

Fire-prone plant communities and palaeoclimate of a Late Cretaceous fluvial to estuarine environment, Pecínov quarry, Czech Republic

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(Received 1 December 2000; accepted 19 June 2001)

Abstract – The botanical identity and facies distribution of fossil charcoal is described from Middle to Late Cenomanian (90–94 Ma) fluvial to estuarine units at Pecínov quarry, near Prague, Czech Republic. Braided alluvial facies associations contain charred conifer woods (family Pinaceae) possibly derived from upland forest fires, and abundant charred angiosperm woods, flowers and inflorescences (families Lauraceae and ?Platanaceae) derived from riparian gallery forest fires (Unit 2). Retrogradational coastal salt marsh facies associations contain abundant charred conifer wood (families Cheirolepidiaceae and Cupressaceae/Taxodiaceae) derived from fires in halophytic backswamp forest, and rare pinaceous charred cones and lauraceous angiosperm wood washed downstream from fires further inland (Units 3–4). Progradational coastal facies associations within an estuary mouth setting contain abundant charred conifer wood (family Cupressaceae/Taxodiaceae), common taxodiaceous conifer and angiosperm leaves, fern rachises, and lycopsid stems derived from fires in mesic backswamp taxodiaceous forests and supra-tidal fern-lycopsid thickets (Unit 5). Growth rings in angiosperm and conifer woods, leaf physiognomy and computer models indicate that climate was equable, warm and humid, but that there was a short annual dry season; most fires probably occurred during these annual drought periods. The abundance of charcoal and the diversity of taxa preserved in this state indicate that nearly all plant communities were fire-prone. Physiognomically, the Pecínov flora resembles present-day seasonally-dry subtropical forests where fires are a common occurrence.

1. Introduction

Natural, lightning-initiated fires occur today in every vegetation biome including everwet tropical rainforest and frigid tundra (Racine, Dennis & Patterson, 1985; Sanford *et al.* 1985). Recently, the importance of fire in influencing earth surface processes has received considerable attention; it is now known that fire plays a crucial role in the global carbon cycle (Clark, 1997), shapes the character and evolutionary development of many terrestrial ecosystems (Walter, 1973) and alters cycles of erosion and deposition (Meyer & Wells, 1997). The frequency, geographic area and intensity of fire events in a given region, and thus their impact on plant ecology and the physical environment, are strongly influenced by rainfall magnitude and seasonality (Chandler *et al.* 1983). Regions with everwet, non-seasonal climates are characterized by large, low frequency (every 100–1000 years), high intensity fire events, whilst in seasonally-dry regions fires occur much more frequently (annually in some places) but are of smaller size and lower intensity (Scott & Jones, 1994; Falcon-Lang, 2000).

Recently there has been great interest in trying to understand the nature and significance of fire in Pre-Quaternary times (Scott, Moore & Brayshaw, 2000). The occurrence of Pre-Quaternary fires may be recognized by the presence of fossil charcoal incorporated into sedimentary and extrusive igneous rocks (Scott, 1989, 1990). Early workers called this substance fusain and came to conflicting conclusions about its origin (see Robinson, Chaloner & Jones, 1997, for a review), but recent chemical and physical studies have confirmed that fusain is fossilized charcoal, the product of wildfire (Jones & Chaloner, 1991). An important feature of all charcoal is its exquisite preservation of three-dimensional plant anatomy, a condition related to the fact that the plant material was made chemically inert through loss of volatiles before it entered the geological record (Scott, 1989).

Recent work on Carboniferous charcoal deposits has demonstrated that a wealth of palaeoecological data may be extracted from this remarkable fossil material (Scott & Jones, 1994). For example, through a comparison of the distribution of charred and uncharred plant fossils within the facies context, discrete fire-prone plant communities may be identified (Batten, 1998; Falcon-Lang, 1998, 1999a, 2000; Falcon-Lang & Scott, 2000). Additionally, integration

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of these data with information concerning the magnitude and seasonality of rainfall (from growth rings, leaf physiognomy, palaeosols and climate models) allows ecosystems characterized by small seasonal fires to be distinguished from those punctuated by rare catastrophic conflagrations (Scott & Jones, 1994; Falcon-Lang, 1999*b,c*, 2000).

In this paper we document the occurrence of charcoal in the Cretaceous Bohemian Basin of the Czech Republic (Uličný & Špičáková, 1996). Earlier studies of Cretaceous charcoal have generally been limited to describing the beautifully preserved anatomy of plant organs such as flowers, leaves and woods (Alvin, 1974; Friis & Skarby, 1981; Herendeen, 1991*a*) with relatively little attention given to the palaeoecological significance of fire (Harris, 1958; Batten, 1974; Lamberson *et al.* 1996; Falcon-Lang, Cantrill & Nichols, 2001). Here we apply the various approaches used to analyse Carboniferous charcoal (described above) to understand for the first time the nature and role of fire in the Late Cretaceous terrestrial ecosystems of Central Europe.

2. Geological setting

During the Late Cretaceous period the Earth experienced an equable greenhouse climate; polar ice caps were absent or at least comparatively small, and eustatic sea-level was high (Francis & Frakes, 1993; Price, 1999). Central Europe lay on the southern margins of the Laurasian continent at a palaeolatitude of 40° N, and consisted of a large island with subdued topography (Eastern European Island) surrounded by shallow epeiric seas (Golonka, Ross & Scotese, 1994; Smith, Smith & Funnel, 1994). During the Cenomanian age, a system of strike-slip basins, termed the Bohemian Cretaceous Basin, formed on the northwest margins of Eastern European Island in response to compression transmitted from the Alpine–Carpathian collision zone to the south (Uličný & Špičáková, 1996; Fig. 1*a*). During the early stages of basin evolution it was characterized by a series of broad palaeovalleys, whose strikes followed lineaments in the Variscan basement. During a stepwise sea-level rise in Middle to Late Cenomanian times, the palaeovalleys became filled with a succession of fluvial deposits overlain by first estuarine/coastal facies and later open marine shelf facies (Uličný & Špičáková, 1996; Uličný, 2001).

The charcoal deposits described in this paper are from Pecínov quarry, approximately 40 km northwest of Prague, Czech Republic, an outcrop on the south-west margins of the Bohemian Basin (Fig. 1*b*; latitude 50°07'48", longitude 13°54'54"). Pecínov quarry was situated near the axis of a 5 km wide, NE-striking palaeovalley bounded by local palaeo-highs (Fig. 1*c*). It contains a 30–35 m thick succession of Cenomanian–Turonian strata, which overlies Upper Carboniferous clastic units with a pronounced unconformity (Fig. 2).

We examined only the lower 18–20 m of the Pecínov section, the Peruc and Korycany members of Peruc–Korycany Formation, which span the Middle to Upper Cenomanian stage (90–94 Ma; Čech *et al.* 1980).

3. Sedimentary facies and plant assemblages, Pecínov quarry

3.a. Description and interpretation

The sedimentary facies and plant assemblages of these beds have already been described in great detail (Uličný & Špičáková, 1996; Uličný *et al.* 1997*a,b*). Here we just give a brief summary of that data to set the background for our study of the charcoal. Five depositional units have been recognized in the Peruc and Korycany members at Pecínov Quarry, and their properties are summarized in Table 1 and Figure 2.

Unit 1 represents the deposits of a gravelly braided river channel in the proximal part of a palaeovalley, which was dominantly vegetated by lauraceous angiosperm gallery forest. Unit 2 is interpreted as the deposit of a large tidally-influenced braided river system in the medial part of the palaeovalley, colonized by mixed angiosperm–gymnosperm forest, with gymnosperms becoming increasingly common towards the coast. Unit 3A consists of the deposits of supra-tidal marshes dissected by sinuous tidal creeks, which were covered by putatively halophytic taxodioid–cheirolepid backswamp conifer forests (cf. Tu *et al.* 1999). Unit 3B represents a supra-tidal salt marsh peat, seaward of the backswamp, which accumulated beneath cheirolepid conifer and ginkgoalean shrubland (cf. Gomez *et al.* 2000). Unit 4 represents the deposit of a tidal flat/sub-tidal channel complex; these beds lack macro-plant fossils and were probably unvegetated. Unit 5 is interpreted as representing the progradation of a tide-dominated coastline, Unit 5A being an ebb-tidal delta deposit and Unit 5B representing inter- and supra-tidal deposits of the late-stage estuarine mouth fill. These beds contain plant assemblages that were derived from a variety of mesic, taxodioid conifer, backswamp forests and supra-tidal marsh floras (Uličný *et al.* 1997*b*).

3.b. Environmental and ecological synthesis

Uličný & Špičáková (1996) interpreted the five depositional units as parasequences (*sensu* Van Wagoner *et al.* 1990) on the basis of identifying marine flooding surfaces or their correlative equivalent at the top of each unit. Units 1–4, which represent a transition from braided alluvial to estuarine facies, were collectively interpreted as a transgressive systems tract. Unit 5, which represents a progradational coastal facies, was interpreted as a highstand systems tract (Uličný & Špičáková, 1996). Alluvial environments in the proximal to medial part of the palaeovalley (Units 1–2)

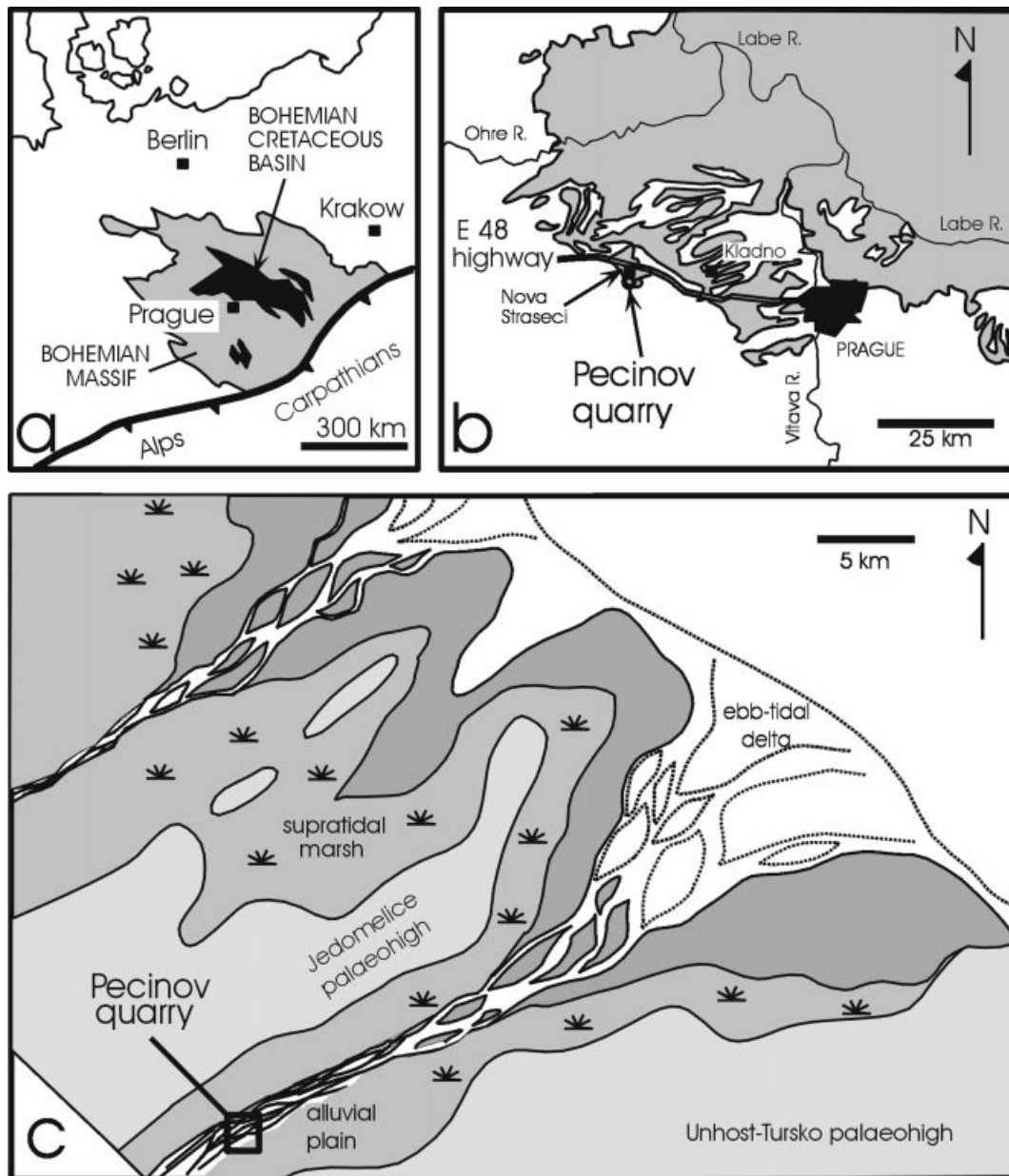


Figure 1. Geological setting. (a) Location of the Bohemian Cretaceous Basin in Central Europe. (b) Location of Pecinov quarry, 30 km west of Prague, Czech Republic. Grey area indicates limits of the Cretaceous rocks. (c) Summary palaeogeographic reconstruction during the deposition of Unit 1 (based on facies and isopach data in Uličný & Špičáková, 1996).

were dominated by angiosperm gallery forests, with conifers and cycadophytes becoming increasingly abundant towards the coast (Units 3–5). Retrograding coastal environments were dominated by putatively halophytic cheirolepid/taxodioid/ginkgo conifer forests and scrub (Unit 3–4) whilst prograding coastal environments were dominated by mesic taxodioid conifer/fern forests (Unit 5). The difference in character of coastal vegetation in Unit 3–4 compared to Unit 5 probably relates to variable edaphic conditions; retrogradational coastal soils would have been more susceptible to saline intrusion than those of progradational coastlines, which explains the predominance of

halophytic cheirolepid vegetation in these former units (cf. Batten, 1974).

4. Charcoal assemblages

Fossil charcoal occurs in great abundance in the Cenomanian units of Pecinov quarry; only in Unit 1 was no charcoal found. Charcoal abundance was quantified using a 400 cm² acetate quadrat on bedding surface exposures (H. Falcon-Lang, unpub. Ph.D. thesis, Univ. London, 1998). Samples were collected from Units 2–5, macerated in 40% HCl for one week to remove carbonates and in 40% HF for two

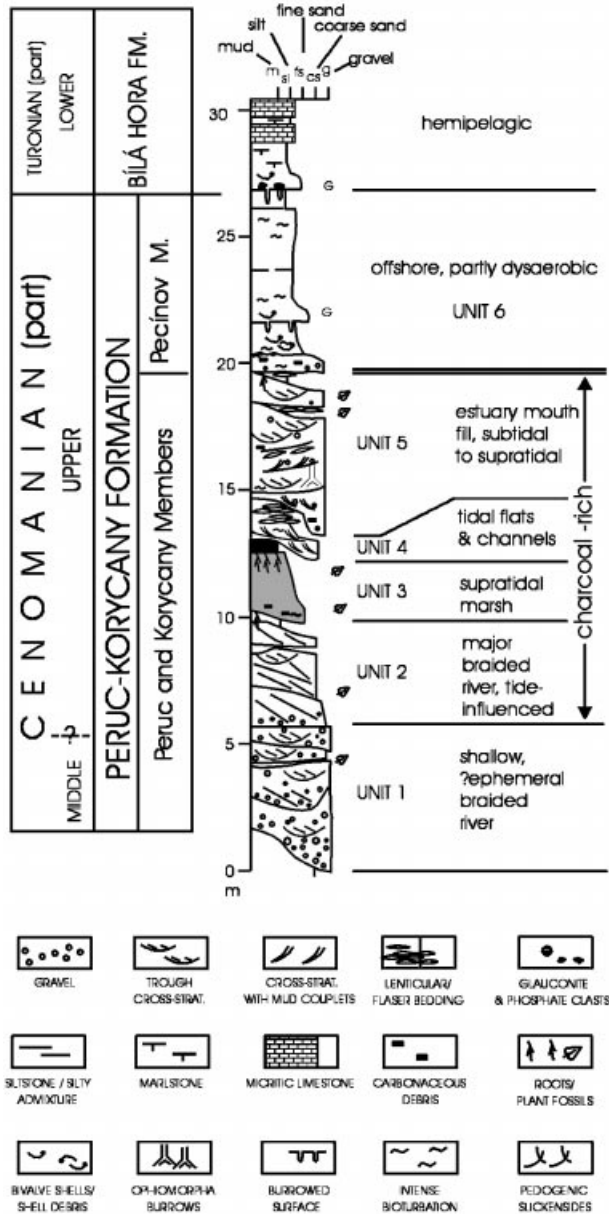


Figure 2. Interpreted log of Cenomanian–Turonian succession in Pecínov Quarry (Uličný *et al.* 1997a).

weeks to remove silicates, mounted on stubs using carbon tabs or ‘Q.D. colloidal silver’, and examined with the aid of a Cambridge S-360 Scanning Electron Microscope. Most charcoal exhibits high quality anatomical preservation and gaseous eruption structures (Jones, 1993) indicating that it was formed from burned living tissue. Some charcoal exhibits poorer preservation due to cellular degradation (mainly by fungi), the emplacement of frass-filled chambers, and physical squashing, all of which demonstrably took place prior to charring; this latter charcoal was therefore probably formed from burned partially decomposed litter material.

4.a. Unit 2: Tidally influenced braided river

Equidimensional blocks of charred wood (0.1–3 cm long), partially charred laths of wood (up to 17 cm long), and <1 mm non-woody charcoal fragments occur in several facies within this unit. In coarse-grained associations (Assemblage 2A), they occur in channel bases associated with lag deposits (up to 5% bedding surface cover), as discontinuous lenses at the base of trough cross-bedded units (up to 90% cover), and as isolated fragments in the fore-sets of the cross-beds, increasing in abundance towards the base of the set (up to 8% cover). Some charcoal clasts have rounded corners but most are angular. Charcoal is also present in thin bar top mudstone beds (Assemblage 2B; abundance not quantified).

Assemblage 2A contains of a mixture of coniferopsid and angiosperm woods. The coniferopsids are mainly represented by branch material as indicated by the small diameter (<2 cm) of the woody cylinders, the presence of a parenchymatous pith at the centre of one specimen, and spiral thickening (interpreted as reaction wood: Creber, 1975) in another. They are characterized by tracheids with contiguous or scattered circular bordered pits on their radial walls and 1–2 pinoid pits occur in each cross-field. Rays are uniseriate, 1–7 cells high, possess smooth walls, and contain resin ducts. In transverse section, growth rings are present and circular resin ducts (50 µm diameter) occur throughout the ring increment. Under the scheme of Kräusel (1949) these would be classified as *Pinuxylon*; they show close similarities to the family Pinaceae.

The rest of the charcoal in Assemblage 2A is angiosperm wood; this material ranges from small branches (10–12 mm diameter) to fragments of large trunks. The first type of angiosperm wood in this unit is characterized by solitary vessels or by rarely radial multiples of 2–4 (Fig. 3a); vessel arrangement is diffuse porous (25–35 vessels per square millimetre). Vessel elements are oval to circular in cross-section, moderately small (35–110 µm diameter), and possess simple perforation plates with only 5 bars. Tyloses are ubiquitous (Fig. 3b). Intervascular pitting of vessel walls typically consists of 7–9 rows of alternately-arranged small (4–6 µm diameter) pits with oblique apertures (Fig. 3c). Fibres are septate. Rays are heterocellular with upright marginal cells, 2–3 seriate, and up to 16 cells high (Fig. 3d–e). Growth rings are present. This wood type exhibits a very close similarity with charred wood specimens of *Paraphyllanthoxylon*-type from the mid-Cretaceous Potomac Group of eastern North America (Herendeen, 1991a), which are similar to present-day wood of the family Lauraceae (Metcalf & Chalke, 1950; Metcalf, 1987; Herendeen, Wheeler & Baas, 1999). Our specimens are also probably lauraceous because they occur in facies association with lauraceous leaves (*Grevilleophyllum* and *Myrtophyllum*),

Table 1. Summary of facies and macroplant data from Pecínov quarry, near Prague (Uličný *et al.* 1997a,b)

| Facies | Facies description | Facies interpretation | Dominant uncharred fossil plants |
|--------|--|---|---|
| 1 | Channelized sandstone-conglomerate unit containing low-angle, metre-scale cross stratification | Gravelly braided river channels | Angiosperm leaves (<i>Grevilleophyllum</i> , <i>Myrtophyllum</i> , <i>Platanus</i> : 88% of flora) and cycadophyte leaves (<i>Nilsonia</i>) in fine-grained abandoned channels |
| 2 | Channelized, heterolithic sandstone-conglomerate unit containing metre-scale, mudstone-draped cross stratification | Tidally-influenced braided river channels | Angiosperm leaves (<i>Grevilleophyllum</i> , <i>Myrtophyllum</i> , <i>Platanus</i> : 61% of flora), cycad leaves (<i>Pecopteris</i> , <i>Pseudoclenis</i>), pinaceous conifer cones (<i>Pityostrobus</i>), and fern fronds (<i>Cladophlebis</i>) in mudstone drapes; unidentified logs in master channel bases |
| 3A | Rooted mudstone unit incised by channels containing inclined heterolithic stratification | Supra-tidal marsh dissected by sinuous tidal creeks | Cheirolepid and taxodioid conifer foliage (<i>Frenelopsis</i> , <i>Ceratostrobos</i> , <i>Cunninghamites</i> , <i>?Sequoia</i>) dominant in channel deposits, with minor angiosperms (<i>Cocculphyllum</i> and <i>?Diospyros</i>), ginkgos (<i>Nehvizdya</i>), and ferns |
| 3B | Carbonaceous mudstone unit with roots | Salt marsh peat | Cheirolepid conifer and ginkgo foliage only (<i>Frenelopsis</i> , <i>Eretmophyllum</i>) |
| 4 | Heterolithic laminite unit with flaser bedding incised by crossed-bedded channels | Tidal flat and sub-tidal channel complex | Macro-plant fossils rare; palynomorph assemblage is rich in lycosid spores with rare conifer and angiosperm pollen |
| 5A | Sandstone unit containing mud-draped planar cross-stratification and lateral accretionary channel fills | Ebb-tidal delta complex | Large (20 cm) blocks of silicified conifer wood (<i>Cupressinoxylon</i>), and silicified trunks of <i>Tempskya</i> tree-ferns (> 10 cm diameter) |
| 5B | Mudstone unit containing channels with heterolithic fills | Estuarine mouth deposits | Taxodioid conifer foliage (<i>Brachyphyllum</i> , <i>Cunninghamites</i> , <i>Sphenolepsis</i>), with rare bennettites (<i>Nilssoniopteris</i>), ferns, lycosids and angiosperm leaves |

inflorescences and flowers (*Mauldinia*) (Uličný *et al.* 1997b; Eklund & Kvaček, 1998).

The second type of angiosperm wood (less common) is characterized by solitary, diffuse porous vessel arrangement. Vessel elements occur with very high density (375 vessels per square millimetre); they are oval in cross-section, extremely small (15–20 µm diameter) and possess long scalariform perforation plates (Fig. 3f). Rays are composed of upright parenchyma (50 µm high; 15 µm diameter). Growth rings are absent. These woods are compared to charred specimens of *Iceacinoxylon* described by Herendeen (1991b) from the mid-Cretaceous Potomac Group of eastern North America, which he tentatively assigned to the Platanaceae. Although *Platanus* dominates the Pecínov leaf assemblage, specimens of *Iceacinoxylon*-type cannot presently be assigned to family level with confidence.

Several other angiosperm woods are also present in very small quantities, including one characterized by very small (20 µm diameter), oval, exclusively solitary, diffuse porous vessels, which occur with very low density (8–15 vessels per square millimetre). This and other rare angiosperm woods cannot at this stage be identified.

Assemblage 2B contains highly abundant charred angiosperm wood fragments of *Paraphyllanthoxylon*-type and cf. *Iceacinoxylon*-type, identical to that in Assemblage 2A, together with charred lauraceous inflorescences and flowers of *Mauldinia*-type (Eklund & Kvaček, 1998).

4.b. Unit 3: Supra-tidal marsh

Charcoal occurs as discrete layers in horizontally bedded mudstone units (up to 10% cover) in Unit 3A, but is rarer in Unit 3B. The 3A assemblage is dominantly composed of 0.1–3 cm, poorly sorted, slightly rounded, equidimensional blocks of pycnoxylic coniferopsid wood.

One type of coniferopsid wood consists of tracheids (30–45 µm diameter), which exhibit uniseriate, circular, dominantly contiguous, bordered pits (8–12 µm diameter) with circular apertures (4–5 µm diameter) on radial walls (Fig. 4a). Small circular bordered pits on the tangential tracheid walls are also rarely present. The cross-field is characterized by 1 or locally 2 circular cupressoid pits (10 µm diameter) with large oval apertures (7 µm diameter) per field (Fig. 4b). Rays are uniseriate and 1–28 (mode 1–10) cells high (Fig. 4c). Growth rings are present. Under the scheme of Kräusel (1949), these specimens would be assigned to the genus *Cupressinoxylon*, a wood-type that bears closest similarity to extant, taxodioid and cupressoid conifers (Greguss, 1955, 1972). Considerable variation occurs amongst the many specimens of *Cupressinoxylon* studied, suggesting that several species may be represented in this group.

Another type of coniferopsid wood consists of tracheids (30–40 µm diameter) which exhibit uniseriate rows of circular, contiguous pits (15 µm diameter) with circular apertures (8 µm diameter) on the radial walls (Fig. 4d). Locally biseriate, alternate, circular

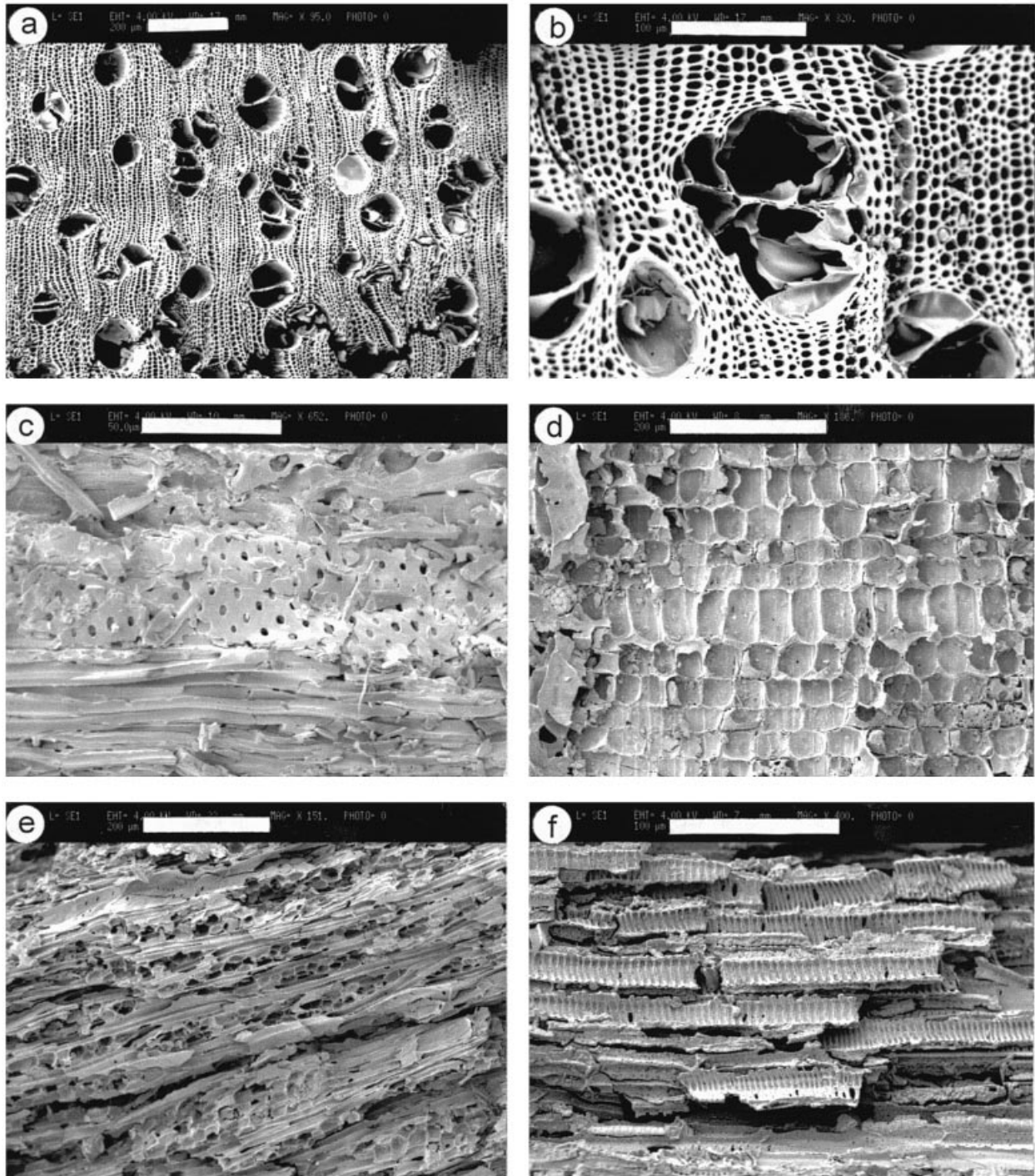


Figure 3. Angiosperm wood charcoal from Units 2 and 4 (SEMs). (a–e) *Paraphyllanthoxylon* (Lauraceae). (a) Solitary to radially multiple vessels, transverse view, scale bar (SB) = 200 µm long; (b) tyloses, transverse view, SB = 100 µm long; (c) alternate, multi-seriate intervacular pitting, radial view, SB = 50 µm long; (d) heterocellular ray, radial view, SB = 200 µm long; (e) 2–3-seriate rays, tangential view, SB = 200 µm long; (f) long scalariform perforation plates, *Icacinoxylon* (?Platanaceae), SB = 100 µm long.

bordered pitting is present. Tangential walls also have rare circular bordered pits. Cross-field pitting consists of 2–13 cupressoid pits (7.5 µm diameter) with oblique oval apertures (2–3 µm diameter) in each field (Fig. 4e). Rays are uniseriate and 1–12 (mode 1–4) cells high (Fig. 4f). Growth rings are present. Under the scheme of Kräusel (1949) this wood type would be called

Protocupressinoxylon. The Pecinov woods are almost identical to Lower Cretaceous woods associated with *Pseudofrenolopsis parceramosa* (Fontaine) Watson from the Wealden of southern England (Alvin, Fraser & Spicer, 1981; Francis, 1987), and are therefore assigned to the extinct conifer family Cheirolepidiaceae.

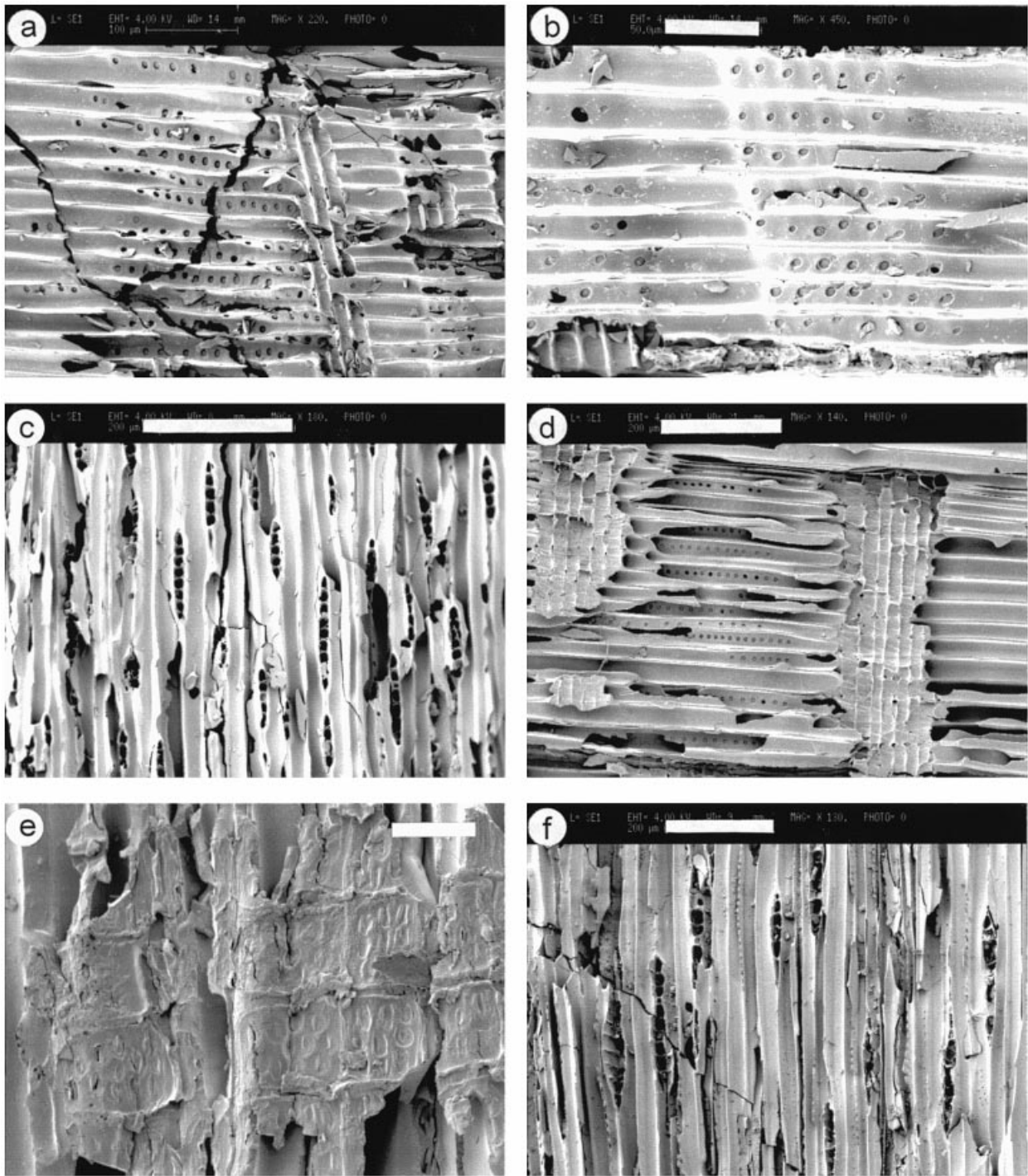


Figure 4. Conifer wood charcoal from Units 3A and 4 (SEMs). (a–c) *Cupressinoxylon* (Cupressaceae/Taxodiaceae). (a) Circular, uniseriate bordered tracheid pitting, radial view, SB = 100 μ m long; (b) 1 cupressoid pit per cross-field, radial view, SB = 50 μ m long; (c) uniseriate rays, tangential view, SB = 200 μ m long. (d–f) *Protocupressinoxylon* (Cheirolepidiaceae). (d) uniseriate bordered pitting and rays, radial view, SB = 200 μ m long; (e) 2–13 cupressoid pits per cross-field, radial view, SB = 200 μ m long; (f) uniseriate rays, tangential view, SB = 200 μ m long.

4.c. Unit 4: Inter-tidal to sub-tidal flats

Rounded equidimensional blocks of wood charcoal (1–3 cm long), and rare charred cones (up to 2 cm long) occur with great abundance in the coarse-grained heterolithic channel deposits. Charcoal is

mainly confined to the mudstone drapes covering the fore-sets of planar cross-bedding (20–100% cover), but is also present in much lower abundance (<10% cover) in the coarse-grained part of the tidal couplet (cf. Falcon-Lang, 1998).

One fragment of lauraceous angiosperm wood of

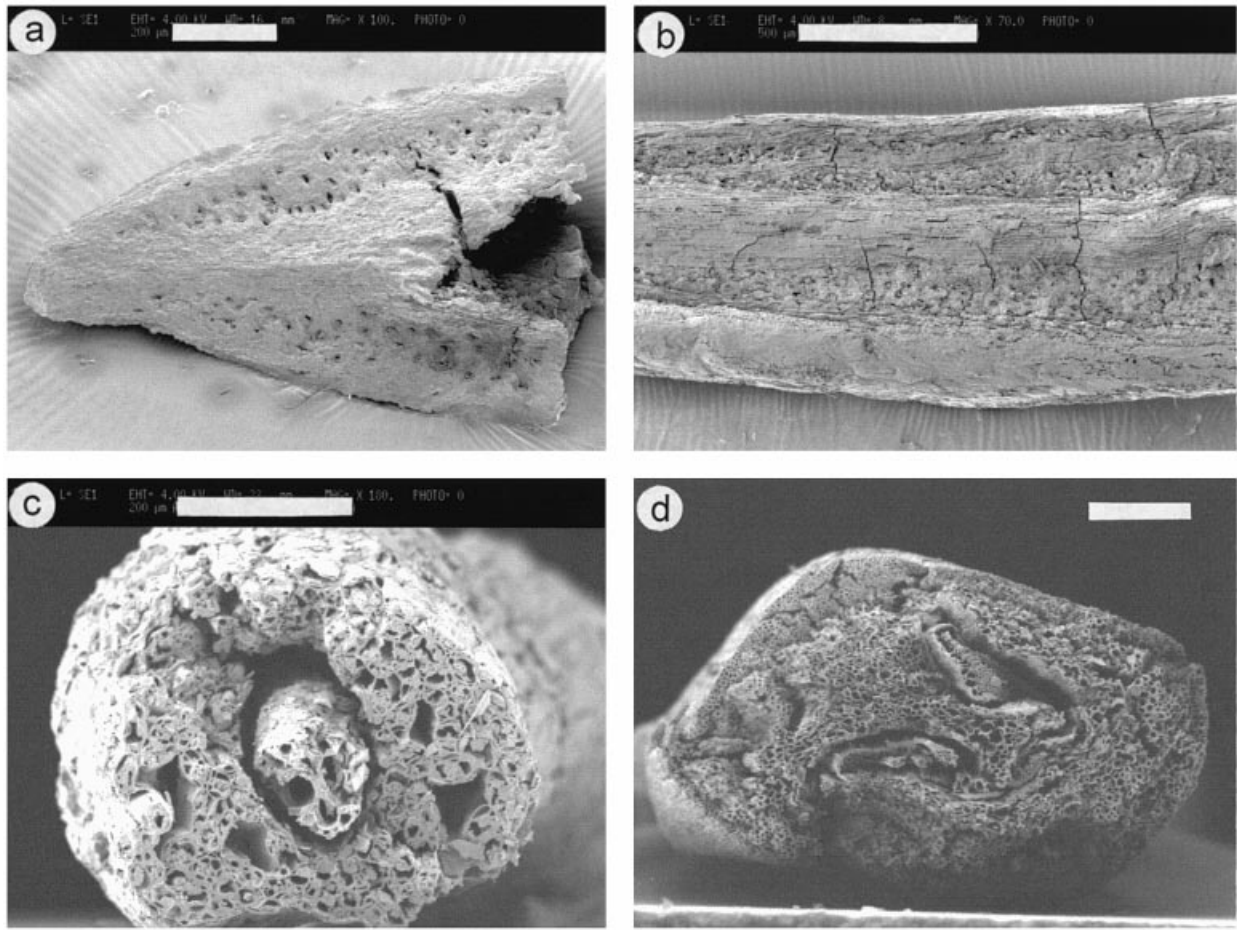


Figure 5. Charcoal from Unit 5B (SEMs). (a) *Sphenolepis*-type conifer leaf (Taxodiaceae), SB = 200 µm long; (b) *Cunninghamites*-type conifer leaf (Taxodiaceae), SB = 500 µm long; (c) unidentified lycopod stem, SB = 200 µm long; (d) unidentified fern rachis, transverse view, SB = 300 µm long.

Paraphyllanthoxylon-type is present (Fig. 3a–e), but by far the most abundant charred taxa in Unit 4 are conifer woods of *Protocupressinoxylon* (Cheirolepidiaceae) and *Cupressinoxylon* (Cupressaceae/Taxodiaceae) types. In addition to the woods, a single putative taxodiaceous cone (16 mm long), and pinaceous cone-scale of *Pityostrobus* occur.

4.d. Unit 5: Ebb-tidal delta

In Unit 5A, large (1–3 cm), slightly rounded blocks of charred wood occur in channel bases (rare), in lenses at the base of trough cross-bedded units (up to 15–20% cover), and in the fore-sets of trough and planar cross-beds (1–2% cover). Smaller (1–5 mm) non-woody charcoal fragments also occur in the fine-grained mudstone drapes of Unit 5B.

The woods of Unit 5A consist entirely of *Cupressinoxylon* (Cupressaceae/Taxodiaceae). Charcoal in the mudstone of Unit 5B is much more diverse. In addition to wood fragments of *Cupressinoxylon* there are common leaf fragments belonging to the taxodiaceous conifers *Sphenolepis* (Fig. 5a) and *Cunninghamites*

(Fig. 5b), and rare fragments of unidentified angiosperm leaves with v-shaped petioles. Also present are abundant lycopsid stems with scalariformly thickened exarch steles (0.5–1 mm diameter) (Fig. 5c), and several types of unidentified fern stems with complex steles (1–2 mm diameter) (Fig. 5d).

5. Palaeoclimatic data

Before the fire ecology of the Pecínov ecosystem can be interpreted it is important to ascertain the probable magnitude and seasonality of rainfall experienced by the Cenomanian vegetation, because as noted in the introduction this parameter strongly influences fire frequency, intensity and size (Chandler *et al.* 1983). Two palaeoclimatic indicators are used: growth rings in woods and leaf physiognomy.

5.a. Growth rings

5.a.1. Charred woods

In Unit 2, growth rings are entirely absent or subtly developed in all the diffuse-porous angiosperm woods. Where they do occur, they are of very irregular width,

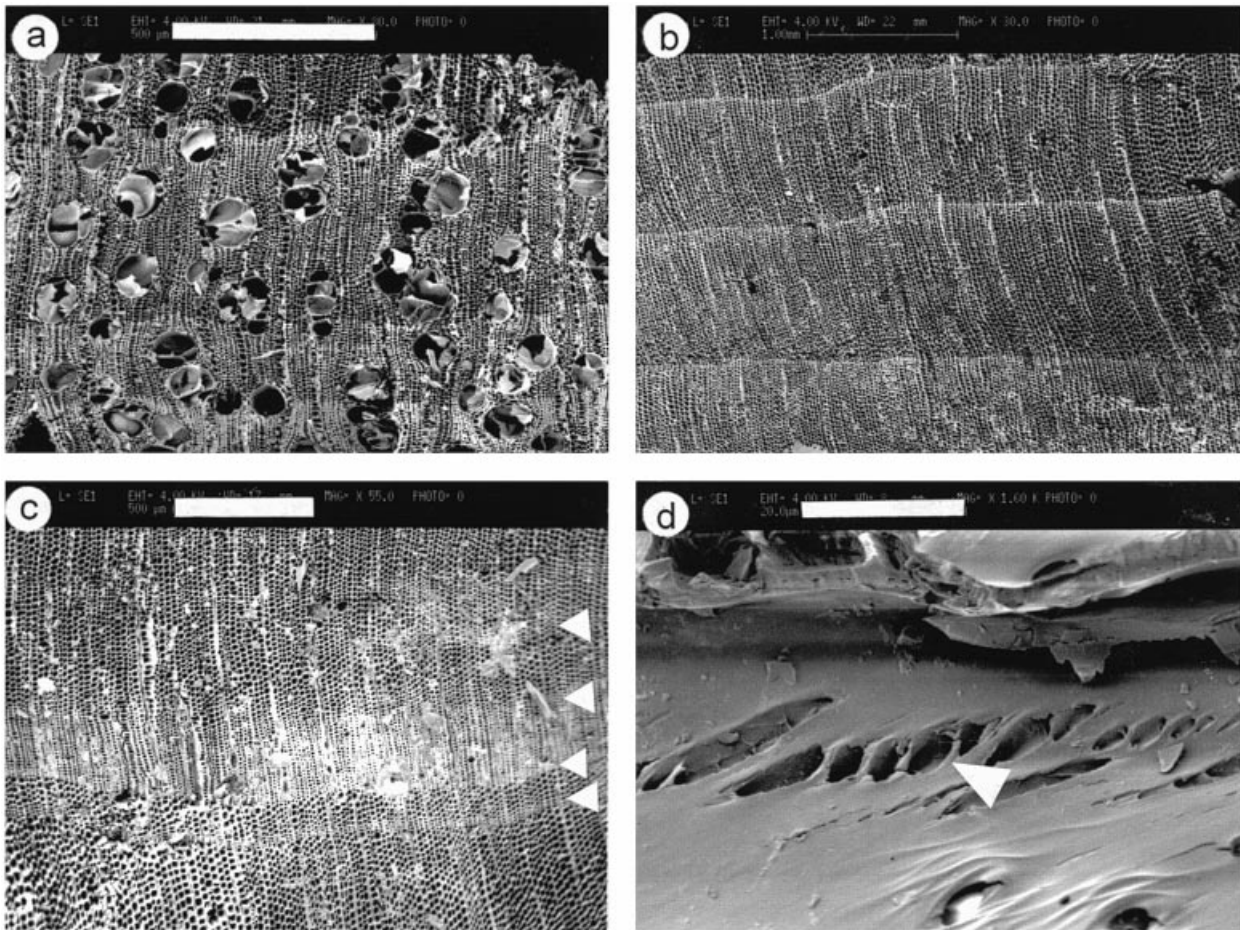


Figure 6. Climate-indicative structures in charred and uncharred woods. Growth rings in (a) charred *Paraphyllanthoxylon*, Unit 4, SB = 500 μm long; (b) charred *Protocupressinoxylon*, Unit 4, SB = 1000 μm long; (c) charred *Cupressinoxylon* showing composite growth zone composed of multiple false rings (arrowed), Unit 4, SB = 500 μm long. (d) Checking in charred *Pinuxylon* (arrowed), Unit 2, tangential view, SB = 20 μm long.

such that a 0.2 mm ring increment may be succeeded by >3 mm lacking rings (Fig. 6a). Rare *Pinuxylon* conifer woods in the same unit exhibit very marked growth rings (up to 4 mm wide) defined by 20–30 latewood cells. Earlywood cells are 30 μm diameter and latewood cells are 10 μm diameter; the earlywood:latewood boundary is abrupt. ‘Checking’, a taphonomic feature formed during the desiccation of the xylem wall (Jones, 1993), is present in several specimens (Fig. 6d).

In Units 3–5 all the conifer woods exhibit very well-defined growth rings. Several centimetre-sized blocks of *Cupressinoxylon* contain very short ring sequences (1–2 rings) composed of increments typically 2.5 mm wide. Earlywood cells are up to 45 μm diameter and latewood cells typically 10–15 μm in diameter. Unlike normal temperate growth rings, ring boundaries are only weakly asymmetrical, that is, they are defined by a gradual decline in tracheid diameter followed by only a moderately abrupt increase in tracheid diameter. These growth interruptions are typically 5–15 cells wide, and composed of multiple fluctuations in cell

size. Typically 2–4 minor false rings occur in the 0.4 mm before the main ring boundary, and usually a major false ring occurs in the 0.2 mm after the main ring boundary (Fig. 6c).

Specimens of *Protocupressinoxylon* wood exhibit relatively long (3–12) sequences of growth rings with subtle, asymmetric boundaries (Fig. 6b). Mean ring width ranges from 0.72–1.16 mm for individual specimens ($n=5$); maximum ring width is 1.45 mm and minimum ring width is 0.3 mm ($n=32$). Mean sensitivity of specimens with ring sequence lengths of >5 are 0.354 (Fritts, 1976). No false rings occur.

5.a.2. Permineralized woods

A single large block of permineralized (uncharred) wood of *Cupressinoxylon* was found in Unit 5A. This was derived from the outer part of a trunk, approximately 20 cm in diameter. It contains a ring sequence 22 increments long; mean ring width is 2.93 mm (individual increments range from 1.3–5.0 mm) and mean sensitivity is 0.274 (Fritts, 1976). Cell by cell measure-

ments taken across a representative section of the wood show that ring boundaries are pronounced with earlywood tracheids of 45–55 µm diameter succeeded by a very few latewood tracheids of 16 µm diameter. Using the method of Creber & Chaloner (1984) for calculating earlywood : latewood ratio, latewood comprises 25–29% of the ring increment. Commonly ring boundaries are composed of composite ‘interruptions’ as in charred specimens of *Cupressinoxylon*, with false rings occurring both before and after the main ring boundary.

5.a.3. Interpretation

The occurrence of growth rings in nearly all of the woods analysed indicates that the trees grew under a distinctly seasonal climate (Creber, 1977). Rings with diffuse (weakly asymmetrical) boundaries in some *Cupressinoxylon* specimens are very similar to those formed in present-day subtropical climates where temperatures do not fall sufficiently low during the winter months to cause complete cambial dormancy (Schweingruber, 1992; Woodcock & Ignas, 1994). The development of several false rings, both before and after the main ring boundary, probably indicates the occurrence of successive droughts late and early in the growing season (Francis, 1984, 1987). Seasonality in rainfall rather than temperature may have been the primary environmental cause of growth ring formation (cf. Ash, 1983). The presence of ‘checking’ in some woods confirms the occurrence of occasional extreme droughts (Jones, 1993). The more weakly defined ring boundaries in the angiosperm woods compared with the conifers probably reflect poorly understood differences in the cambial response of the two groups to climate (Tomlinson, 1980; Poole, 1999). Alternatively the complete absence or weakly defined nature of rings in the angiosperm woods may imply that these plants were growing on permanently moist riparian soils unaffected by drought. However, this interpretation is in conflict with vessel diameter evidence; all these woods have rather small vessels, a feature that may indicate that the plants were adapted to growing under water-stressed conditions (Wing & Boucher, 1998).

5.b. Leaf physiognomy

5.b.1. Qualitative and quantitative observations

The flora contains lauraceous angiosperm leaves such as *Myrtophyllum*, which are very large (5 cm by 25 cm) and others such as *Grevilleophyllum*, which possesses a drip-tip and a thick cuticle. Many of these and other climate-indicative features were quantitatively analysed using the CLAMP technique by Kvaček, Spicer & Herman (2000), a taxon-independent, multi-variant technique for ascertaining palaeoclimatic parameters (Wolfe, 1993). We merely review those findings here.

5.b.2. Interpretation

The results of the qualitative and CLAMP analysis of the flora supports interpretations based on growth rings, and indicates that climate was warm year-round with a short (2.5 month) annual drought when growth ceased. The numerical climate parameters produced by CLAMP are as follows: mean annual temperature (17.3 °C), warm month mean temperature (22.7 °C), cold month mean temperature (11.6 °C), mean annual precipitation (1468 mm), precipitation during driest three months (180 mm), and growing season length (9.5 months). These climate parameters are very similar to those predicted by computer models which calculate that warm month mean temperature was 20–24 °C and cold month mean temperature was 12–16 °C (Valdes, Sellwood & Price, 1996).

6. Discussion

A spatially complex mosaic of intergrading plant communities grew in a variety of inland and coastal environments at Pecínov during the Middle to Late Cenomanian age (Uličný *et al.* 1997b). Abundant charcoal representing every major plant group described from the compression plant fossil record, indicate that all the Pecínov plant communities were fire-prone. The mixture of both charred living tissue and partially decomposed litter material in these deposits may imply the occurrence of predominantly surface fires (Scott, 1989).

6.a. Fire-prone communities

Charcoal in the tidally-influenced braided river channels (Unit 2) was probably derived from two sources. Charred angiosperm wood, flowers and inflorescences in mud-drapes formed during low discharge (Assemblage 2B) have probably only been transported short distances; fragile charred flowers are unlikely to have survived high-energy conditions for long periods. In addition, recent experiments have shown that different plant organs rapidly become separated during transport due to their variable hydrodynamic properties (Nichols *et al.* 2000). The mixture of angiosperm organs in Assemblage 2B were therefore probably transported in suspension from local fires in riparian angiosperm gallery forests.

Pinaceous conifer wood charcoal, which is abundant in the braided channel sandstone units (Assemblage 2A), may have been transported over much longer distances, however. Centimetre-sized blocks of pinaceous wood charcoal float for up to eight days, and may be subsequently transported in the bedload for much longer periods (Nichols *et al.* 2000). For example, observations in modern tidally-influenced braided channels suggest that wood charcoal may be transported for hundreds of years, periodically being deposited in bars before being reworked during

later bar deflation (Blong & Gillespie, 1978). Most of the Pecínov charcoal in Assemblage 2A occurs in the bottomsets and fore-sets of trough cross-bedding, suggesting that it was transported as bedload and deposited during dune slip-face avalanching (cf. Vaughn & Nichols, 1995; Nichols *et al.* 2000). It is tentatively suggested that pinaceous charcoal in Assemblage 2A may record fires from deep within the hinterland, perhaps even from upland conifer forests (cf. Falcon-Lang & Scott, 2000).

Charred conifer wood (Cheirolepidiaceae and Taxodiaceae/Cupressaceae) in retrogradational coastal marsh facies (Assemblage 3A and 4) occurs in lower energy deposits where it was deposited from suspension. It was probably derived from fires in halophytic cheirolepidaceous and taxodiaceous coastal backswamp forests. The cheirolepids may have inhabited a slightly harsher environment than coeval taxodiaceous conifers as indicated by the much narrower growth rings with greater year-to-year width variability in the former. Previous studies of cheirolepid trees associated with hypersaline lagoonal facies have recorded similar narrow rings (1.13 mm) with high year-to-year variability (Francis, 1984) to those described here, whereas cheirolepids in alluvial plain settings generally have wider rings (2.94 mm) with more regular year-to-year sequences (Francis, 1987). Cheirolepid charcoal is common in Late Mesozoic rocks suggesting that this group was particularly fire-prone (Harris, 1957, 1958; Alvin, Fraser & Spicer, 1981; Francis, 1983). Several fire adaptations have been noted in fossil material such as thick fire-resistant barks implied by the abundance of charred bark remains (Harris, 1957, 1958) and the ability to shed shoots during extreme droughts when most fires would likely have occurred (Watson & Alvin, 1996). Rare angiosperm wood charcoal and pinaceous conifer cones in sub-tidal channels (Assemblage 4) may have been transported/reworked from fires further inland.

Charred conifer wood (Taxodiaceae/Cupressaceae) (Assemblage 5A), and taxodiaceous conifer and angiosperm leaves, ferns and lycopods (Assemblage 5B) in progradational coastal facies indicate fires in more mesic coastal taxodiaceous backswamp forests and in supra-tidal fern-lycopod thickets. Some Cretaceous lycopods and ferns from southern England may have exhibited fire-adaptations such as subterranean tubers/rhizomes, which facilitated post-fire resprouting (Watson & Alvin, 1996). A similar situation is envisaged for Pecínov with the supra-tidal thickets being completely destroyed by fires during the dry season, only to resprout following the first rains.

6.b. Comparison with present-day subtropical forests

Palaeoclimatic analysis drawing upon evidence from growth rings, leaf physiognomy and computer models indicates that an equable, warm (MAT 17.3 °C),

humid (rainfall 1500 mm.a⁻¹) climate punctuated by a two month long annual drought period prevailed over the Czech Republic during the Cenomanian age (Valdes, Sellwood & Price, 1996; Kvaček, Spicer & Herman, 2000); most fires probably ignited during the dry periods when vegetation was most flammable. In terms of leaf physiognomy, the Pecínov floras are similar to present-day seasonally-dry subtropical forests, although a few temperate elements also occur (Walter, 1973). This interpretation is supported by Beerling, Woodward & Valdes (1999) who modelled terrestrial primary productivity for the mid-Cretaceous Earth; they predicted the existence of a high productivity vegetation biome over Central Europe (14 t.ha⁻¹.yr⁻¹ of carbon).

Fires are common in many seasonally-dry subtropical forest communities and occur with a relatively high frequency (about once every 50–100 years). Some trees in this setting exhibit fire adaptations such as thick corky barks (Sarmiento & Monastero, 1983), deep vertical rooting systems, the ability to basally sprout from lignotubers, and reproductive cycles closely dependent on fire occurrence (Gill, 1981). The Pecínov humid subtropical forests may have been more fire-prone than their modern equivalents because of putatively higher atmospheric oxygen levels (*c.* 26%) during Cretaceous times (Berner & Canfield, 1989; Robinson, 1991). However, recent studies of Cretaceous fire ecology (Lamberson *et al.* 1996) suggest that fire-frequency in some Albian peat mires was identical to that of modern peat-forming environments, and that Cretaceous atmospheric oxygen concentrations were not much different from present-day values.

6.c. Charcoal taphonomy

Two main factors may have been responsible for the incorporation of large quantities of charcoal into the Peruc-Korycany Formation. First, charcoal production is high in humid, seasonally-dry subtropical environments (Stocks & Kauffman, 1997). Under dry savannah conditions, there is little standing vegetation biomass (mainly grasses), and fires burn efficiently producing soluble ash. Under everwet rainforest conditions, vegetation is dense but fires occur only very rarely (Sandford *et al.* 1985). However, under intermediate conditions like the seasonally-dry subtropical forests envisaged to have covered the Pecínov region during the Cenomanian age, standing biomass is high, fires occur commonly and burn inefficiently to produce large volumes of charcoal (Stocks & Kauffman, 1997).

Secondly, tidally-influenced environments act as sites for the concentration of charred plant material. Charcoal is a highly buoyant substance requiring many days to settle in turbulent waters (Nichols *et al.* 2000). In tide-dominated estuarine settings, such as the macrotidal Pecínov estuary as interpreted by

Uličný *et al.* (1997a), charcoal delivered to the coastline by rivers is likely to have become trapped within the tidal channels in the estuarine funnel by the action of the tides for sufficient time for it to become waterlogged and settle (cf. Falcon-Lang, 1998). It may be significant that charcoal is absent in the Pecínov section only in fluvial Unit 1 where there was no tidal influence. The large volumes of charcoal at Pecínov quarry are therefore probably due to a combination of high charcoal production in a humid subtropical forest biome and charcoal concentration by tidal processes.

Acknowledgements. This paper was prepared in the course of a post-doctoral fellowship to HJFL at the British Antarctic Survey (BAS). We thank Mike Tabecki (BAS) for assisting with charcoal maceration, Pete Bucktrout (BAS) for preparing photographic plates, and Ken Robinson (BAS) for helping with Scanning Electron Microscopy. The manuscript benefited from the reviews of Geoff Creber and David Batten.

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