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Growth interruptions in silicified conifer woods from the Upper Cretaceous Two Medicine Formation, Montana, USA: implications for palaeoclimate and dinosaur palaeoecology

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Abstract

Taphonomic studies suggest that most dinosaur bone assemblages in the Upper Cretaceous (Campanian) Two Medicine Formation of Montana originated from drought-induced mass mortalities on the floodplain. This hypothesis is tested further by studying intra-annual growth patterns in silicified woods of cupressaceous/taxodiaceous conifers found in association with dinosaur bone material at a palaeolatitude of 48°N. True growth rings are completely absent, but growth interruptions characterised by concentric, variably persistent zones, 1–8 latewood cells wide are common. Interruptions are irregularly spaced so that, for example, four interruptions may occur along a radius of only 25 cells in one specimen, whilst in another specimen a radius more than 650 cells wide may completely lack interruptions. Irregular growth patterns like this occur in Upper Cretaceous woods across a broad latitudinal belt in the US Western Interior demonstrating that they resulted from regional climatic forcing rather than localised phenomena. Growth interruptions record the occurrence of short-term, aperiodic disturbances to tree growth, under an equable, megathermal climate that was otherwise favourable for continuous, year-round cambial activity. The only probable cause of growth interruption formation were drought-induced fluctuations in the water table and resultant water stress. Growth patterns suggest that sufficient water for uninhibited growth was continuously available for years at a time, but when water stress did occur, it did so repeatedly over a very few months. Comparison with present-day East Africa, where trees show very similar growth patterns, implies that the equable, but erratically humid, environment of the Late Cretaceous Western Interior was exactly the kind of setting where mass mortalities amongst megafauna might be expected. Like East Africa, this environment would have had sufficient carrying capacity to permit large herds of megafauna to develop under normal conditions, but when repeated phases of droughts struck, such populations would have been highly vulnerable.

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1. Introduction

The Upper Cretaceous Two Medicine Formation of northwest Montana, USA, ranks amongst the world's most productive dinosaur-bearing for-

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mations (Rogers, 1997). Dinosaur remains have been described from this fluvio–deltaic unit since the beginning of the twentieth century (Gilmore, 1914, 1917), and at present at least 14 genera of dinosaurs are known from the Formation (Rogers, 1990; Varricchio and Horner, 1993; Sampson, 1995). The most spectacular discoveries have been of a number of dinosaur nests which preserve both hatched and unhatched eggs containing intact embryos, and associated bones of juvenile hatchlings of the hadrosaur *Maiasaura* (Horner and Makela, 1979; Horner, 1982; Horner and Currie, 1994). In addition, a large number of low-diversity bonebeds dominated either by hadrosaurs, lambeosaurs or ceratopsians have been excavated (Gilmore, 1917; Rogers, 1990; Varricchio and Horner, 1993), together with one higher-diversity bone assemblage containing both iguanodontoids and theropods (Varricchio, 1995). Many of these bonebeds are parautochthonous as indicated by the degree of skeletal articulation (Varricchio and Horner, 1993).

These bone assemblages have provided tantalising insights into many aspects of dinosaur ecology ranging from their social structure (Horner and Makela, 1979; Horner, 1982) to their thermoregulation (Barrick et al., 1996). Lately, there has been considerable interest in the taphonomy of this material, and the palaeoecological implications of these data. Whilst some of the hadrosaur nesting sites may have been instantaneously buried by volcanic ash falls (Horner, 1994) or by clastic sediments from fluvio–deltaic crevasse splay events (Lorenz and Gavin, 1984), the larger majority of the bonebed material is believed to represent the parautochthonous remains of drought-induced mass mortalities on the floodplain (Rogers, 1990; Varricchio and Horner, 1993; Varricchio, 1995). The evidence for drought-induced mass death is fourfold (cf. Shipman, 1975). First, much of the bone material occurs in the fine-grained deposits of inactive river channels interpreted as waterholes (or oxbow lakes), left following cessation in fluvial discharge. Second, the associated sedimentary sequence contains calcrete palaeosols indicating a seasonally dry climate (Goudie, 1983). Third, the vertebrate assemblages contain a preponderance of sub-adult

animals, the age class most vulnerable to drought-mortality according to recent studies (Conybeare and Haynes, 1984; Rogers, 1990). Fourth, most skeletal assemblages are pauci-specific or mono-specific. This is a feature common to many modern vertebrate assemblages resulting from drought-induced mortalities related to the varying susceptibility of different species to adverse conditions (Conybeare and Haynes, 1984; Rogers, 1990; Schwartz and Gillette, 1994).

Nevertheless, direct evidence for frequent and sustained droughts during the deposition of dinosaur-bearing units in the Two Medicine Formation is still lacking. The best way of analysing palaeoclimate on a sufficiently fine scale to detect drought events is by studying growth rings in fossil woods (Creber, 1977; Creber and Chaloner, 1984; Francis, 1984; Falcon-Lang, 1999). Under environmentally favourable conditions, wood is continuously deposited centripetally by the vascular cambium of trees. However, at the onset of unfavourable conditions such as low winter temperature, drought, or insect defoliation, cambial activity ceases, resulting in the formation of a growth ring in the wood marked by a concentric layer of higher density secondary xylem tissue termed latewood (Fritts, 1976). Wood therefore represents an important palaeoenvironmental archive, providing a continuous intra-annual record of what growing conditions were like in the vicinity of the tree over a period of decades to centuries (Creber, 1977; Creber and Francis, 1999). In this paper, I describe and analyse the patterns of growth seen in fragments of anatomically preserved wood from the Two Medicine Formation to analyse the Late Cretaceous climate of north-west Montana, and to further test the hypothesis that dinosaur skeletal accumulations resulted from drought-induced mass mortalities.

2. Geological setting

The Upper Cretaceous Two Medicine Formation is a ~600-m-thick sedimentary package, exposed for approximately 220 km in highland plains to the east of Glacier National Park in northwestern Montana (Fig. 1). It represents the

most proximal part of a mollasse-type, non-marine wedge deposited between the actively rising Elkhorn Mountain Range to the west and the meridionally orientated Western Interior Seaway to the east, at a palaeolatitude of 48°N (Lorenz and Gavin, 1984; Golonka et al., 1994; Smith et al., 1994). The formation was deposited in a fluvio-deltaic setting, and is bounded by the transgressive shallow marine units of the underlying Virgelle Formation and overlying Bearpaw Formation (Varricchio, 1993; Rogers, 1998). $^{40}\text{Ar}/^{39}\text{Ar}$ radiometric dating of plagioclase and biotite in common bentonite layers above and close to the base of the formation constrain its age between 74 and 83 Ma and place it in the latter part of the Campanian Stage of the Upper Cretaceous (Rogers et al., 1993).

The fossil woods described in this paper were collected from the Seven Mile Hill locality of the Old Trail Museum, 10 km south of Choteau in northwest Montana, south of US Highway 287 (Fig. 1; G. J. Dyke, pers. commun., 2001). At this site a 70-m-thick succession is exposed from near the base of the Two Medicine Formation. Three main sedimentary facies occur. First, there are up to 10-m-thick green/grey mudstone units containing root and burrow traces, rare dinosaur bones and abundant aquatic fresh/brackish water gastropods, together with rare impersistent calcrete layers. This facies is interpreted as the deposits of freshwater lakes or brackish bays in a lower deltaic plain setting (Varricchio, 1993) with calcrete layers indicating periods of emergence and pedogenesis under a seasonally dry climate (Goudie, 1983). Second, there are 1–7-m-thick, erosionally-based, fine- to medium-grained sandstone lenses. These are typically only a few tens of metres wide, contain a coarse basal lag of reworked calcrete nodules, mudstone rip-up clasts, dinosaur bones, permineralised wood, and molluscan fragments, and they fine upward. This facies is interpreted as the deposits of small, tributary river channels on the delta plain (Varricchio, 1993). Third, <1-m-thick bentonite layers and one crystal tuff layer occur. These represent the deposits of repeated volcanic ash falls and a single hot pyroclastic flow, respectively, which probably originated from the nearby Elk-

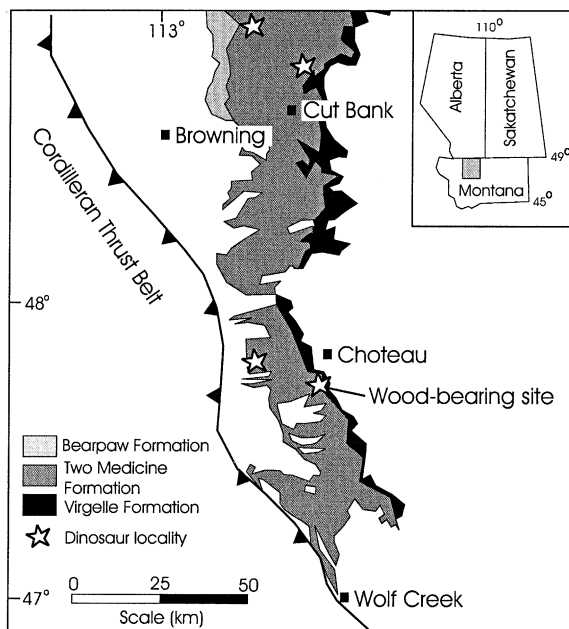


Fig. 1. Location details of area studied. Northwest Montana showing the outcrop of the Two Medicine Formation and the position of the wood-bearing and dinosaur-bearing sites. Inset: situation of Montana; stippled area depicts region of larger map.

horn Mountain Volcanic belt (Roberts and Hendrix, 2000).

The unique crystal tuff layer occurs 105 m above the base of the Two Medicine Formation at Seven Mile Hill and has been $^{40}\text{Ar}/^{39}\text{Ar}$ dated to $80.0 \text{ Ma} \pm 0.1 \text{ my}$ (Rogers et al., 1993). The fossil woods discussed here occur in a channel lag deposit associated with rare dinosaur bones, approximately 60 m above the crystal tuff (Fig. 2). The fossil woods are angular, have long-axes of up to 5–15 cm, and a few fragments exhibit a high degree of anatomical preservation due to silicification. Examination of growth ring boundary curvature, which is always straight or undulating, indicates that these specimens represent fragments of much larger tree trunks, of at least 20–30 cm in diameter. Charred tree trunks within the crystal tuff unit nearby range in diameter from 20 cm to 1 m (Roberts and Hendrix, 2000), implying that the diameter estimates of Seven Mile Hill material may be conservative.

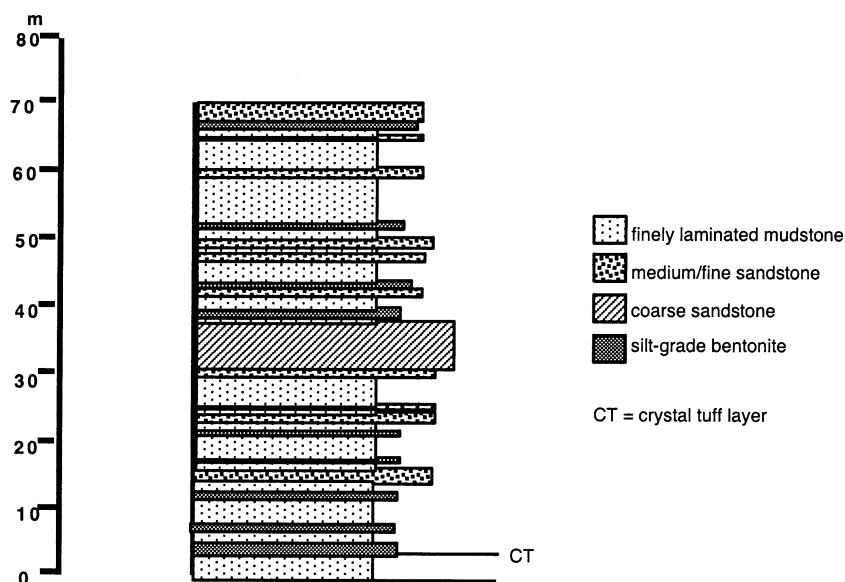


Fig. 2. Sedimentary log of wood-bearing section, Seven Miles Hill, near Choteau, Montana. Crystal tuff is argon dated at 80 Ma (Rogers et al., 1993).

3. Fossil woods

3.1. Materials and methods

Standard 6×4-cm petrographic thin sections were prepared for the six best-preserved wood fragments, orientated along three planes, radial longitudinal section (RLS), tangential longitudinal section (TLS) and transverse section (TS). These specimens were assigned the accession numbers TMF1–6, and are now stored in the Palaeontology Research collection of the Department of Earth Sciences, Dalhousie University, Canada. The thin sections were described in detail with the aid of an Olympus BH-2 transmission light microscope using a combined qualitative and quantitative approach (Phillips, 1948; Falcon-Lang and Cantrill, 2000, 2001). All specimens consisted of pycnoxylic conifer wood belonging to a single form taxon and were classified to generic level using the scheme of Krausel (1949).

3.2. Description

In RLS tracheids are characterised by circular bordered pits (15–18 µm diameter) possessing a

large circular aperture (7 µm diameter) (Fig. 3A). Tracheid pitting is dominantly uniseriate (91%) with biseriate, opposite to sub-opposite pitting separated by bars of Sanio (9%) confined to the ends of the widest tracheids (Fig. 3A,B). Adjacent tracheid pits are either contiguous (63% of instances), spaced greater than half of one pit diameter apart (34%), or squashed together so that adjacent pit borders are distorted into ovals (3%)(Fig. 3B). Rays are thin-walled, and composed of parenchymatous cells, 30 µm in length, 12–17 µm in height, and 10–12.5 µm in width. Ray tracheids are absent. Cross-field pitting is characterised by 1–4 elliptical (7.5×5 µm diameter), obliquely oriented cupressoid or taxodioid pits with elliptical apertures per field (Fig. 3C). Checking is weakly developed in some tracheids (cf. Jones, 1993).

In TLS, rays are highly abundant, being spaced only 1–3 tracheids apart (8–12 per linear mm). In addition, they are almost always uniseriate, typically being 1–30 cells high, although rare examples are up to 58 cells high and possess short biseriate zones up to 5 cells in length (Fig. 3D). Latewood tracheids commonly possess abundant small, circular bordered pits (7.5 µm diameter) on

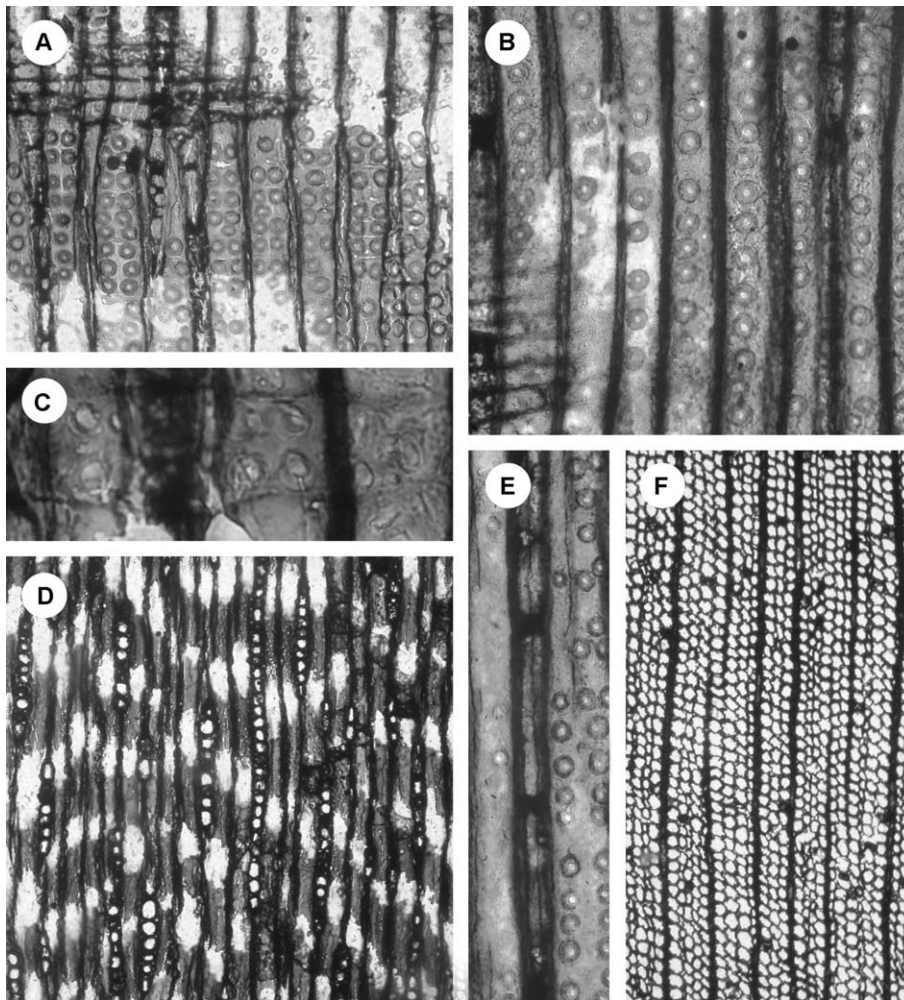


Fig. 3. Two Medicine Formation wood of *Cupressinoxylon*/*Taxodioxydon*-type. (A) Biseriate, opposite tracheid pitting exhibiting bars of Sanio, RLS, TMFc, $\times 150$. (B) Uniseriate bordered pits, RLS, TM3c, $\times 200$. (C) 3–4 cupressoid and taxodioid cross-field pitting, RLS, TM3c, 375. (D) Tall, uniseriate, closely-spaced rays, RLS, TM3b, $\times 75$. (E) Axial parenchyma, TLS, TM3b, $\times 225$. (F) Uniform size rows of tracheids and closely spaced rays, TS, TMF3a, $\times 40$.

their tangential walls (Fig. 3E). Axial parenchyma is common, being composed of vertically elongate cells 30–40 μm in height and 5–10 μm diameter (Fig. 3E).

In TS, common ‘growth features’ with subtle to more marked ring boundaries occur, and will be described in detail in Section 3.3. Resin ducts are absent, but resin-filled axial parenchyma is commonly present, and randomly distributed throughout each growth increment (Fig. 3F). Rays are up to 5.1 mm in length. Tracheids are angular and rectangular in cross-section (Fig. 3F). Although

the wood is generally excellently preserved, locally diamond-shaped cracks (1 mm long) and with long-axes orientated radially, are present between adjacent files of tracheids, occurring in clusters close to the growth features (Fig. 4B).

3.3. Palaeobotanical identity

Under the classification scheme of Krausel (1949), these woods would be named either *Cupressinoxylon* or *Taxodioxydon* because both cupressoid and taxodioid cross-field pit-types occur.

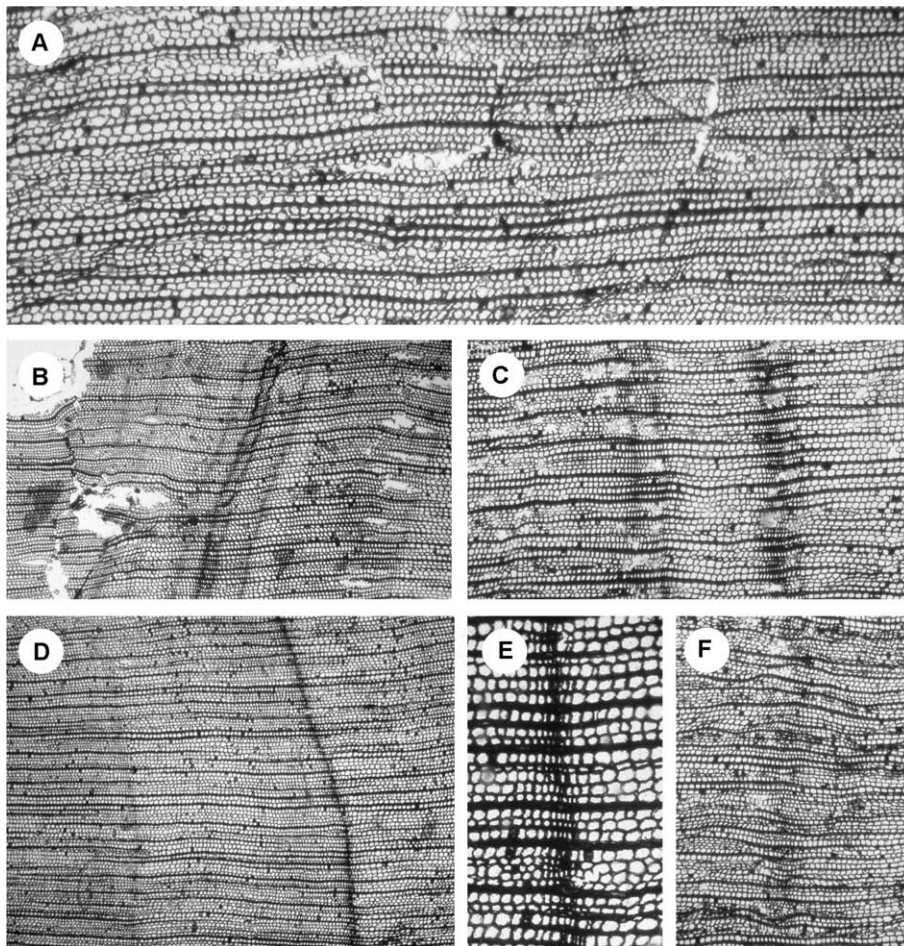


Fig. 4. Examples of growth interruptions in *Cupressinoxylon*/*Taxodioxylon* from the Two Medicine Formation in TS. (A) Growth interruptions are locally absent for a considerable distance, TM1a, $\times 25$. (B) Closely spaced zones of variably persistent growth interruptions, TM6a, $\times 12$. (C) Some growth interruptions have 'double' boundaries, TM3a, $\times 15$. (D) Variably developed interruptions, TM6a, $\times 12$. (E) The most marked growth boundary in the Two Medicine wood assemblage, TM6a, $\times 40$. (F) A typical weakly developed interruption, TM6a, $\times 15$.

The woods compare most closely with silicified specimens of *Taxodioxylon cryptomerioides* Schönfeld from the Campanian Oldman Formation of nearby Alberta, Canada (Ramanujan, 1972), which differs in its shorter rays (1–20 cells high). However, as ray height varies with the developmental age of the wood (Falcon-Lang and Cantrill, 2000), the samples may nevertheless belong to this species. The samples are also similar to a Maastrichtian specimen of *Taxodioxylon drumhellerense* Ramanujan and Stewart (1969)

from Alberta, which differs more significantly in having both taxodioid and glyptostroboid cross-field pits. Another close match is with *Cupressinoxylon coloradense* (Knowlton, 1917) from the Maastrichtian of Colorado, but precise comparison is limited due to the incomplete description of Knowlton's specimen.

Comparison of the Two Medicine Formation material with modern conifer woods indicates a close affinity with either the extant Cupressaceae or Taxodiaceae families (Greguss, 1955, 1972),

but due to the numerous shared anatomical characteristics of woods of these groups, it is difficult to ascertain precisely which of the two families the fossil wood specimens belong to (Phillips, 1948). This question may ultimately prove to be academic because a recent revision of the Order Coniferales has proposed that Taxodiaceae should be absorbed into Cupressaceae (Farjon, 1998). Attribution of the wood specimens to the Cupressaceae/Taxodiaceae is also strongly supported by the presence of taxodiaceous and cupressaceous foliage in the Two Medicine Formation (Crabtree, 1987; Wing and Boucher, 1998), and by abundant taxodiaceous and cupressaceous pollen in its correlative equivalent, the Campanian Belly River Formation, southern Alberta (Jerzykiewicz and Sweet, 1988).

3.4. Palaeo-ecosystem reconstruction

Studies of the facies distribution of plant parts in the Two Medicine Formation suggest that disturbed river channel margin environments were largely colonised by high diversity communities of shrubby angiosperms (Crabtree, 1987), as seen in other Late Cretaceous Northern mid-latitude floodplain assemblages from North America and Europe (Wing and Boucher, 1998; Falcon-Lang et al., 2001b). In contrast, more distal inter-channel regions of the floodbasin appear to have supported open woodlands of taxodiaceous/cupressaceous conifers as indicated by occasional in situ petrified forests overlain by thick mudstone units (Wolfe and Upchurch, 1987; Roberts and Hendrix, 2000). The allochthonous wood specimens described in this paper were presumably sourced from one such floodbasin woodland.

Three lines of evidence suggest that dinosaurs lived in close association with these conifer woodlands in the Choteau region of Montana. First, the fossil wood fragments studied here occur in facies association with dinosaur bones. Second, at another nearby site charred dinosaur bones and Cupressaceae/Taxodiaceae conifer logs are found mixed together in a crystal tuff near Choteau, recording a single biological community suddenly overwhelmed by a hot pyroclastic flow (Roberts

and Hendrix, 2000). And third, but most compelling of all, at a third site permineralised dinosaur coprolites associated with nesting grounds and bonebeds in the Choteau region contain the remains of Cupressaceae/Taxodiaceae wood, indicating that herbivorous dinosaurs such as *Maia-saura* browsed amongst the forests (Chin and Gill, 1996).

4. Analysis of wood growth patterns

True growth rings, defined here as being continuous around the tree's circumference and having a distinctly asymmetric boundary (Fritts, 1976; Creber and Chaloner, 1984), are completely absent in the Two Medicine Formation woods. However, the woods do contain a large number and wide variety of what Schweingruber (1992, 1996) has termed 'growth interruptions' or 'growth zones', features most commonly seen in low latitude trees today. In order to understand the nature of the climate under which dinosaurs lived, growth patterns in the *Taxodioxylo*/*Cupressinoxylo* specimens were examined in transverse thin section. In addition to these qualitative observations, detailed quantitative cell-by-cell measurements of successive tracheid radial diameters (including the cell walls) were made along the wood radii with the aid of a graduated scale mounted in the microscope eyepiece. Five adjacent rows of cells were measured for each specimen, and then averaged using the method of Falcon-Lang (1999). Mean Sensitivity statistical analysis was also applied to the growth interruption sequences using the equation:

$$MS = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(x_{t+1} - x_t)}{x_{t+1} + x_t} \right|$$

where x is the distance between adjacent growth interruptions, n is the number of growth increments in the sequence analysed, and t is the year number of each increment. The Mean Sensitivity technique was developed to quantify the year-to-year variability in sequences of true growth ring widths (Fritts, 1976). Whilst true annual rings are not present and therefore this statistic is used in an unconventional manner, its

application to the growth interruptions does give a good numerical measure of their spacing variability, and is thus very valuable in helping to describe the phenomenon observed.

4.1. Description of ring boundary types

The growth interruptions consist of concentric, variably persistent zones characterised by tracheids with smaller than normal radial diameters (analogous to the latewood tracheids of true growth rings). Although a complete continuum of growth interruptions exist in these woods, it is useful to informally describe two end-member types. At one end of the spectrum are those with more marked growth boundaries that are continuous around the partial circuit of the largest specimens (15 cm), and are defined by a gradual decline in cell diameter from 40–45 μm to 12–20 μm over approximately 4–8 latewood cells. The subsequent reversion to 40 μm diameter cells occur abruptly over 1–2 cells and gives the growth interruption zone weakly asymmetric boundaries (Fig. 4D,E). At the other end of the spectrum are zones with much more subtle growth boundaries. In many cases, these cannot be traced laterally around the stem for more than about 10 cm before they either fade out or wedge out to merge with an earlier-produced growth interruption. They are defined by a rapid decline in cell diameter from 40 μm to approximately 20–25 μm over 1–3 latewood cells, followed by an equally rapid

rise back up to the normal tracheid diameter, and therefore have symmetrical growth boundaries (Fig. 4B–D,F).

Two further general properties of these interruptions are noteworthy. First, the smaller tracheids that mark the interruptions do not have preferentially thickened cell walls (Fig. 4E). In fact, their cell walls are often slightly thinner (4–5 μm) in comparison with those seen in the normal-sized tracheids (5–6 μm). Second, a concentric zone (< 10 cells wide) of unusually large diameter (up to 50–60 μm) tracheids often occurs immediately after the growth interruptions (Fig. 4B,C).

4.2. Description of ring boundary spacing

The distribution of growth interruptions in the woody trunks is highly spatially irregular. Only short continuous sequences of growth interruptions, ranging from 10 to 19 ring increments, are observable in the Two Medicine Formation thin sections due to patchy silicification, cellular crushing and their irregular occurrence. Individual growth interruptions are spaced between 0.12 mm and 29.07 mm apart (mean 1.81 mm, $n=65$). Individual wood fragments possess Mean Sensitivity values that range from 0.412 to 0.878 with a mean value of 0.639 ($n=6$). Compared with the ring spacing in modern temperate ring sequences, these values demonstrate highly irregular growth patterns; temperate ring are considered irregular (or ‘sensitive’) if year-to-year

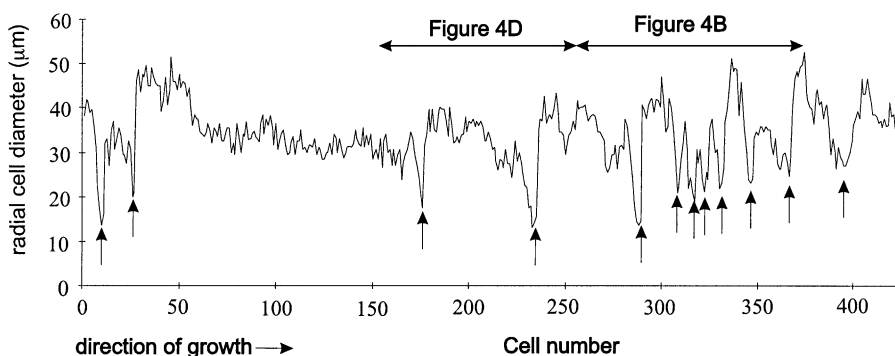


Fig. 5. Numerical representation of growth rings in Specimen TM6a. Growth is left to right. Arrows indicate subtle growth interruption boundaries.

ring widths give mean sensitivities >0.3 (Fritts, 1976).

However, these statistics do not communicate the irregular distribution of growth interruptions as adequately as a qualitative description. For example, one specimen (TMF1a), almost completely lacks growth interruptions altogether (Fig. 4A). It contains zones 4–29 mm wide (i.e. approximately 90–650 cells wide) composed of rows of tracheids consistently 36–53 μm in diameter, separated by very weakly developed growth interruptions. Other specimens, e.g. TMF2a–5a, contain a large number of growth interruptions spaced 0.2–1.3 mm apart, with boundaries often defined by two very closely adjacent interruptions that grade into each other (Fig. 4C). In Fig. 5, cell-by-cell growth patterns are shown for part of a particularly well-preserved sequence in specimen TMF6a. This specimen contains a highly irregular growth pattern with some zones lacking interruptions over 150 cells whilst another shows four interruptions over a radius of only 25 cells (Fig. 4B).

4.3. Review of regional-scale

Campanian–Maastrichtian tree growth patterns

As only a small number of wood specimens with sufficient anatomical preservation to examine growth patterns were found at the Seven Mile Hill locality, additional growth data from approximately contemporaneous deposits across the region were collected through a literature review. This approach not only increases sample size but also improves understanding of the extent of the geographical area over which similar tree growth patterns occurred. The palaeogeographic location of additional wood sites was ascertained using Fred Ziegler's base maps located at <http://pgap.uchicago.edu/movies.html> (Fig. 6)

The regional review shows that fossil conifer woods exhibit qualitatively identical growth patterns to those described here in detail from the Two Medicine Formation over a wide palaeolatitude range from 34–48°N along the margins of the Western Interior Seaway. For example, specimens of *Cupressinoxylon* conifer wood from the Maastrichtian Vermejo Formation of Colorado

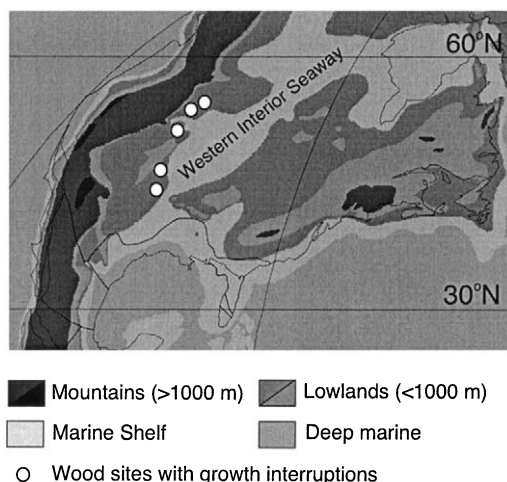


Fig. 6. Global palaeogeographic map (<http://pgap.uchicago.edu/movies.html>) showing position of Montana on the margins of the Western Interior Seaway, USA, and the location of wood-bearing sites showing growth interruptions

(palaeolatitude 34°N) contain either multiple, closely spaced growth interruptions (1–2 mm apart) defined by a narrow latewood band 3–4 (rarely 6) cells wide or completely lacked rings (Knowlton, 1917). Conifer wood from the Campanian–Maastrichtian of New Mexico, Montana and Wyoming (palaeolatitude 35–44°N) exhibit continuous uninhibited growth or with weakly delineated growth interruptions (Wolfe and Upchurch, 1987). Finally, conifer woods from the Two Medicine Formation itself (palaeolatitude 48°N), have previously been described briefly as possessing growth interruptions of highly variable thickness, closely comparable to those noted here (Crabtree, 1987).

In contrast, at lower palaeolatitudes ($<30^\circ\text{N}$) Campanian–Maastrichtian woods from Arizona, Utah, Idaho, and Texas exhibit continuous growth, completely lacking any growth ring features whatsoever (Spackman, 1948; Thayne et al., 1985; Lehman and Wheeler, 2001), whilst at higher palaeolatitudes ($>55^\circ\text{N}$) specimens of *Cupressinoxylon* (Penhallow, 1908) and *Taxodioxyton* (Ramanujan and Stewart, 1969; Ramanujan, 1972) contain true growth rings, continuous around the trunk circumference, possessing well-marked, asymmetrical ring boundaries defined by numerous latewood cells.

5. Interpretation of growth patterns

In summary, growth features in the Two Medicine Formation are quite unlike true growth rings exhibited by most present-day temperate-zone conifers (cf. Greguss, 1972), but bear a close resemblance to what Schweingruber (1992) has described as growth interruptions in subtropical and tropical woods. In addition, these Late Cretaceous growth interruptions are not geographically localised phenomena but in fact characterise a broad latitudinal belt along the Western Interior Seaway. The palaeoclimatic significance of growth interruptions has generated much confusion and debate (Ash and Creber, 1992), and as a preamble to interpreting the palaeoclimatic significance of these structures it is worth beginning by examining how their nature and origin differs from that of true growth rings.

5.1. Formation of growth interruptions

Wood is produced by the vascular cambium (Creber and Chaloner, 1984). As new tracheids pass out of the cambial zone they undergo a phase of radial expansion followed by a phase of wall thickening (Ford et al., 1978). The factors that control the degree to which tracheids radially expand and thicken, and hence the growth patterns observed in the wood, are complex. The three most important factors influencing tracheid maturation are the supply of photosynthate and growth promoting phytohormones, and the turgor of the cambial derivative cell (Schweingruber, 1996).

Under temperate climatic conditions, falling temperatures and shortening photoperiod during late summer/early autumn inhibit the rate of production and transport of photosynthate and growth promoting phytohormones, at a time when water supply is also declining. This leads to a reduction in the number of cells in the cambial zone, and causes newly formed tracheids to spend longer in the zone of cell wall thickening relative to the zone of cell expansion (Creber and Chaloner, 1984; Uggla et al., 1998). A transition from large diameter, thin-walled earlywood tracheids to small diameter, thick-walled latewood

tracheids is therefore seen in the latewood. During winter, cambial activity completely ceases, and when it reactivates under optimum spring growing conditions, large earlywood tracheids are produced. This process gives rise to a true growth ring. True growth rings may be also formed in seasonal tropical regions with a long dry season, where drought induces long-term cambial dormancy (e.g. Rao and Rajput, 1999), but in contrast these do not necessarily represent annual increments of growth (Duke et al., 1981; Ash, 1983; Falcon-Lang, 1999).

In environments where cambial activity can potentially occur continuously (e.g. in the non-seasonal tropics), short-term disturbances to growth may occur which influence patterns of wood development in a qualitatively different way to that manifesting in true growth rings (Jacoby, 1989). Examples of such disturbances are droughts, floods, fires, wind damage, unusually low temperatures, synchronous coning/leaf flushing, or insect-attack (Fritts, 1976; Ash, 1983; Dechamps, 1984; Schweingruber, 1992, 1996; Young et al., 1993). Each disturbance has the potential to limit the degree to which tracheids in the cambial zone undergo expansion and wall thickening. The growth interruptions that result have a symmetrical or weakly asymmetrical ring boundary, exhibiting a gradual decline and subsequent gradual rise in tracheid diameter, and are produced by a temporary slowing down, but not switching off, of cambial activity (Schweingruber, 1992, 1996). In addition, they typically fade out around the trunk circuit because phytohormonal response to weak short-term disturbances is imprecisely synchronised growth throughout an individual tree (Larsen, 1956). Growth interruptions are therefore distinctly different from true growth rings with respect to their morphology and origin; the former result from a temporary slowing down of cambial activity, the latter are produced by a complete cessation of cambial activity (Creber and Chaloner, 1984). Growth interruptions may also occur in temperate woods, which contain true growth rings, having resulted from short-term disturbances during the growing season. In this context growth interruptions have been termed false rings (Fritts, 1976).

5.2. Interpretation of Late Cretaceous growth interruptions

The complete absence of true growth rings in the woods of the Two Medicine Formation and adjacent coeval localities between 34 and 48° of palaeolatitude indicate that these trees grew under conditions that were potentially favourable for continuous cambial activity year-round. Two independent strands of data support this interpretation. First, the results of mid-Cretaceous computer climate models suggest that mean winter temperatures for the Western Interior of the USA were 16–20°C, and summer mean temperatures were 20–24°C (Valdes et al., 1996). Second, leaf physiognomic data suggest that NW Montana lay in the transition zone between a non-seasonal megathermal climate and a weakly seasonal mesothermal climate, a region with a mean annual temperature close to 20°C, and a mean annual temperature range of only 8°C (Wolfe and Upchurch, 1987). Summer–winter temperature contrast was probably reduced by the ameliorating effect of the Western Interior Seaway (Valdes et al., 1996).

However, the presence of growth interruptions in Western Interior fossil woods indicates that trees growing in this megathermal environment were subject to repeated growth disturbances. The highly irregular spacing of the growth interruptions (<5 to >650 cells apart; Mean Sensitivity 0.639) indicates that this growth disturbance process entirely lacked any periodicity whatsoever. Assuming a conservative tracheid production rate of ca. 1 cell per day (cf. Ford et al., 1978), the four interruptions closely-spaced across a file only 25 cells wide in TMF6a may represent repeated disturbances in less than a single month. In contrast, specimen TMF1, which largely lacks interruptions, likely represent many years of undisturbed growth. Furthermore, the differing degrees to which the growth interruptions are developed in these woods, suggest that the intensity and duration of the disturbance events were also highly variable.

In the Late Cretaceous Western Interior, two environmental phenomena could potentially have given rise to the repeated, aperiodic, and

variably intense environmental disturbances recorded by the growth interruptions; these are drought (e.g. Ash, 1983) and flooding (e.g. Young et al., 1993). However, drought is the overwhelmingly most likely of the two causes for four intrinsic reasons. First, growth interruptions are common to woods over 14 degrees of latitude indicating that they formed in response to regional climatic phenomena rather than being features related to the local vagaries of floodplain hydrology. Second, the fossil woods contain features like diamond-shaped cracks and checking, similar to features known in modern woods to be created by the wood drying out during growth (Jones, 1993; Schweingruber, 1996). Third, growth interruptions caused by flooding are usually accompanied by the development of rounded tracheid, with intercellular spaces (Hook, 1984; Falcon-Lang et al., 2001a), a feature not present in the Two Medicine woods. Fourth, zones composed of unusually large diameter tracheids that follow many of the growth interruptions indicate that disturbance events ended by a rapid return to optimum growing conditions, a feature that has been related to an increase in water availability and cellular turgor after rains (Ford et al., 1978).

Several independent lines of evidence support a drought-induced origin for the growth interruptions. First, angiosperm leaves in the Two Medicine Formation are coriaceous but lack drip tips, a physiognomy associated with seasonally dry environments (Crabtree, 1987). Second, charcoal is common in the Two Medicine Formation, indicating the occurrence of fires and implying drought (Carpenter, 1987). Third, studies of Campanian palaeosols at a palaeolatitude of 40°N in New Mexico indicate the operation of a humid climate with an annual precipitation of 750–1000 mm yr⁻¹ (Mack, 1992), whilst Maastrichtian palaeosols at a palaeolatitude of 49°N in Montana are believed to have formed under seasonally humid climates with a marked (but not severe) dry season and a mean annual rainfall of 900–1200 mm yr⁻¹ (Retallack, 1994; Buck and Mack, 1995). Fourth, the results of non-parametric climate models have implied slight rainfall seasonality over Late Cretaceous Montana, with

summers being humid but winters being rather drier (Golonka et al., 1994).

However, there may not have been a simple direct linkage between drought and growth interruption formation. Droughts lead to the physiological water stress of trees by depressing the local water table (Little, 1975). Irregular growth interruption patterns therefore probably reflect drought-induced fluctuations in water table, and this mediating process may have introduced a greater degree of aperiodicity into the growth interruption patterns observed, compared with the actual aperiodicity of the rainfall.

5.3. Comparison with present-day East African growth patterns

The interpretation of the Two Medicine Formation wood growth patterns as indicating drought-interrupted growth under a megathermal climate is strongly supported through comparison

with woods from present-day seasonal, megathermal regimes in East Africa. The woods of a wide diversity of conifers from this region are held in the collections of the Jodrell Laboratory at the Royal Botanic Gardens, Kew, UK, and exhibit identical growth patterns to those described in this paper. For example, trunk wood of *Juniperus procera* Hochst ex Endlicher from Somalia and Kenya (a cupressaceous conifer related to those studied from the Two Medicine Formation) exhibits wide radii lacking any growth features (Fig. 7A) or contains irregularly spaced growth interruptions characterised by symmetrical to weakly asymmetric growth (Fig. 7B). Other pinaceous conifers such as *Pinus oocarpa* Schiede and Schltdl from Uganda contain common well-developed symmetrical growth interruptions (Fig. 7C), and asymmetric growth interruptions that often exhibit a double boundary composed of two closely spaced interruptions (Fig. 7D). This latter feature is very similar to the double interruptions

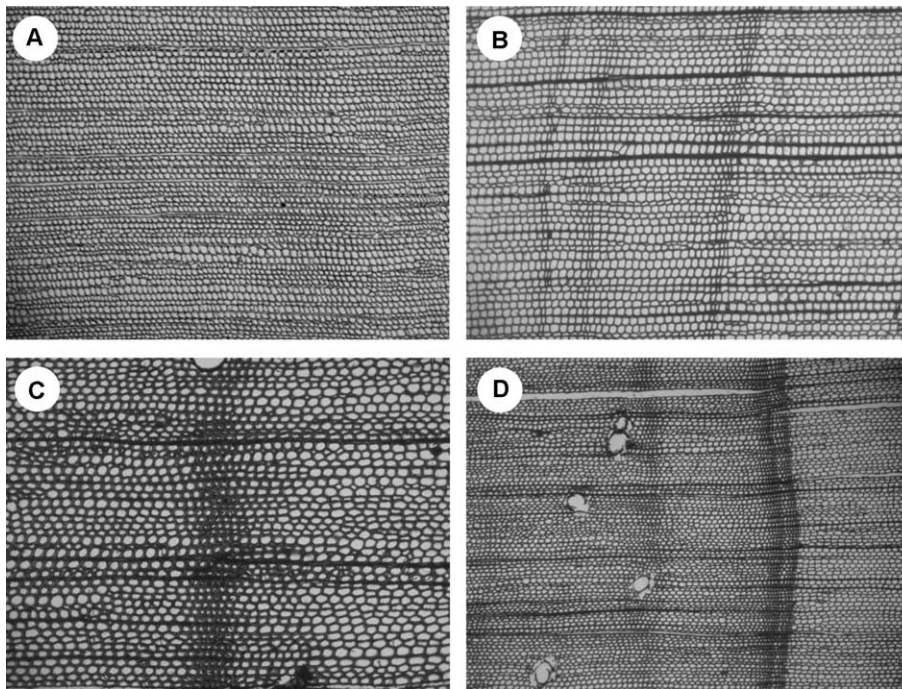


Fig. 7. Examples of growth interruptions in conifer woods from East Africa. All specimens stored at Jodrell Laboratory, Royal Botanic Gardens, Kew. (A,B) *Juniperus procera* and (C,D) *Pinus oocarpa*. (A) Growth interruptions are locally absent, $\times 12$. (B) Irregularly spaced weak interruptions, $\times 15$. (C) Marked symmetrical growth interruption, $\times 12$. (D) Marked asymmetrical 'double' interruptions, $\times 15$.

seen in the Two Medicine sample, TM3a (cf. Fig. 4C). Still other podocarpaceous conifers such as *Podocarpus milanjanus* Rendle and *Afrocarpus mannii* (Hook) Page from Tanzania and Uganda have even more weakly developed growth features exhibiting only the faintest interruptions (not figured), and then only rarely. All the East African conifers described grew in near-equatorial settings where annual temperature variability is minimal and irregular growth interruption patterns are entirely the result of erratic rainfall and seasonal droughts (Jacoby, 1989).

6. Discussion

In summary, growth patterns in Late Cretaceous woods of the Western Interior suggest the operation of megathermal climates punctuated by erratic seasonal rainfall. The only other site documented in the fossil record that contains abundant woods with very similar patterns of growth to those documented from the Two Medicine Formation, and surrounding areas, is the Upper Triassic Chinle Formation of Arizona, USA (Ash and Creber, 1992). Growth interruptions at this site have been interpreted as recording either drought-induced fluctuating water table or perhaps free-running endogenous rhythms (Ash and Creber, 1992). The absence of true growth rings, despite abundant independent evidence for rainfall seasonality, has been linked to the palaeovalley setting of the fossil forests, which may have maintained an artificially high water table, and rendered the trees less sensitive to regional climate (Demko et al., 1998). Comparison with the Chinle Formation is highly significant because this unit, like the Two Medicine Formation, contains rich mono-specific or pauci-specific bonebeds of dicyonodonts and early dinosaurs believed to have originated from drought-induced mass mortalities (Schwartz and Gillette, 1994; Fiorillo et al., 2000).

It is interesting that at both the Cretaceous Two Medicine Formation and the Triassic Chinle Formation sites, trees producing weakly defined growth interruptions, and drought-induced bonebeds co-occur. I suggest that this is no coinci-

dence, and that such types of geological environment actually possess the optimum conditions for causing drought-induced mass mortalities. Wood growth patterns indicate that in both settings, the trees could grow continuously for long periods, but when water stress did occur it did so repeatedly for one to several months. During long favourable environmental phases when water availability was unlimiting for many years, the ecosystem carrying capacity of the region would have been high, and large populations of megafauna could develop. However, when droughts began to lower the water table, as they did so with an erratic aperiodicity, these populations would have become very vulnerable and mass mortality would have followed.

Very similar population dynamics are seen in East Africa amongst elephant herds where as previously noted, climate is megathermal with a seasonal rainfall distribution (Owen-Smith, 1988). Under normal conditions rainfall is regular, and water availability is high. However, due to the erratic vagaries of tropical climate, rainfall occasionally fails, the rivers dry up, and water holes become rarer. Megafauna that need to drink every few hours become restricted in their movements to a within a few kilometres of the remaining water holes. If the droughts persist, vegetation in the vicinity of the water holes is quickly completely consumed, and the megafauna die of starvation in very large numbers (Conybeare and Haynes, 1984; Haynes, 1988).

In conclusion, analysis of the growth interruption patterns seen in the conifer woods of the Two Medicine Formation and surrounding regions indicate the existence of a megathermal climate with erratic rainfall. Megafaunal populations would have been highly unstable under such conditions, and the new data presented in this paper therefore strongly support the hypothesis that para-autochthonous dinosaur bonebeds originated from drought-induced mass mortalities.

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