the British Isles (Scott & Galtier, 1996). However, until recently their value as palaeoclimatic indicators has been neglected (Bateman & Rothwell, 1990).

In an earlier paper (Falcon-Lang, 1999), I examined fossil woods and leaves from the Lower Carboniferous (Asbian–Brigantian) rocks of northern Britain. This study concluded that at this time Britain experienced a seasonal tropical climate, characterized by dry seasons of irregular duration and non-annual frequency, similar to present-day north Australia and East Africa. In this second paper, I present a detailed quantitative analysis of growth rings in Arundian fossil woods from Creevagh Head, County Mayo, Ireland. In addition, a semi-quantitative overview of growth-ring frequency in woods from a further nine Late Courceyan–Arundian localities in northern Britain is also provided. These data are used to understand more clearly the palaeoclimate of the British Isles during the Courceyan–Arundian period.

2. Creevagh Head

2.a. Geological setting

Fossil wood occurs abundantly in a 28-m-thick sequence at Creevagh Head, near Ballycastle, North Mayo, Ireland (Irish National Grid Reference, G16324115; see Fig. 1). These rocks belong to the upper part of the Moyny Limestone Formation and are of Arundian age (343–345 Ma; Graham, 1996). Five coastal marine sedimentary facies have been described from this locality (Falcon-Lang, 1998). These record deposition on tidal flats (Facies 1), in large, estuarine channels (Facies 2), in small, meandering tidal creeks (Facies 3), in oligohaline lagoons

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* Current address: British Antarctic Survey, High Cross, Madingley Rd, Cambridge CB3 OET. E-mail: HJFL@pcmail.nerc-bas.ac.uk

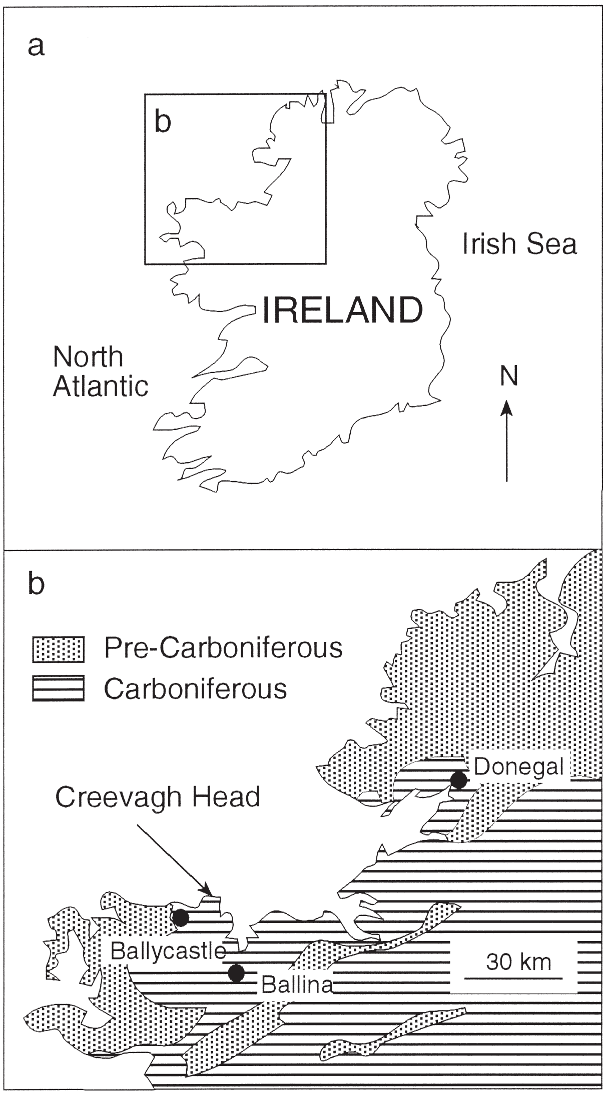

Figure 1. (a) Ireland (b) Location details and regional geology of Creevagh Head in western Ireland (reprinted from Falcon-Lang (1998) with the permission of Elsevier Science).

(Facies 4), and in shallow marine bays (Facies 5). One 2-m-thick estuarine creek deposit (Facies 3; the 'Lithostratigraphic Unit 8' of Falcon-Lang, 1998) contains very large quantities of fossil wood, anatomically preserved as charcoal (fusain; Scott, 1989). This unit has been interpreted by Falcon-Lang (1998) to represent the product of a hinterland wildfire event that exerted a catastrophic effect on downstream coastal environments and biotas.

2.b. General description of charred wood

One hundred charred wood fragments, 1–6 cm in size, were collected from Lithostratigraphic Unit 8 (Falcon-Lang, 1998) at Creevagh Head. These were sectioned transversely using a microtome, and then placed in 40% HF for one week in order to remove any clay minerals. Specimens were then fixed to aluminum stubs using 'Electrodag,' and examined using a Hitachi S2400 Scanning Electron Microscope (SEM).

All charcoal fragments consist of pycnoxylic gymnosperm wood, and are attributed with reservation to the genus *Dadoxylon* (Falcon-Lang, 1998). Before undertaking a palaeoclimatic analysis of growth rings in these woods, it is important to ascertain from which part of the original tree these fragments came (i.e. roots, trunk or branches), because the position of growth in the tree influences growth-ring morphology (Chapman, 1994). Wood from the roots, basal stumps and branches are of least use for growth-ring palaeoclimate analysis, because they record the effects of gravity and buttressing in addition to palaeoclimatic influences (Chapman, 1994).

One of the Creevagh Head specimens consists of a complete stem cross-section (3.5 mm radius) composed of a parenchymous pith surrounded by a woody cylinder. A characteristic feature of all the other wood fragments is that they exhibit a triangular, wedge-like shape in transverse section (Fig. 2a), indicating that they were also derived from stems of relatively small radius. Because files of cells in these woods are strongly convergent in one direction (when viewed in transverse section), it was possible to project this convergence backwards to a point of intersection, thereby determining the approximate minimum stem radius from which each wood fragment was derived (Fig. 3a). Projected stem radii were found to range from 5 to 46 mm (mean 17.2 mm, $N = 96$; Fig. 3b). However, it is known that during the charring process, the volume of wood contracts by approximately one third (Scott & Jones, 1991). Correcting for this contraction, an original mean stem radius of approximately 25.8 mm (range 7.5 to 69 mm) seems probable. In addition, reaction wood (Creber, 1975) is absent from all specimens; this suggests that the wood fragments were derived from small (1.5–13.8 cm diameter) vertical trunks, rather than from branches. Trunk wood, such as this, is likely to give a clear palaeoclimate signal (Chapman, 1994).

2.c. Description of growth rings

In this paper, the term 'ring boundary' is used to describe the transition from the latewood of one growth ring to the earlywood of the following ring, and the term 'ring increment' is used to describe the distance between two ring boundaries (Fig. 4b). Sufficient preservation of wood anatomy required to distinguish growth rings was only present in 25 of the 100 specimens (the transverse section of 31 specimens was obscured by pyritization; 44 specimens were badly crushed). Of the 25 well-preserved fragments, 19 (76%) contain growth rings. Given the small size (1–6 cm) of the charcoal fragments, ring sequences in any one specimen were typically short (3–29 growth increments; mean nine growth increments; $N = 19$).

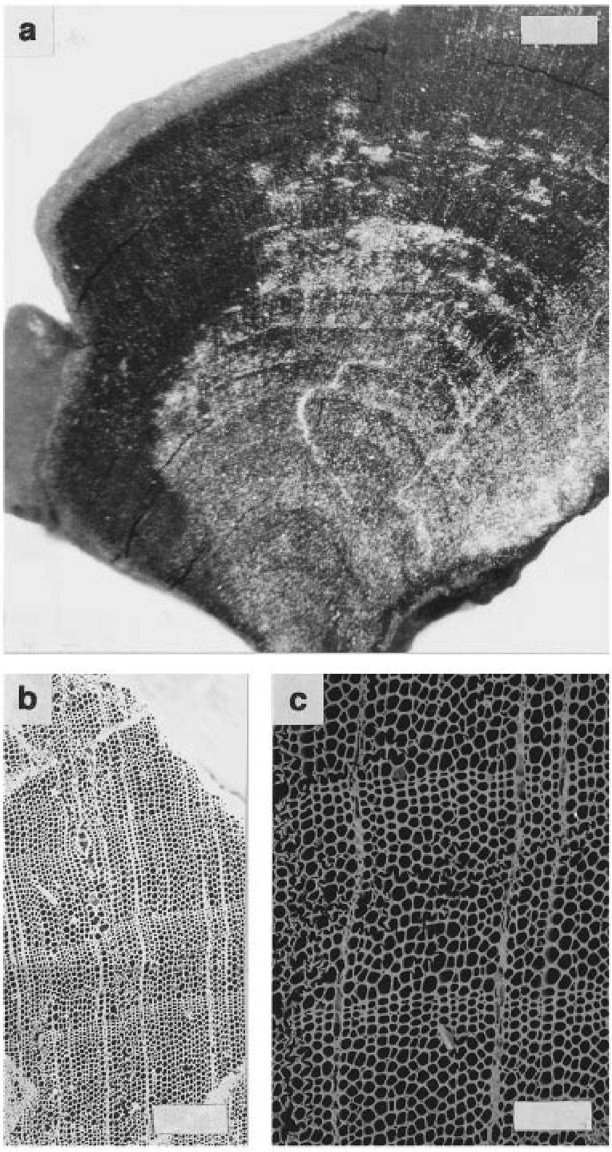

Figure 2. Charred fossil wood from Creevagh Head, County Mayo, Ireland. (a) Transverse section of wood fragment showing growth rings picked out by pyritization (white areas). The scale bar is 2 mm (Specimen NM16). (b) SEM image of ring sequence (Specimen NM4). The scale bar is 250 µm. (c) SEM image of single growth increment, showing very subtle ring boundaries (Specimen NM4). The scale bar is 100 µm. All specimens will be lodged in the Natural History Museum, London following this study.

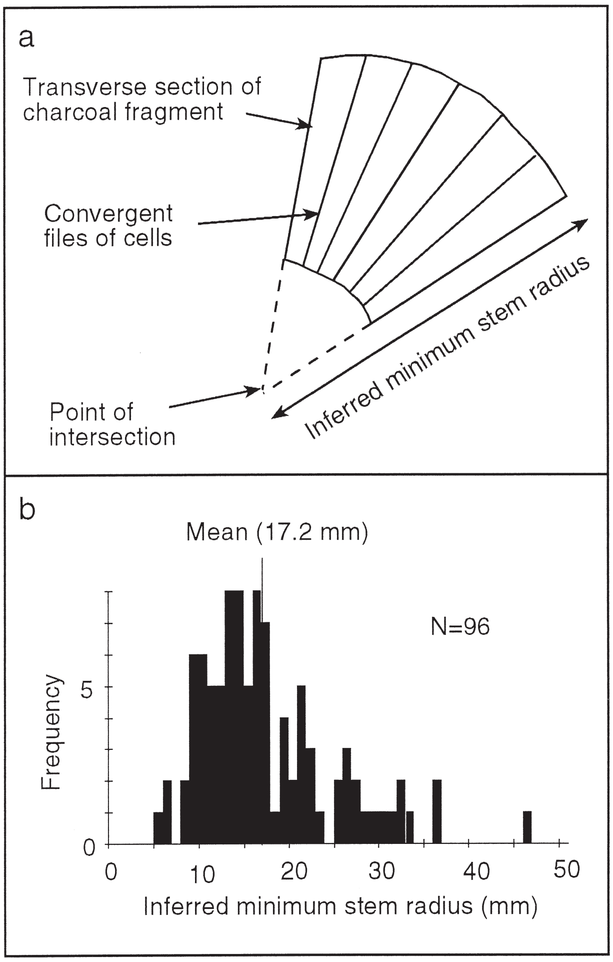

Figure 3. (a) Diagram showing the method of inferring the original minimum stem diameter from small wood fragments by projecting backwards convergent files of cells to a point of intersection. (b) Inferred stem diameters derived from wood fragments collected at Creevagh Head (not corrected for contraction occurring during charring).

Compared with growth rings in *Pinus sylvestris* growing in modern temperate latitudes, these *Dadoxylon* growth rings have very subtle ring boundaries (Fig. 2). In the single specimen where a complete cross-section is preserved, ring boundaries are discontinuous around the stem circumference (Fig. 4). In addition, in all specimens ring increments are very narrow, ranging from 0.2 mm to 2.8 mm (mean 0.83 mm; $N = 143$; Fig. 5a), and highly variable in width from one increment to the next (Fig. 5b). Again, correcting for contraction associated with charring of the wood fragments (Scott & Jones, 1991), original mean ring incremental widths are likely to have been 1.24 mm (range 0.3–4.2 mm).

2.d. Numerical analysis of growth rings

Photo-montages of several ring sequences were taken at 40 x magnification with the SEM, a scale at which individual cells could be easily discerned (Fig. 2b). These were examined with a binocular microscope. Radial diameters of individual cells across each growth increment were measured to an accuracy of 0.5 µm using a ruler mounted in the eye-piece of the microscope. Where possible ten adjacent files of cells were measured for each growth ring, with a minimum of six measured rows in crushed samples. Where one file of cells was too poorly preserved to measure, counting continued along an adjacent file (Creber & Chaloner, 1984). Data from each of the 6–10 files measured were averaged to produce the final plots. A slightly different number of cells was present in each

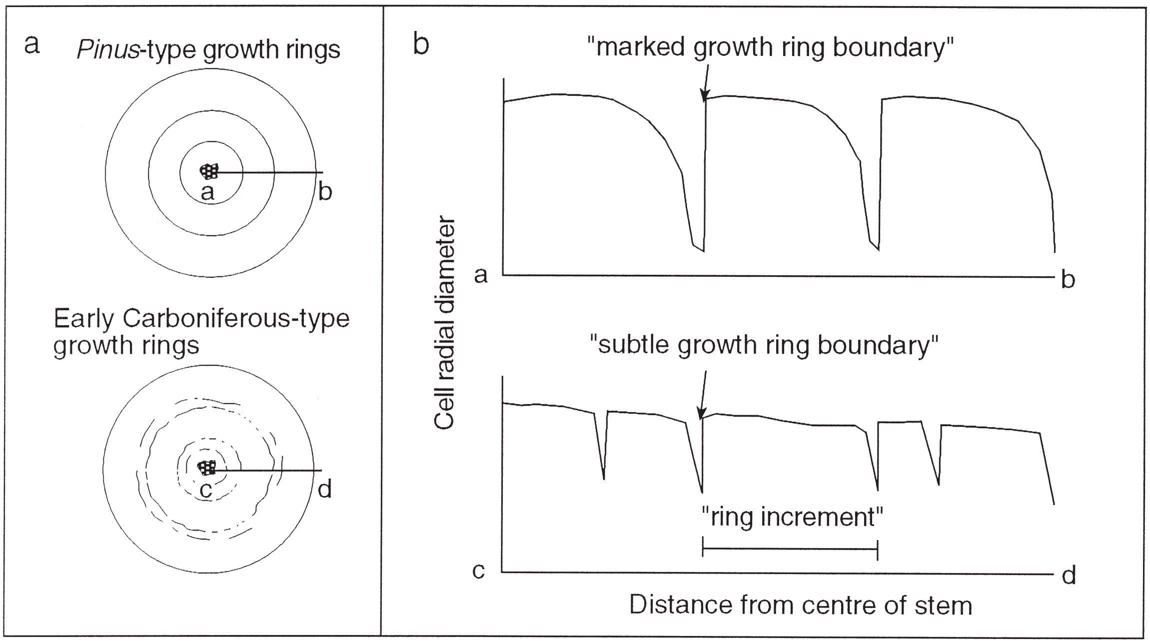

Figure 4. Comparison of growth rings in *Pinus sylvestris* and Courceyan–Arundian woods of the British Isles (reprinted from Falcon-Lang, 1999). (a) Growth rings in stem cross section. *P. sylvestris* exhibits continuous ring boundaries. Courceyan–Arundian woods exhibit discontinuous ring boundaries. (b) Variation in cell radial diameter across growth rings. Growth is left to right. *P. sylvestris* exhibits 'marked' ring boundaries defined by many small latewood cells. Courceyan–Arundian woods exhibit 'subtle' ring boundaries defined by 2–6 moderate-sized latewood cells.

measured file. Therefore to create meaningful average plots, data from the shorter sequences were stretched out by adding spaces into the spreadsheet, so that data from the ring boundaries matched up exactly.

Data for two of the specimens are plotted in Figure 6, giving a numerical representation of the style of growth rings in these specimens of *Dadoxylon*. Each growth ring typically begins with earlywood cells 30–35 µm in radial diameter. This value declines slightly across the ring increment to 23–30 µm with an abrupt reduction in radial diameter to 12–17 µm in the terminal 2–6 latewood tracheids. Values then return to 30–35 µm at the start of the new ring. Rings with rather subtle boundaries composed of only a very few latewood tracheids are very characteristic of these woods. False rings (Creber & Chaloner, 1984) are also a characteristic feature, and may occur at any point within the growth ring, but most commonly towards the end of the growth interval (Fig. 6).

3. Overview of Courceyan–Arundian growth-ring frequency

In order to obtain an indication of the regional frequency of growth rings in British woods of Courceyan–Arundian age, a review of published literature was also undertaken. Nine localities yielding fossil woods, all belonging to the Cementstone Group of northern Britain, have been described by earlier workers (Fig. 7a, b). These are: Oxroad Bay, Cove, Castleton Bay, Burnmouth, Edrom, Langton Burn, Lennel Brae (all late Courceyan), Glenarbuck (Chadian–Arundian) and Loch Humphrey Burn (Arundian). In total, the photographs or written descriptions of 53 specimens of wood were given in these published papers (see Table 1); of these, 29 (40 %) exhibited growth rings. Of particular note is a specimen of *Eristophyton beinertianum* (Göeppert) Zalessky from Lennel Brae, Berwickshire, which exhibited a sequence of 40 growth increments (Absalom, 1931).

All these Courceyan–Arundian woods possess growth rings very similar to those described from Creevagh Head. They have ring increments of variable width within single specimens; measurements taken from published plates indicate that ring increments vary between approximately 0.2 mm and 4 mm in width. Furthermore, in specimens where the entire stem cross-section is largely preserved, ring boundaries are discontinuous around the circumference, such that ring sequences on one side of the stem cannot always be exactly correlated with ones on the other side.

4. Palaeoclimatic interpretation of growth rings

It is clear that growth rings are moderately common in fossil woods from the Early Carboniferous (Courceyan–Arundian) palaeotropics of the British Isles; of the 77 wood specimens examined from both Creevagh Head and the Cementstone Group localities, 52 % exhibit growth rings. However, these growth rings are different from the rings of temperate woods such as *Pinus sylvestris*; they have much more subtle, discontinuous ring boundaries defined only by a very few (2–6) late-

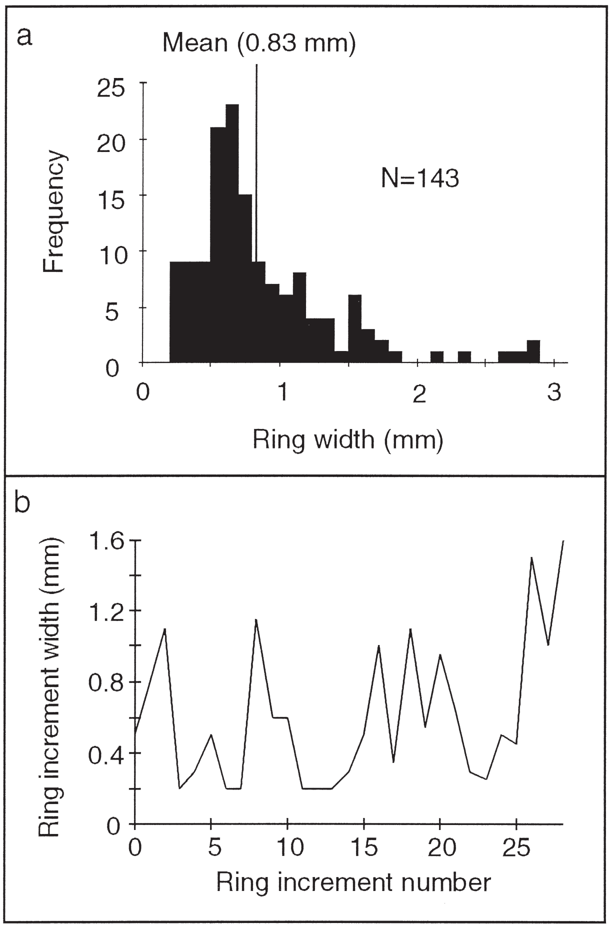

Figure 5. Growth-ring incremental widths in woods from Creevagh Head. (a) Histogram of ring incremental width versus frequency (not corrected for contraction during charring). (b) Plot of 29 consecutive ring incremental widths in the largest wood specimen (Specimen NM21) at Creevagh Head.

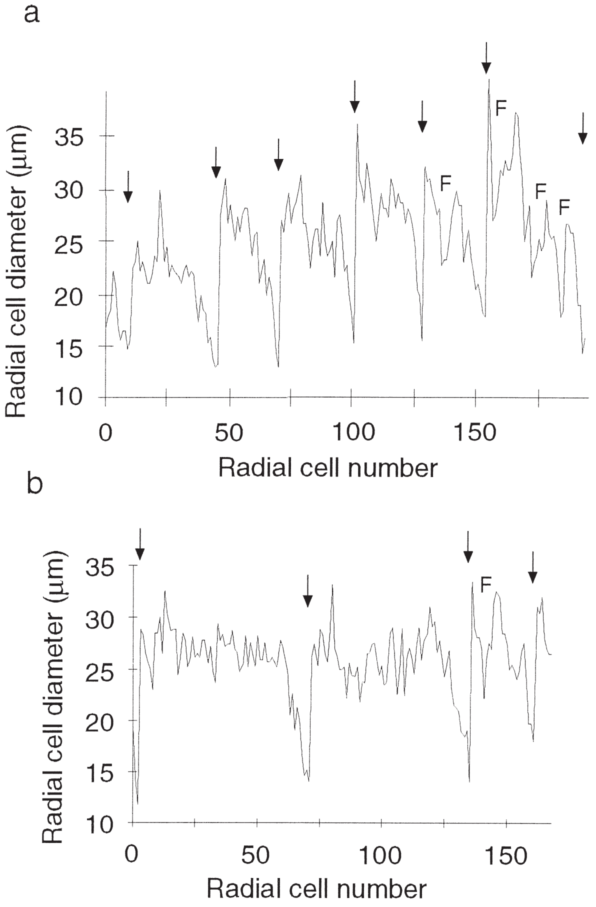

Figure 6. Numerical depiction of some of the growth rings observed in *Dadoxylon*-type wood from Creevagh Head. The arrow marks growth ring boundaries. F indicates 'false ring'. Growth is left to right in all specimens. (a) Specimen NM4. (b) Specimen NM16.

wood cells, and possess ring increments of extremely narrow and irregular width (Fig. 4). These Carboniferous growth rings bear closest similarity to the growth rings of modern tropical conifers growing in the southern hemisphere. In two earlier papers, these British Carboniferous woods, containing only weakly developed rings, were interpreted as indicating growth under a uniform, non-seasonal palaeoclimate (Chaloner & Creber, 1973; Creber & Chaloner, 1984). However, recent advances in the understanding of tree rings in tropical conifers challenge this interpretation (Jacoby, 1989). I argue here that the Early Carboniferous (Courceyan–Arundian) growth rings described in fact indicate tree growth under a markedly seasonal climate (cf. Falcon-Lang, 1999).

4.a. Controls on growth ring formation in modern tropical conifer woods

Growth-ring formation in modern conifer woods is dictated by an endogenous rhythm that originates in the lateral and apical meristems, and is controlled by the cycle of leaf flushing and abscission (Creber & Chaloner, 1984). At the beginning of the growing season, the production of a new set of leaves sends a hormonal impulse down the trunk, activating the vascular cambium and initiating a new growth ring. Towards the end of the growing season, when leaves are abscissed, this hormonal impulse declines, and a ring boundary is formed (Creber & Chaloner, 1984).

In temperate latitudes, leaf flushing is closely synchronized with photoperiod and temperature, so that growth rings in the wood reflect climatic seasonality. In tropical latitudes, where temperature and photoperiod are nearly constant year-round, seasonality is largely the product of intra-annual variations in rainfall (Rumney, 1968). If this is sufficiently intense, the endogenous rhythm of tropical tree growth may become locked on to rainfall seasonality, leaf flushing broadly coinciding with the beginning of the wet season and leaf abscission with the beginning of the dry season (Jacoby, 1989).

As a consequence of this, in the seasonal tropics of Northern Australia (e.g., Ash, 1983a, 1983b), Southeast

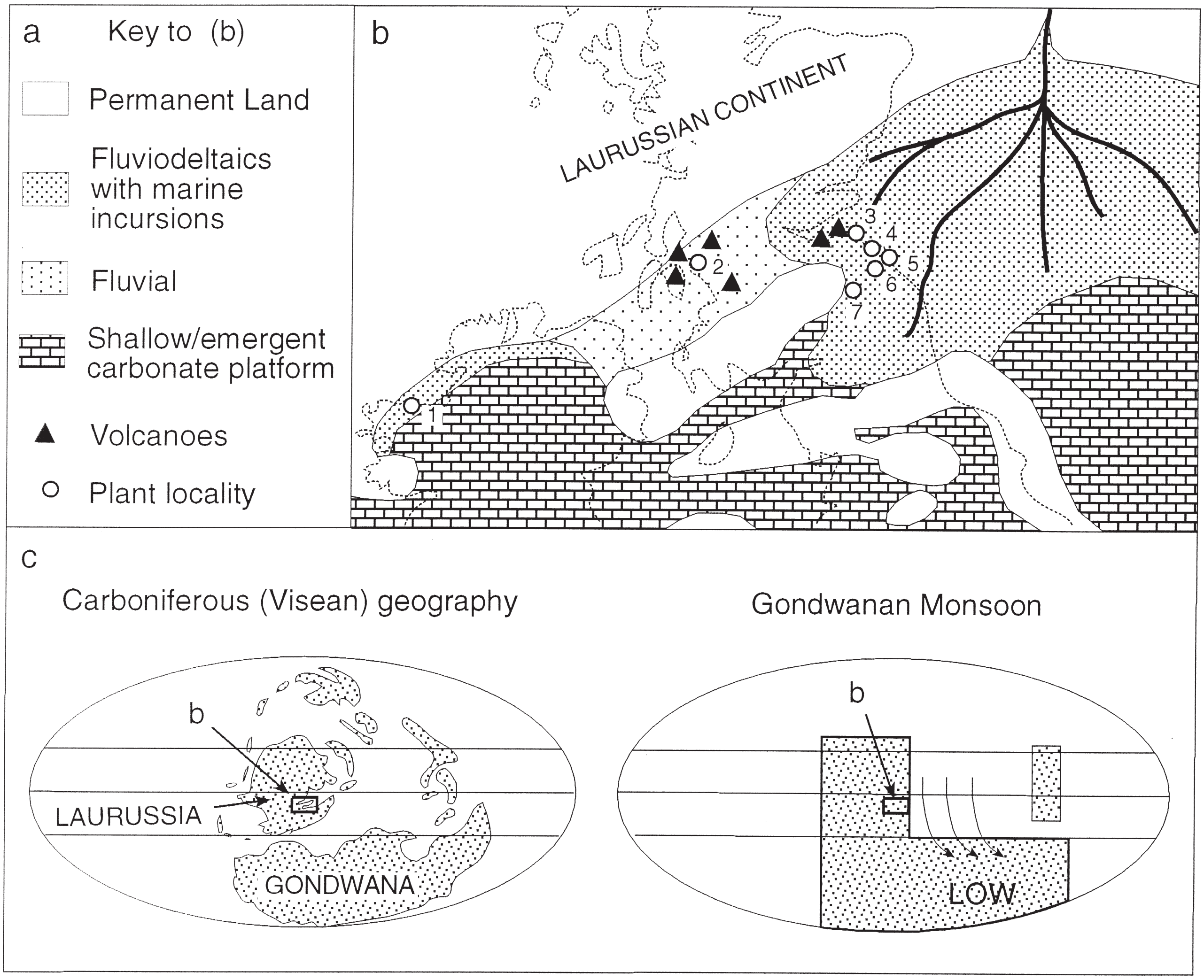

Figure 7. Palaeogeography of sites studied. (a) Key to (b). (b) Arundian palaeography of northern British Isles showing the position of the fossil-wood-bearing localities examined. Plant localities are: 1, Creevagh Head; 2, Glenarbuck and Loch Humphrey Burn; 3, Oxroad Bay and Castleton Bay; 4, Cove; 5, Burnmouth; 6, Edrom and Langton Burn; and 7, Lennel Brae (Scott & Galtier, 1996). (c) Early Carboniferous (Viséan) global palaeogeogeography. LOW indicates a large atmospheric low pressure over Gondwana during the southern hemisphere summer driving monsoonal circulation over equatorial Laurussia (modified from Golonka, Ross & Scotese, 1994; Wright, 1990).

Asia (e.g., Duke, Birch & Williams, 1981; D'Arrigo *et al.* 1997), East Africa (e.g., Amobi, 1973), and South America (e.g., Vetter & Botosso, 1989), growth-ring formation closely reflects rainfall seasonality. Under humid tropical climates, however, where seasonality in rainfall, temperature and photoperiod is lacking, the endogenous rhythm of tree growth may become 'free-running' (Ash & Creber, 1992). Growth rings may still be formed under such circumstances but are unrelated to climatic factors. However, in most cases, these may be easily distinguished from climatically induced growth rings; they possess extremely subtle, discontinuous ring boundaries, and are typically symmetrical about the ring boundary (Ash & Creber, 1992).

In addition to these external climatic factors, growth ring morphology is also strongly dictated by internal (genetic) influences. For example, in a study of tree growth in Florida, Tomlinson (1980) found a wide spectrum of growth responses to that climate, with some species producing marked ring boundaries, others subtle ring boundaries, and still others no growth rings at all. In conifers, the markedness of growth-ring boundaries produced (under a given climate) is closely linked to the mean lifespan of the tree's leaves. For example, the leaves of *Pinus sylvestris* are abscissed after only 1–3 years; a new season's flush of leaves thus contributes around 45% of the total photosynthetically active leaves (Creber & Chaloner, 1984). The hormonal impulse produced by this new leaf flush is large when compared to the background levels of hormone production generated by the older leaves, hence, a marked ring boundary is formed.

However, many araucarian and podocarp conifers hold active leaves for much longer periods (Creber & Chaloner, 1984). For example, a specimen *Araucaria araucana* growing in Surrey (UK) held active leaves for

Table 1. Frequency of growth-ring occurrences in Courceyan–Arundian woods from northern Britain

Locality	Flora with secondary xylem	Radius of wood specimen	Growth-ring frequency
Glenarbuck	*Endoxylon zonatum* (Kidston) Scott	8 mm	1/2[9, 17]
Loch Humphrey Burn	*Eristophyton fasiculare* Scott	?	2/2[15]
	Eristophyton waltoni Lacey	12 mm	2/2[18]
	Protopitys scotica Walton	2–6 mm	1/1[9]
Oxroad Bay	*Ameylon bovius* Barnard	1–22 mm	3/3[2, 3]
	Bilignea solida Scott	4 mm	0/1[3]
	Eristophyton waltoni Lacey	5–21 mm	0/2[13]
	Stenomyelon tuedianum Kidston	?	2/3[8]
	Tetrastichia bupatides Gordon	?	0/1[7]
	Triradioxylon sp.	?	0/1[3, 10]
	Unknown gymnosperm	3 mm	1/1[3]
Cove	*Ameylon equivius* Barnard	25 mm	1/1[2]
	Eristophyton waltoni Lacey	5 mm	0/1[13]
Castleton Bay	*Eristophyton beinertianum* (Goeppert) Zalessky	3–20 mm	0/4[5, 13]
	Eristophyton waltoni Lacey	4–12 mm	1/6[5]
	Stenomyelon tuedianum Kidston	1.5 mm	0/3[14]
Burnmouth	*Eristophyton beinertianum* (Goeppert) Zalessky	3–9 mm	0/2[13]
	Stenomyelon heterangioides Long	?	0/1[11]
Edrom	*Eristophyton beinertianum* (Goeppert) Zalessky	4–17 mm	0/4[13]
	Pitus sp.	3 mm	3/3[12, 15]
	Stenomyelon heterangioides Long	?	0/1[11]
	Stenomyelon primaevum Long	?	0/1[11]
Langton Burn	*Stenomyelon* sp.	4 mm	0/2[4]
Lennel Brae	*Eristophyton beinertianum* (Goeppert) Zalessky	19 mm	1/1[1]
	Pitus antiqua Witham	4 mm	1/1[6, 12]
	Stenomyelon tuedianum Kidston	?	2/2[16]

[1]Absalom (1931), [2]Barnard (1962), [3]Bateman & Rothwell (1990), [4]Calder (1938), [5]Galtier & Scott (1989), [6]Gordon (1935), [7]Gordon (1938), [8]Kidston & Gywnne-Vaughan (1912), [9]Lacey (1953), [10]Long (1961), [11]Long (1964), [12]Long (1979), [13]Long (1987), [14]Scott and Galtier (1988), [15]Scott (1902), [16]Scott (1923), [17]Scott (1924), [18]Smith (1962).

3–17 years (unpub. data, British Antarctic Survey), whilst specimens of *Podocarpus elongatus* growing in southern Africa held leaves for 4–8 years (Midgley, Bond & Geldenhuys, 1995) and *Halocarpus bidwilli* growing in New Zealand held leaves for 3–20 years (Ogden & Stewart, 1995). As a consequence of this great longevity of leaves, a new leaf flush may account for $< 15\%$ of the total photosynthetically-active leaf mass. The hormonal impulse triggered by this new leaf flush in araucarian and podocarp conifers is thus relatively small and the subsequent ring boundary produced is rather subtle (Creber & Chaloner, 1984).

4.b. Phenology of Early Carboniferous (Courceyan–Arundian) trees

In order to understand the palaeoclimatic significance of the Early Carboniferous growth rings documented in this study, it is important to ascertain whether the endogenous rhythm of tree growth was 'locked' on a climatic seasonality or more-or-less 'free-running'. It is also crucial to know how long these trees held photosynthetically active leaves, because this factor strongly influences the markedness of the growth ring produced (Falcon-Lang, 1999).

4.b.1. Locked versus free-running endogeneous rhythms

In my recent analysis of Early Carboniferous (Asbian–Brigantian) growth rings from northern Britain (Falcon-Lang, 1999), I found a close link between edaphic drought and growth-ring frequency. Growth-ring frequency was highest at localities where independent sedimentological evidence suggested that well-drained soil conditions prevailed. Similarly, growth rings were rare in woods interpreted to have grown in permanently water-logged settings. These data implied that growth-ring production in these woods was related to external (climatic) not internal (free-running) causes. Unfortunately, it is not possible to apply a similar palaeoenvironmental analysis to growth-ring frequency in the Courceyan–Arundian woods discussed here; most wood fragments are allochthonous and may have grown in edaphic settings quite unlike those in which they were finally deposited. Furthermore, interpretations of edaphic conditions based on sedimentological data for most of the ten localities in question are rather poorly constrained.

However, it is noted that several species documented in Table 1 exhibit growth rings at one locality and not at others (e.g. *Eristophyton waltoni* Lacey). These data thus favour the interpretation that growth-ring formation was the product of an endogenous rhythm locked on to environmental conditions rather than a free-running cycle. In addition, the growth rings described here are asymmetrical across the ring boundary (Fig. 2), unlike those produced by a free-running endogenous rhythm, which typically are symmetrical either side of the ring boundary (Ash & Creber, 1992).

4.b.2. Life-span of Early Carboniferous gymnosperm leaf fronds

The Early Carboniferous gymnosperms discussed in this paper appear to have retained active leaves for long periods, like modern araucarian and podocarp conifers. This conclusion is based on the length of the leaf traces preserved in some Early Carboniferous stems. Leaf traces are small vascular bundles that pass through the wood and connect the living leaves to the centre of the stem. Leaf longevity, therefore, may be determined by measuring the number of growth rings through which the leaf trace passes (W. G. Chaloner, pers. comm. 1997).

Unfortunately very few examples of leaf traces have been described from the Early Carboniferous period of Britain. Galtier & Scott (1994) described a branch of the genus *Pitus* from the Early Carboniferous (Brigantian) East Kirkton locality, Scotland; this contained a leaf trace that extended through secondary xylem for about 15 mm, before being occluded by parenchyma. Given that growth increments in Asbian–Brigantian woods are typically 0.35–3 mm in width, and assuming that each growth increment is representative of one year's growth, a 15-mm-long leaf trace may indicate that these trees held their leaves for more than five years (Falcon-Lang, 1999). In another example, Lacey (1953) described a specimen of *Eristophyton waltoni* from Loch Humphrey Burn (Table 1), in which leaf traces penetrated through 3–4 growth-ring increments before being occluded. These leaf-trace data therefore imply that the wood anatomy of the Courceyan–Arundian trees discussed here would not have been particularly sensitive to rainfall seasonality, like modern araucarian and podocarp conifers. This brings into question the assumption that growth rings with subtle ring boundaries equate with weakly developed climate seasonality.

4.c. Comparison with tropical araucarian conifers

Several growth-ring studies have been undertaken on araucarian conifers growing in the seasonal (monsoonal) tropics that may provide useful analogues for the Courceyan–Arundian growth rings (Ash, 1983a; Ogden, 1981; Detienne, 1989). For example, Ash (1983a) studied the woods of *Agathis robusta* growing in the seasonal tropics of north Australia (latitude 17° S) that exhibited growth rings very similar to those described here from the Early Carboniferous period. These growth rings possessed increments of narrow variable widths (0.1–3 mm), and subtle, discontinuous ring boundaries defined by only 1–3 latewood cells. Ash (1983a) demonstrated that these *Agathis* growth rings were formed during the intense three-month dry season of Queensland's monsoonal climate. To emphasize that these growth rings were indeed climate-induced structures, Whitmore (1966) noted that specimens of *A. macrophylla* growing in the everwet (non-seasonal) tropics of southeast Asia (11° S) were not producing rings at all. It is possible then that the subtle Courceyan–Arundian rings may record a tropical seasonality of comparable intensity to that of north Australia.

In addition, the growth rings studied by Ash (1983a) in *Agathis* were also characterized by highly variable ring increments similar to those described from the Courceyan–Arundian (Fig. 5b). Two factors were found to be important in the production of variable ring increments in *Agathis*. First, tropical rainfall seasonality lacks an absolute regularity (Rumney, 1968). For example, one to two wet seasons and one to two dry seasons may occur each year, and each dry spell may be sufficiently severe to induce growth-ring formation (Ash, 1983a; Nieuwolt, 1977). During his three-year study, Ash (1983a) found that trees typically produced 3–4 rings. Second, the rate of vascular cambium division in araucarians fluctuates greatly with time (Ash, 1983a). Some trunks are fast-growing and produce wide ring increments, while coeval slow-growing trunks form narrow ring increments or are completely dormant. The variability of ring-increment widths encountered in the Courceyan–Arundian woods may therefore also reflect the operation of these two processes. Rings widths vary between 0.1 and 3.6 mm in modern araucarian conifers (Ash, 1983a; Enright, 1995; Ogden & Stewart, 1995), and such values are closely similar to the Carboniferous example described here, which possess 0.2–4.2-mm-wide ring increments.

Finally, Ash (1985) noted in *A. vitiensis* growing in Fiji that cambial activity migrates in a wave around the circumference of the trunk during the growing season, producing growth rings with discontinuous ring boundaries. This may also account for the discontinuity of rings exhibited by the Carboniferous material. In addition, the occurrence of numerous 'false rings' within the Courceyan–Arundian woods suggests that the wet (growing) season was punctuated by irregular droughts (Creber & Chaloner, 1984).

4.d. Palaeoclimatic and phytogeographic models

More than 65% of the land area in the tropical zone today experiences seasonal rainfall. This seasonality is linked to monsoonal circulation generated by the large, mid-latitude, equator-parallel Asian continent (Rumney, 1968). Given the near-equatorial palaeo latitude of the British Isles during the Courceyan–Arundian period, rainfall seasonality would most probably also have been the result of a monsoonal climate (Wright, 1990). Global palaeogeogeography, dominated by the large, mid-latitude, equator-parallel Gondwanan continent, would have been particularly conducive for monsoonal circulation over the tropics of Laurussian Britain during Early Carboniferous time (Fig. 7c). For example during the northern hemisphere summer, the Intertropical Convergence Zone (ITCZ), where the highest tropical rainfall occurs, would have been positioned over the British Isles, giving a rainy season. However, during the southern hemisphere summer, the Gondwanan continent would have rapidly heated up, producing a zone of intensely low atmospheric pressure. This low-pressure zone would have pulled the position of the ITCZ southward, causing a dry season over the British Isles (cf. Parrish, 1993).

Recent work has suggested that the gymnospermous plant communities that dominated northern Britain during the Asbian–Brigantian monsoonal climate may best be described in terms of a tropical savanna-type biome (Falcon-Lang, 1999). It is likely therefore that a similar phytogeographic model also holds true for the gymnosperm-dominated vegetation that occupied the British Isles during the Courceyan–Arundian monsoonal phase. Monsoonal conditions over Britain appear to have finally broken down by the end of the Namurian (Rowley *et al.* 1985), with savannas being replaced by rainforests (Falcon-Lang, 1999). This shift in circulation patterns was probably due to the formation of the equatorial Hercynian mountains, which caused orographic lifting of tropical air masses and led to the fixation of the ITCZ close to the British Isles (Rowley *et al.* 1985).

5. Conclusions

(1) Subtly developed growth rings are described from British palaeotropical woods of Courceyan–Arundian age, and are interpreted to have formed in response to a seasonal tropical climate.
(2) Leaf-trace data indicate that Early Carboniferous gymnosperms maintained photosynthetically-active leaves for several years, similar to modern araucarian conifers. As a consequence, their wood anatomy would not have been particularly sensitive to climate, and growth rings, although subtly developed, may record intense rainfall seasonality.
(3) The occurrence of growth rings with variable incremental widths and common false rings implies that this climatic seasonality may not necessarily have had an absolute annual rhythm; several dry seasons of variable duration may have occurred each year.
(4) Palaeoclimatic models suggest that palaeotropical rainfall seasonality was probably linked to the operation of the Gondwanan monsoon.

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