A NEW ANATOMICALLY PRESERVED GINKGOALEAN GENUS FROM THE UPPER CRETACEOUS (CENOMANIAN) OF THE CZECH REPUBLIC

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ABSTRACT. A new genus of ginkgoalean woody branch, Pecinovicladus kvaceki gen. et sp. nov., is described from the Upper Cretaceous (mid to late Cenomanian) Peruc-Korycany Formation at Pecin Quarry, near Prague, Czech Republic. Eighteen branch specimens, anatomically preserved as charcoal, the product of wildfire, occur as allochthonous assemblages in intertidal facies and as parauthochthonous assemblages in supratidal salt marsh facies. Primary branches range from 7–13 mm in diameter, and are composed of a central, parenchymatous pith, a medial pycnoxylic xylem layer, and an outer periderm layer. Closely spaced, helically arranged leaf bases and rare secondary branch scars characterize the exterior. The branches are confidently referred to the Ginkgoales on the basis of a variety of diagnostic xylem features, most notably the presence of inflated axial parenchyma containing moulds of crystals, and by the precise anatomical correspondence of the leaf bases to those of detached, but facies-associated Nehvizdya obtusa leaves of known ginkgoalean affinity. The newly described ginkgoalean, together with cheirolepidiaceous conifers, formed fire-prone vegetation in halophytic salt marsh environments under a seasonal, subtropical climate.

KEY WORDS: Cretaceous, Cenomanian, Ginkgoales, charcoal, fire, wood.

THE Upper Cretaceous (Cenomanian) floras of Peruc-Korycany Formation, Bohemian Massif, Czech Republic are the richest, most abundant and well-preserved compression floras of this age in North America and Europe (Kvaček and Dilcher 2000). Systematic study of the fossil plants began in the late nineteenth and early twentieth century with the seminal works of Velenovsky (1882, 1883, 1884, 1885, 1888, 1889) and Bayer (1900, 1914, 1921), and culminated with the publication in four volumes of the Cretaceous Flora of Bohemia (Velenovsky and Viníklář 1926, 1927, 1929, 1931). Following a long dearth in serious study, Kvaček and co-workers have recently described many important new collections (Kvaček 1995, 1997, 1999, 2000, 2002; Kvaček and Knobloch 1997; Knobloch and Kvaček 1997; Eklund and Kvaček 1998; Kvaček and Dilcher 2000; Kvaček and Pacltová 2001).

In total, at least 136 genera containing 291 species are now recognized (Kvaček, unpublished data). Angiosperms are the most diverse element of the flora comprising 57 per cent of the species richness, including members of the families Annonaceae, Chloranthaceae, Lauraceae, and Platanaceae (Kvaček 2002). Conifers comprise a further 21 per cent of the species richness including members of the families Araucariaceae, Cheirolepidiaceae, Cupressaceae, Pinaceae, and Taxodiaceae (Kvaček and Dilcher 2000). Ferns, representing the families Matoniaceae and Schizeaceae, amongst others, comprise 18 per cent of the species richness (Pátova and Kvaček 2002). The remainder of the flora consists of lycopsids, pteridosperms, cycads, bennettites and ginkgos collectively comprising only 4 per cent of the species richness (Kvaček 1995, 1999; Knobloch and Kvaček 1997).

In September 2000 the important discovery was made that charcoal, the product of wildfires, is extremely abundant in the Peruc-Korycany Formation. A preliminary analysis of this charred material indicates that it comprises woods, stems, leaves, and reproductive structures and includes a very large number of anatomically preserved taxa (Falcon-Lang et al. 2001a), many of which are new to science. Once more fully studied, these charred remains, which represent an entirely new source of palaeobotanical data for the Peruc-Korycany Formation, will significantly augment our knowledge of the terrestrial biodiversity and ecology of Central Europe during Cenomanian times.
This paper represents the first detailed systematic study of the charred material. It describes eighteen woody shoots, which are assigned to a new genus of ginkgoalean branch, *Pecinovicladus kvaceki* gen. et sp. nov. Although gingkoaleans were a diverse and globally widespread group during Cretaceous times (Tralau 1968), prior to this study, they were represented in the Peruc-Korycany Formation by a single species of leaf, *Nehvizdya obtusa* Hlustík (Hlustík 1986; Kvaček 1999; Gomez et al. 2000).

**GEOLOGICAL SETTING**

The Upper Cretaceous Peruc-Korycany Formation (Čech et al. 1980) is a 25-m-thick unit, which crops out widely across the northern part of the Czech Republic (Kvaček and Dilcher 2000). It represents the earliest strata to be deposited in a system of strike-slip basins (termed the Bohemian Basin), which formed in Central Europe in Cenomanian times in response to compression transmitted from the Alpine-Carpathian collision zone to the south (Uličný and Špičáková 1996). During the early stages of basin evolution, the Czech Republic region was characterized by a series of broad palaeovalleys, whose strikes followed lineaments in the Variscan basement (Uličný and Špičáková 1996; Uličný 2001). Following a stepwise sea-level rise through mid to late Cenomanian times, the palaeovalleys were infilled with a fluvial–estuarine succession, the Peruc-Korycany Formation (Uličný and Špičáková 1996).

At Pecinov Quarry, near Prague (Text-fig. 1; latitude 50°07′48″N, longitude 13°54′54″E), a complete section through the Peruc-Korycany Formation is exposed, where it overlies Upper Carboniferous fluvial deposits with a pronounced unconformity. At this locality, five depositional units occur, each interpreted as a parasequence on the basis of the identification of a marine flooding surface or its correlative equivalent at their top (Uličný and Špičáková 1996). Units 1–4, which represent a transition from braided alluvial to estuarine facies, are collectively interpreted as a transgressive systems tract, while Unit 5, which represents a progradational coastal facies, is interpreted as a highstand systems tract (Text-fig. 2; Uličný and Špičáková 1996).

**FACIES CONTEXT OF STUDY MATERIAL**

The ginkgoalean branches described in this paper occur in Unit 3 of Pecinov Quarry (Uličný et al. 1997). This 1·1–3·5-m-thick unit consists of a lower layer of dark grey to black, pyritic mudstone containing
marine acritarchs and fine-grained channel sandstone bodies exhibiting inclined heterolithic stratification (Unit 3A). Associated compression floral remains possess a low species richness (n = 11) consisting of ginkgos, conifers, angiosperms and ferns (Uličný et al. 1997; Table 1). Falcon-Lang et al. (2001a) additionally reported the occurrence of conifer wood charcoal from these beds. An upper layer consists of a black, carbonaceous, laminated mudstone unit, which exhibits a strongly rooted base (Unit 3B). Associated compression floral remains possess very low species richness (n = 5) consisting of ginkgos, conifers and ferns (Table 1).

The beds of Unit 3A are interpreted as the deposits of upper intertidal salt marshes cut by sinuous tidal creeks fringing an estuarine mouth setting (Uličný and Špičáková 1996). Plant material is clearly allochthonous in this depositional setting, and interpreted as being variously derived from taxodiaceous conifer-dominated backswamps and supratidal halophytic communities dominated by ginkgos and cheirolepidiaceous conifers (Uličný et al. 1997). The upper rooted beds of Unit 3B represent the deposits of supratidal salt marsh peats (Uličný and Špičáková 1996). Given the low-energy environment envisaged,
Fossil plant taxa in Unit 3 of Pecínov Quarry (compressions only) | Upper intertidal salt marsh flat | Supratidal salt marsh peat
---|---|---
Ferns | | |
*Onychiopsis* sp. | Rare | Absent
*Gleichenites* sp. | Absent | Rare
Ginkgoaleans | | |
*Nehvizyda obtusa* Hlustík (Gomez) | Common | Abundant
Conifers | | |
*Ceratostrobus sequoiaphyllus* Velenovský | Abundant | Rare
*Dammarites albens* Presl *in Sternberg* | Common | Rare
*Frenelopsis alata* (K. Fiestmantel) Knobloch | Abundant | Abundant
*Sequoia heterophylla* Velenovský | Common | Absent
*Sequoia crispa* (Velenovský) Kvaček | Common | Absent
Angiosperms | | |
*Cocculophyllum cinnamomeum* Velenovský | Common | Absent
*Diospyros cretacea* Velenovský and Viníklář | Common | Absent
*Magnolia amplifolia* Heer | Common | Absent
*Pseudoasterophyllites cretaceus* (K. Fiestmantel) Velenovský | Common | Absent
Species richness | 11 | 5
Interpretation of plant taphonomy | allochthonous | parautochthonous

plant material is probably parautochthonous and is interpreted as representing supratidal halophytic communities co-dominated by ginkgos and cheirolepidiaceous conifers (Uličný *et al.* 1997).

**MATERIAL AND METHODS**

The ginkgoalean branches were mostly collected *ex situ* from talus deposits at the base of Unit 3, but a few specimens were found within the sediments themselves in both Units 3A and 3B. In total 18 specimens were collected. Specimens were placed in 40 per cent HCl for three days to remove carbonates. Following washing in distilled water, they were transferred into polypropylene containers with screw top lids and treated with 48 per cent HF for two weeks to remove adhering silicate grains. Specimens were then washed in distilled water for one week and allowed to dry. Analysis of the gross morphology of the branches was undertaken with a Nikon stereo-microscope. Four of the most complete specimens were then attached to 2-cm-diameter aluminum stubs with electro-conducting resin, gold coated with a splutter coater, and examined with a Hitachi S-3200 Scanning Electron Microscope (SEM) housed at the National Research Council, Halifax, Canada. Following external examination, specimens were then split in half with a scalpel blade, and their internal anatomy was again examined with the SEM.

In the following descriptive section, the term ‘view’ (e.g. radial longitudinal view, RLV; tangential longitudinal view, TLV; transverse view, TV) is used throughout rather than ‘section’ because only surface analysis can be undertaken with the SEM. All the specimens have been charred. Woody material has been shown to contract by approximately one third during charring (Scott 1989), and this should be taken into account when interpreting all anatomical measurements given in the text. In the descriptions I have generally followed the terminology of Esau (1977).
Order Ginkgoales Gorozhankin, 1904
Family Ginkgoaceae Engler, in Engler and Prantl 1887
Genus Pecinovicladus gen. nov.

Derivation of name. Meaning a branch from Pecínov Quarry.

Diagnosis. Shoots constructed of an inner parenchymatous pith, a medial pycnoxylic xylem cylinder containing inflated axial parenchyma, crystalline moulds, and mucilage canals, and an outer periderm layer. Exterior of shoots bear prominent, helically arranged leaf scars, and/or randomly arranged secondary branches.

Remarks. Although complete anatomically preserved woody shoots of this type are not previously known, isolated fragments of Ginkgoxylon gruetii Pons and Vozenin-Serra wood have been described from Cenomanian deposits in France (Pons and Vozenin-Serra 1992), which are nearly identical to the secondary xylem of Pecinovicladus. However, this wood species cannot be absorbed into the new Pecinovicladus genus because gymnosperm wood has a highly conservative anatomy (Falcon-Lang and Cantrill 2000), and it is likely that Ginkgoxylon gruetii may be a characteristic wood of, not just Pecinovicladus, but also related taxa.

Pecinovicladus kvaceki sp. nov.

Text-figures 3–10

Derivation of name. In honour of Jiri Kvaček (National Museum, Prague), who has made an enormous recent contribution to our understanding of Cenomanian plants and ecosystems in Central Europe.

Holotype. F02912 collected from Unit 3, Pecínov Quarry, near Prague, Czech Republic (latitude 50°07′48″N, longitude 13°54′54″E), and stored in the Palaeontology Collection of the National Museum of Prague, Czech Republic.

Material. Seventeen additional specimens collected from the same locality and unit with National Museum of Prague accession numbers F02909–F02926.

Diagnosis. Slender shoots (c. 7–13 mm diameter); pith, parenchymatous and broad (c. 1.6–2.2 mm diameter); xylem radius, narrow (c. 0.5–1.8 mm radius); cambial radius, very narrow (c. 55 μm wide), and periderm radius, narrow (c. 1.6–2.5 mm wide). Metaxylem cells exhibit interspersed scalariform
thickening and bordered pitting. Secondary xylem exhibits irregular tracheid arrangement with intermixed wide and narrow files, both opposite and alternate tracheid pitting, and low rays (1–7 cells high). Periderm exhibits sieve cells. Leaf bases broad (c. 2·7–3·5 mm wide, c. 1·45 mm high), and contain at least six vascular strands.

**Detailed anatomical description**

**General**. Specimens consist of primary branches ranging from 7–13 mm in diameter (fragments up to 24 mm long) and bearing numerous pronounced leaf scars, or a mixture of leaf scars and small secondary branch scars (Text-fig. 3).
They possess a siphonostelic structure, being composed of a central pith (1.6–2.2 mm diameter), surrounded by a medial xylem layer (0.5–1.8 mm radius) and an outer periderm layer (1.8–2.5 mm radius; Text-fig. 4A–B). Generally branches of greater diameter possess a relatively narrow pith and periderm layer and a relatively wider xylem layer.

**Pith.** The 1.6–2.2-mm-diameter pith is composed of vertically orientated, elongate parenchyma cells, up to 280 μm high, and 50–130 μm in diameter (Text-fig. 4C). Some cells may be contorted along their length. Parenchyma cells possess thick cell walls (5–8 μm thick), and a few examples exhibit irregular pitting on longitudinal walls, whilst others are resin-filled (Text-fig. 5A–B).

**Protoxylem and metaxylem.** Distinct protoxylem poles were not observed, but protoxylem arrangement is obscured by numerous leaf gaps and associated leaf traces (see below for more details). Metaxylem tracheids (4–10 μm diameter) exhibit pronounced scalariform wall thickening (Text-fig. 5C). Locally scalariform-thickened tracheids are very short (150 μm long), and occur as ‘outgrowths’ from larger adjacent tracheid walls (Text-fig. 5D). Scalariform bars are typically spaced 4–8 μm apart. Isolated, circular bordered pits are commonly interspersed with the scalariform bars. Where rays occur they are exclusively one cell high, one cell wide, and 1–2 cells long, and composed of cells 15–30 μm wide, 20–40 μm high, and 45–55 μm long. They exhibit 1–2 cupressoid cross-field pits (6–7 μm diameter) per field (Text-fig. 5E). Isolated inflated axial parenchyma cells (20–30 μm diameter, 18–20 μm high) also locally occur (see below for full description of these; Text-fig. 5F). An additional feature of the primary xylem is the presence of a few, large, scattered mucilage ducts (70–110 μm diameter, >1.1 mm high) which superficially resemble inflated axial parenchyma in transverse view, but are distinguished by their slightly greater diameter, and when viewed longitudinally, by their lack of horizontal partitions and much greater height. Mucilage ducts are surrounded by axial parenchyma, as clearly seen in longitudinal view (Text-fig. 7A–B).

**Secondary xylem.** The secondary xylem is pycnoxylic. It is composed of thin-walled (2 μm thick) tracheids of highly variable diameter, ranging from 7–26 μm in radial diameter, and 4–22 μm in tangential diameter. In transverse view, tracheid arrangement is irregular with some files composed of very narrow (7 μm) tracheids interspersed with others composed of wide (28 μm) tracheids. Secondary xylem tracheids locally possess scalariform-thickening interspersed with isolated bordered pits, but much less commonly than seen in the metaxylem. The dominant architectural feature of these more mature tracheids is uniseriate or rarely biseriate, circular, bordering pitting (Text-fig. 6A–B). Pit borders are 7–12 μm in diameter, whilst apertures are 3–8 μm in diameter. Where biseriate, pits may have an opposite, alternate or mixed arrangement.

Rays are common, being spaced 5–11 tracheids apart in transverse view. They may be uniseriate or rarely biseriate, 100–550 μm long, and are composed of cells 40–110 μm long, 7–25 μm wide, 21–35 μm high, with 0.8-μm-thick walls. Rays are very short, ranging from 1–7 cells high, but most commonly 1–3 cells high (Text-fig. 6C–D). Transverse walls may locally exhibit rare, circular, irregular, simple pits. Cross-field pitting on the radial walls is highly variable, consisting of 1–6 pits per field (Text-fig. 6E). Cross-field pits are oval (5–16 μm in diameter) with oblique to circular, taxodioid to cupressoid apertures (4–12 μm diameter).

Axial parenchyma exhibiting 1-μm-thick walls and commonly arranged in vertical files is locally present. It consists of cells 10–18 μm in diameter, and 80–120 μm high. An unusual feature of the secondary xylem, as already noted in the metaxylem, is the common occurrence of very large (inflated) axial parenchyma cells (Text-figs 6F, 7C). Although when viewed transversely they may superficially resemble resin ducts of conifers or vessels of angiosperms, they may be clearly distinguished from these phenomena by the follow features. Viewed longitudinally, inflated axial parenchyma may consist of isolated cells, or be arranged in vertical files of 2–5 (rarely up to nine; Text-fig. 7D–F). Individual inflated cells range in diameter from 25–45 μm, have heights of 25–60 μm, typical wall thicknesses of 1–2 μm, and occur with a density of 18–24 per mm² in transverse view. Usually their walls are typically smooth, but locally they may exhibit 1–2 oval pits (5 μm diameter). Some may possess a rhombic geometry and clearly once contained crystals. When viewed transversely, they may be surrounded by up to 5–7 smaller (7–9 μm diameter) parenchyma cells.

Although no growth rings were observed in any specimens, the radial tracheid diameter of one specimen systematically decreases towards the outer margin of the secondary xylem cylinder (from 23 to 5 μm) reminiscent of an earlywood to latewood transition (Text-fig. 6F). The absence of growth rings, despite their common occurrence in associated secondary wood fragments from Unit 3 (Falcon-Lang et al. 2001a), implies that all branch specimens are less than one year old, including the largest specimens bearing small secondary branches.

Cambium. The cambial zone is 55 μm wide, and consists of vertically orientated, elongate cells (18–21 μm diameter, 150–170 μm high; Text-fig. 8A–B, D). A few ray initials are locally observed. They are 1–4 cells high, composed of parenchyma cells 3–4 μm wide, 20–30 μm long, and 8–9 μm high (Text-fig. 8C–E). More prominent, however, are files
(1–5 cells high) of inflated axial parenchyma, composed of cells 20–40 μm wide, 30–40 μm high. The moulds of rhombic crystals (6–21 μm long) are a ubiquitous feature of this zone, and the shape of some inflated axial parenchyma cells indicates that these too originally contained crystals (Text-fig. 8c).

**Periderm.** The periderm layer may be up to 2–5 mm wide. The inner periderm consists of thin walled (2.5–3.1 μm thick) parenchyma cells 35–45 μm in diameter and 30–350 μm long, which may be vertically orientated, or if nearly
TEXT-FIG. 6. Secondary xylem of *Pecinovicladus kvaceki* gen. et sp. nov.; all SEM images. A, tracheids showing spaced, uniseriate, circular bordering pitting, F02909, RLV; ×300. B, tracheids showing biseriate, opposite to alternate bordered pitting, F02910, RLV; ×700. C, short rays (1–3 cells high), F02909, RLV; ×140. D, short rays, one cell high, F02910, TLV; ×300. E, 1–6 irregular cross-field pitting, F02909, RLV; ×500. F, outer part of xylem cylinder showing mucilage canals, inflated axial parenchyma and incipient ring boundary, F02909, TV; ×50.
TEXT FIG. 7. Mucilage canals and inflated axial parenchyma in *Pecinovicladus kvaceki* gen. et sp. nov.; all SEM images.

A, mucilage canals in inner part of xylem, F02909, TV; ×130.
B, mucilage canal surrounded by normal axial parenchyma, F02909, RLV; ×200.
C, mucilage canals and inflated axial parenchyma, F02909, TV; ×170.
D, inflated axial parenchyma in xylem, F02911, RLV; ×580.
E, inflated axial parenchyma (right) in cambium, F02909, TLV; ×195.
F, inflated axial parenchyma surrounded by normal axial parenchyma in xylem, F02909, RLV; ×850.
isodiametric, randomly orientated (Text-fig. 9 A, D). Sieve cells (up to 100 μm diameter, 400 μm long) are common within this parenchymatous matrix exhibiting sieve areas (mostly on the radial walls) with single oval pores (12 by 8 μm) or larger, oval, pore groups (25–30 μm by 10 μm; Text-fig. 9E–F). Several elongate cells with thick cell walls are resin-filled (45 μm diameter, up to 270 μm long) and are interpreted as fibres (Text-fig. 9C). Rays were rarely observed, but when locally present are very short (1–2 cells high). The structure of the outer periderm is more disordered. It consists of longitudinally fissured cells, some very large (40–250 μm diameter) with very thick walls (10–20 μm thick; Text-fig. 9A–B).

Leaf traces and leaf bases. Viewed transversely, numerous parenchymatous leaf gaps and associated leaf traces are clearly visible in the primary branches (Text-fig. 4A–A). At the point where the leaf trace departs from the secondary xylem into the periderm, it is typically 1.0–1.5 mm in diameter (Text-fig. 10A). At this location it consists of a vascular bundle composed of an oval xylem strand on the adaxial side and a crescent-shaped phloem strand on the abaxial side.

At a point 2 mm outside the periderm, the leaf bases are well preserved, and helically arranged (Text-fig. 3). Phyllotaxy could not be precisely determined from the very short branch portions preserved intact (up to 24 mm long),
but may approximate to a 5/13 arrangement. Leaf bases are oval in cross-section (2.7–3.5 mm wide, 1.45 mm high), and consist of a central, vascular bundle of adaxial xylem and abaxial phloem surrounded by mesophyll and an epidermal layer (Text-fig. 10A). The vascular bundle exhibits a pronounced boudinaging across its width, giving rise to six distinct boudins (each 350–500 μm wide), which presumably separate into individual veins further into the leaf. The xylem strand is 2.6–3.4 mm wide, 400 μm high, and consists of both metaxylem and secondary xylem. Numerous prominent mucilage canals (40–50 μm diameter) occur close to the contact with the phloem. The phloem strand is 2.5–3.3 mm wide, 350 μm high, and also exhibits prominent mucilage canals (80–150 μm diameter).
Branch traces. The largest diameter primary branch specimens typically possess fewer leaf scars, and in their place secondary branch scars (1.8–2.1 mm diameter) occur (Text-figs 4A, 10C). These consist of a 250–800-μm-diameter pith surrounded by a secondary xylem cylinder (0.7–0.8 mm radius; Text-fig. 10E). Leaf gaps and associated leaf traces (up to 450 μm diameter) occur in these secondary branches close to the point of departure from the primary branch, and indicate that the secondary branches bore leaves themselves (Text-fig. 10D).

Affinity

Several lines of evidence, mostly related to distinctive features in the xylem, strongly suggest that these charred branches may be confidently assigned to the gymnosperm order Ginkgoales. First, the xylem of
Pecinov cladus kvaceki contains unusual inflated axial parenchyma cells, which demonstrably once contained crystalline druses. Identical features are seen in modern Ginkgo wood, where the abnormal inflation of axial parenchyma is caused by the internal growth of calcium oxalate crystals (Gunkel and Wetmore 1946a, b; Greguss, 1955; Scott et al. 1962; Li and Li 1991). Amongst extant coniferopsids and angiosperms, this feature is only found in Ginkgo (Srivastava 1963). In studies of Cretaceous–Tertiary fossil woods, the presence of inflated parenchyma has in fact been considered an important diagnostic indicator of ginkgoalean affinity (Scott et al. 1962; Pons and Vozenin-Serra 1992).

Secondly, the tracheids in the secondary xylem of Pecinov cladus exhibit a very irregular arrangement when viewed transversely, consisting of interspersed wide and narrow files. This arrangement is not seen in conifers, and amongst extant gymnosperms is probably peculiar to Ginkgo (Srivastava 1963; Timell 1986; Li and Li 1991). Scott et al. (1962) considered this kind of tracheid arrangement as being an important feature for assigning their fossil wood to Ginkgoales. Examination of wood specimens stored at the Royal Botanic Gardens, Kew confirms the close similarity between the tracheid arrangement of Pecinov cladus and extant Ginkgo, and the relative dissimilarity of Pecinov cladus and extant conifers. Furthermore, taking into account the contraction that occurs during charring the typical diameters of Pecinov cladus tracheids are very similar to those of extant Ginkgo (Mastogiuseppe et al. 1970).

Thirdly, the tracheid wall thickening and ornamentation of Pecinov cladus is characteristically Ginkgo-like. For example, the occurrence of helical thickening with interspersed, scattered bordered pitting in the metaxylem is a feature that is very commonly observed in Pecinov cladus. This feature is never found in conifers, but is peculiar to the Gnetales, Ginkgoales, and angiosperms according to Bierhorst (1960) and Carlquist (1996). In addition, the mixed, alternate-opposite arrangement of bordered pits on radial tracheid walls seen in Pecinov cladus is also typical of Ginkgo (Scott et al. 1962; Srivastava 1963), although it is also seen the extinct Mesozoic conifer family Cheirolepidaeae (Alvin et al. 1981; Francis 1983; Falcon-Lang et al. 2001a).

Fourthly, the occurrence of very low rays [typically 1–3 (up to 7) cells high] is very characteristic of modern and ancient ginkgoaleans (Mastogiuseppe et al. 1970). However, this feature can only be used as supporting evidence for a ginkgoalean affinity because the woods of some extant juvenile conifers (Jane 1962), and several taxa of mature fossil gymnosperms (e.g. Endoxyylon, Lacey 1953), similarly possess low rays.

Fifthly, Pecinov cladus possesses 1–6 oval cross-field pits with oblique aperture. The nature of cross-field pitting is perhaps one of the most important criteria for distinguishing modern and ancient conifer families (Jane 1962). Whilst its importance as a diagnostic feature of Ginkgo has not been proven, it should be noted that extant Ginkgo exhibits very similar cross-field pitting to Pecinov cladus, typically 1–9 oval/oblique cross-field pits per field (Scott et al. 1962; Srivastava 1963).

All these anatomical considerations are also supported by a sixth line of evidence based on facies assemblage data. The leaves of ginkgoaleans, namely Nehvizdy obtusa, are one of the most abundant elements of the flora in Unit 3B (parauthochthonous assemblage), with only the cheirolepidaeae conifer Frenelopsis alata (Fiestmantel) Knobloch being more numerous. N. obtusa is confidently assigned to the Ginkgoales on the basis of its Ginkgo-like ovules, megasporangiophores, and leaf epidermal features (Hlustik 1986; Kvaček 1999; Gomez et al. 2000). Facies association of Pecinov cladus with a low-diversity, parauthochthonous assemblage rich in N. obtusa supports a ginkgoalean affinity. It is significant that the ginkgoalean wood described by Pons and Vozenin-Serra (1992) from the French Cenomanian, which is of identical age to the Czech ginkgoalean branch specimens, occurs in facies association with Nehvizdy andegavense (Pons) Gomez.

Bearing this facies association of Pecinov cladus and N. obtusa in mind, a seventh line of evidence for a ginkgoalean affinity is the very close correspondence that exists between the size and architecture of the charred Pecinov cladus leaf bases and those of N. obtusa. The type specimen of Nehvizdy obtusa has a leaf base 4·1 mm wide, and cuticular studies show that this region possesses six fused veins (c. 400–500 µm wide), which separate further into the leaf (Kvaček 1999). An identical architecture is seen in the Pecinov cladus leaf bases, whose slightly smaller dimensions (2.7–3.5 mm wide leaf bases) can easily be accounted for by the 30 per cent contraction that occurs during charring (Scott 1989). Although not found
in organic connection with one another, it is highly probable that *Pecínovycladus kvaceki* bore *Nehvizya obtusa* leaves.

### DISCUSSION OF PALAEOECOLOGY

Abundant *Pecínovycladus kvaceki* and *Nehvizya obtusa* ginkgoalean remains together with abundant cheirolepidiaceous conifers, rare angiosperms and rare ferns occur in a parauthochthonous assemblage within the salt marsh peat deposits of Unit 3B (Table 1). The very low diversity of this community, and the dominance by only two taxa (ginkgoaleans and cheirolepids), strongly suggest ecologically stressful conditions (Hughes, 1986). The presence of marine acritarchs and the position of Unit 3B in a transgressive sequence stratigraphic setting, confirms the close proximity of marine waters and implies that saline intrusion may have been the main source of ecological stress (Ulicňy et al. 1997). This interpretation is strongly supported by the fact that most plants from Unit 3B have high $^{13}$C/$^{12}$C ratios (Tu et al. 2002) and exhibit leaves with a succulent/xeromorphic character; both observations suggest growth under water-stressed conditions, typical of salt marshes. An exception to this trend is *Nehvizya obtusa*, which lacks obvious xeromorphic characters, and exhibits relatively low $^{13}$C/$^{12}$C ratios. It may be that this ginkgoalean inhabited localized freshwater niches in an otherwise saline environment, perhaps dominantly colonizing the margins of river-dominated creeks, which are known to have dissected the salt marsh.

Further insight in the ecology of the salt marsh ginkgo may be gained from an analysis of growth rings in associated allochthonous woods. Growth ring studies of conifer woods in Unit 3A by Falcon-Lang et al. (2001a) indicates these coastal ecosystems were subjected to a seasonally dry climate. This is supported by the results of CLAMP analysis of angiosperm leaves in the Peruc-Korycany Formation, which imply a humid, subtropical to warm temperate climate with a dry season three months long (Kvacˇek et al. 2000). The abundance of charred plant material in Unit 3 further suggests these halophytic ginkgo-cheirolepid communities were highly fire-prone, with most fires probably igniting during the dry season (Falcon-Lang et al. 2001a).

Although it is evident that the Ginkgoales had a very wide ecological amplitude during Cretaceous times, occurring from pole to pole and inhabiting a range of humid temperate rainforest to subtropical woodland biomes (Spicer and Herman 2001; Falcon-Lang et al. 2001a, b), ginkgoaleans with a very similar ecology to those of Pecínov Quarry are known from several coeval deposits elsewhere in Europe. For example, accumulations of *Ginkgoxylon* wood and *Nehvizya andegavense* leaves (Ginkgoales) and *Frenelopsis* leaves (Cheirolepidiaceae) occur together in Cenomanian deposits near Anjou, northern France (Pons and Vozenin-Serra 1992). These units are interpreted as saline lagoon/barrier island deposits, and $^{13}$C/$^{12}$C analysis of plant material suggests that the cheirolepids grew in saline niches, whilst the ginkgoaleans thrived under saline to freshwater conditions (Tu et al. 1999). In a Spanish example, an association dominated by *Frenelopsis* and *Nehvizya penalveri* Gomez has been reported in Albian units interpreted as the deposits of a lower delta plain setting (Gomez et al. 2000). The presence of marine palynomorphs associated with plant remains again point to a halophytic coastal ecology for these ginkgo-cheirolepid communities.

Continued future studies of the charred material from salt marsh peat units in the Peruc-Korycany Formation, together with ongoing parallel studies of sedimentology, sequence stratigraphy, palynology, growth rings, and carbon isotope ratios, will doubtless further elucidate the diversity and ecology of these interesting halophytic communities.

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