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Martina Dolezych[1]: Taxodiaceous woods in Lusatia (Central Europe), including curiosities in their nomenclature and taxonomy, with a focus on *Taxodioxylon*

Abstract Taxodiaceous woods are among the most investigated in Lusatia (Central Europe) as well as in the European Cenozoic. Although these conifer genera have been known for a long time, the use of the generic names is confusing, especially in regard to their relationships to extant taxa. In Lusatia there occur some *Taxodioxylon* species with affinities to *Sequoia*, *Cryptomeria,* and *Taxodium, Glyptostroboxylon* species with affinities to *Glyptostrobus* and *Cunninghamia,* and also—paradoxically—one *Cupressinoxylon* wood with affinity to *Taiwania*. Extinct taxodiaceous woods also occur: *Quasisequoioxylon* and *Juniperoxylon pachyderma* ex parte. One *Juniperoxylon* was found with *Cupressospermum saxonicum*. The establishment of *Quasisequoioxylon*, a morphogenus, which shares xylotomic characters both with Taxodiaceae and Cupressaceae *s.s.*, is considered to represent the wood of the extinct genus *Quasisequoia*. Rediscovery of the original preparation of *Glyptostrobus tener* Kraus, the basionym for *Glyptostroboxylon tenerum* (Kraus) Conwentz, enabled a detailed re-assessment of this taxon and an emended diagnosis for the genus *Glyptostroboxylon*. The most common morphogenus is *Taxodioxylon*, because the wood species it includes have affinities to many extant genera: *Taxodium*, *Cryptomeria*, *Sequoia*, *Metasequoia,* and *Sequoiadendron*. *Taxodioxylon* was erected by Hartig in 1848 with the type *Taxodioxylon goeppertii*. Gothan emended this taxon in 1905. Greguss and Blokhina have used the names *Sequoioxylon* as well as *Metasequoioxylon*, but these taxa fit under the broadly defined morphogenus *Taxodioxylon*. It is proposed that a revision of *Taxodioxylon* should be made. One *Cupressinoxylon* wood is most similar to *Taiwania*. The xylotomical investigations supplemented by information from other organs, especially dispersed cuticles—using the whole-plant concept—provide data for reconstructing the woody plant communities that contributed to Miocene peat formation in Lusatia. The xylotomical records suggest the transition of a relatively eutrophic stage with *Glyptostrobus*, via a mesotrophic stage with *Sequoia*, *Cunninghamia,* and *Taiwania* towards an oligotrophic habitat with *Cryptomeria*.

Keywords: *Cupressinoxylon, Glyptostroboxylon, Juniperoxylo*n, Lusatia, Miocene, *Quasisequoioxylon*, *Taxodioxylon*, xylotomical investigations

Introduction

Most of the Miocene brown coal exploited in the coal-mining district of Lusatia (Lausitz) is part of the Cenozoic infill of the North German-Polish Basin (Göthel, 2004). After mining of the First Lusatian Seam, ever-increasing opencast excavation during the 20th century focused on the deeper, 7–20 m thick Second Lusatian Seam. Basin wide sequence-stratigraphic interpretation of Miocene sedimentary successions indicates that the Second Lusatian Seam was deposited during the TB2.2 (ca. 17.3–16.4 Ma; late Burdigalian) and TB2.3 (ca. 16.4–14.8 Ma; Langhian) third-order cycles sensu Haq et al. (1988), implying that the Second Seam straddles the boundary between Lower and Middle Miocene (Göthel, 2004).

As a corollary of extensive exploitation, Lusatian brown coals and associated clastic sediments, in particular the Second Seam, have yielded a wealth of palaeobotanical information. Taxonomic and taphonomic interpretation of records of pollen (Thiergart, 1937; Magalowski, 1960; Sontag, 1966; Krutzsch, 1971), seeds (Mai, 2000; Czaja, 2003), and leaf cuticles (Jähnichen, 1965; Litke, 1966; Schneider, 1966–2004) has been used successfully in stratigraphical, sedimentological, facies- and palaeo-environmental analyses of the coal-bearing deposits.

The individual seam layers of the Second Lusatian Seam show a distinctive succession of swamp and bog

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Fig. 1 Geographic position of the localities in Lusatia.

facies types (Schneider, 1969, 1978, 1992, 2004) which can be distinguished on the basis of combined coal-petrographic and palaeobotanical characteristics (Table 1). Facies types are largely determined by nutrient availability and groundwater level, and named after the characterizing vegetation elements.

Methods

The fossil woods were cut into sections 20–25 µm thick. The observations were made using a microscope Leica DM 5500, equipped with a digital camera (DFC 480).

The woods were identified by referring to literature on recent and fossil wood and by comparisons with reference collections of recent and fossil wood from the Laboratory of Palaeobotany and Palynology in Utrecht, the Natural History Museum in Berlin, Senckenberg Naturhistorische Sammlungen in Dresden, and from the author's private collection. Descriptive terms correspond to current wood anatomical terminology (e.g., Kräusel, 1949; Greguss, 1955; Hudson, 1960; Van der Burgh, 1964, 1973; Mathiesen, 1970; Grosser, 1977; IAWA committee, 2004).

History

The locality lies in the classic German mining district of Lusatia. With the beginning of mining activity in the 19th century, autochthonous stump horizons (Fig. 2) and big stumps (Fig. 3) came to the attention of experts as material for palaeobotanical research. Because of its high tensile strength, high pressure resistance, high density, and the often considerable size, mining engi-

Table 1 Palaeobotanical characterization of Lusatian brown coal-facies types (modified from Dolezych, 2005)

Coal-petrographically defined facies types (Schneider 1995)	Characterizing wood	Characterizing cuticles	Facies types (Schneider, 2004)
M	*Juniperoxylon pachyderma*, *Cupressinoxylon kostyniukii*	*Enormicutis saxonica*	X (*Cupressospermum* swamp-forest facies, eutroph)
	Sciadopityoxylon wettsteinii, *Piceoxylon pseudotsugae*	*Sciadopitys tertiaria*, *Cathaya roseltii*	M (*Sciadopitys* bog facies, oligotroph)
	Taxodioxylon cryptomerioides, *Piceoxylon pseudotsugae*	*? Enormicutis conferta*, *Cryptomeria rhenana*, *Cathaya roseltii*	C (cf. *Cryptomeria conferta* bog facies, oligotroph)
P	*Pinuxylon* ssp.	*Pinicutis* spp.	P (*Pinus* woodland facies, oligotroph)
G	(wood generally absent)	*Graminophyllum weylandii*	G (Glumiflorae reed facies)
A	Angiosperm wood types (additionally conifers: *Glyptostroboxylon tenerum* and *Cupressinoxylon cupressoides*)	Angiosperm cuticles (additionally *Cunninghamia* and *Taiwania)*	A (Angiospermous bush-swamp facies, mesotroph)
K	*Taxodioxylon germanicum*, *Taxodioxylon gypsaceum*	*Enormicutis amplicavata*	S (*Sequoia* open canopy-woodland facies, mesotroph)
	Glyptostroboxylon rudolphii	*Enormicutis medicavata*	K (*Glyptostrobus* swamp-forest facies, eutroph)
F	(wood generally absent)	Cuticles of *Salix*, *Alnus*, *Acer*, *Liquidambar* and ferns	F (Riparian-forest facies)

Fig. 2 Autochthonous stumps at opencast mine Marie II, 1895 (Archive LMBV).

Fig. 3 Opencast mine at Zeißholz, about 1920 (Archive LMBV).

Fig. 4 Second Coal Seam (about 10 m high) in the opencast mine at Meuro with a stump horizon of *Taxodioxylon taxodii* Gothan (see arrows).

neers were interested in the nature of fossil wood, but systematic wood-anatomical analysis was hampered by poor preservation.

The first author who attempted to determine the botanical affinity of the remains was Eberdt (1895), who considered the Lusatian wood to represent *Taxodium distichum* L. C. Richard. However, he did not carry out any anatomical investigations and used the apparent similarities in physiognomy. Later Potonié (1895) assumed that all the woods were *Taxodium* based on their external appearance and developed a concept of species-poor *Taxodium*-swamp as the peat forming vegetation.

Gothan (1906) was the first who described the anatomy of these woods from brown coal opencast mine Senftenberg. He identified *Taxodioxylon taxodii* Gothan and *T. sequoianum* (Merklin) Schmalhausen emend. Gothan. Later Striegler & Süss (1984) identified *Sequoioxylon gypsaceum* (Goeppert) Greguss. In this way the peat-forming vegetation was considered to represent a species-poor *Taxodium*-swamp, followed by a nutrient- and species-poor raised forest bog (Gothan, 1906; Kräusel, 1920a) dominated by *Taxodium* and *Sequoia*.

In the past decades, this classic concept of a species-poor *Taxodium*-swamp has been challenged by the results of systematic cuticle analysis of (par)autochthonous leaf fossils (Jähnichen, 1965; Litke, 1966; Schneider, 1978, 1980, 2004). Cuticle analysis played a central role in the establishment of a conceptual model of an autogenic succession of distinctive peat-forming vegetation types in Lusatia, in which an eutrophic marsh represented by swamp woodland with *Glyptostrobus* develops into an oligotrophic bog plant community dominated by *Sciadopitys* (Schneider, 1969, 1978, 1992, 1995, 2004).

It is therefore conceivable that anatomical analysis of predominantly autochthonous, structurally preserved coalified wood could provide essential evidence for corroborating and refining the concept of the existence of more diverse Miocene peat-forming vegetations with 32 morphospecies of fossil woods in Lusatia (Dolezych, 2005). These discoveries and identifications of fossil woods contradict the picture of a Lusatian wood flora poor in species. Of particular importance are *Taxodioxylon* woods, which were often found in autochthonous stump horizons (i.e., Fig. 4).

Xylotomical investigations of taxodiaceous woods

1. *Taxodioxylon* woods

Conifers

Cupressaceae Li *sensu lato* (i.e., incl. Taxodiaceae)

Taxodioxylon sensu Gothan 1905

Taxodioxylon gypsaceum (Goeppert) Kraeusel 1949

Description: (Plate I, 1–2; Figs. 5–6)

Growth rings: Growth rings vary in width. The transition from early- to latewood is gradual.

Tracheids: The lumina are polygonal in cross section.

Bordered pits: Bordered pits in the radial walls of the tracheids occur in two or three adjacent vertical rows (Fig. 5). Crassulae are often present. The diameter of the bordered pits sometimes reaches up to 22 µm. In the tangential walls of the tracheids the pits are considerably smaller, with a diameter of ca. 8–9 µm (Fig. 6).

Axial parenchyma: The parenchyma occurs scattered in several tangential zones. In its longitudinal walls the pits are present (Fig. 6). The horizontal walls of the parenchyma are noticeably thin and smooth (Fig. 6). There are up to 22 cells in a strand of axial parenchyma.

Rays: The horizontal walls are thin, 2–3 µm thick; therefore, they appear to be un-pitted although pits of 1–2 µm are present (Plate I, 2; Fig. 5). The tangential walls are up to 2–3 µm thick and appear to be smooth (Plate I, 2; Fig.5). Indentures are present (Plate I, 2). The cross-fields have taxodioid pits mostly in pairs, glyptostroboid pits to lesser extent, and rarely cupressoid pits (Plate I, 1; Fig. 5). The diameter of pits can reach up to 14 µm, mostly 12–13 µm. The average height of the central cells is ca. 24 µm. The marginal cells are somewhat higher.

Identification

The identification of *Taxodioxylon gypsaceum* (Goeppert) Kraeusel is based on the identification key by Kräusel (1949, p. 168) which uses predominance of taxodioid cross-field pits, the almost smooth horizontal walls in the axial parenchyma, and the smooth ray cell walls to distinguish this species. Van der Burgh (1973, p. 155) mentioned the thin walls of ray parenchyma as being an important feature for differentiating this species from other *Taxodioxylon* species. This description by Van der Burgh (1973) fits exactly the features of the Wetro-fossil.

Taxodioxylon gypsaceum is widely distributed throughout the Tertiary. Van der Burgh & Meijer (1996) discussed the wide range of variation of this morphospecies. These authors pointed out that often natural variability within a morphospecies cannot be assessed, because only a single sample was used for the description of fossil wood. There are several *Taxodioxylon* species that should be reevaluated as they could belong to the same variable species.

Comparison with recent conifer wood indicates that *Taxodioxylon gypsaceum* is anatomically identical with the wood of extant *Sequoia sempervirens* (D. Don) Endlicher, because it has smooth ray cell walls, multiseriate borderd pits, and smooth horizontal axial parenchyma walls, and lacks ray tracheids and the relativly great and mostly two taxodioid cross-field pits

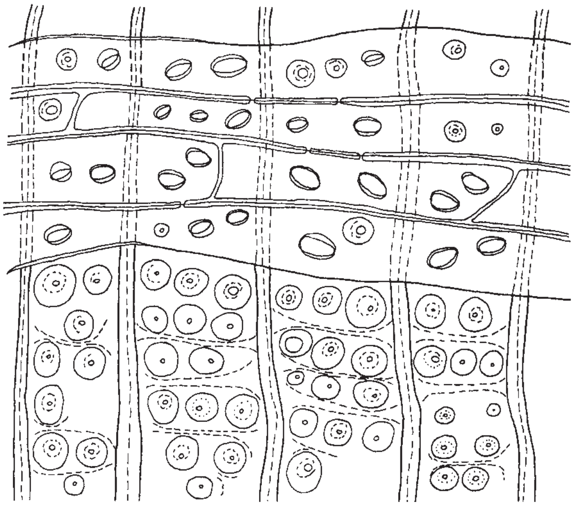

Fig. 5 RS (radial section) of *Taxodioxylon gypsaceum* (Goeppert) Kraeusel showing longitudinal tracheids with two or three rows of pits, crassulae, and smooth walled ray parenchyma with taxodioid cross-field pits, ×400.

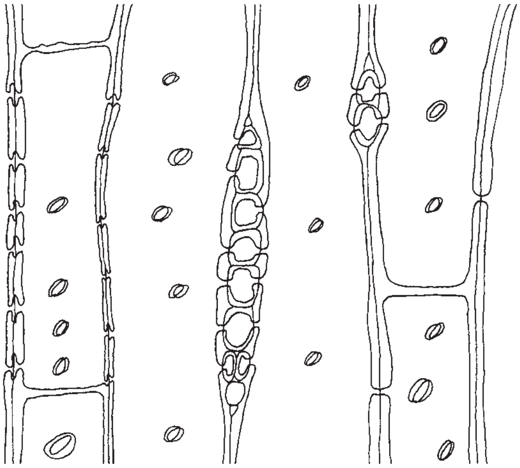

Fig. 6 TLS (tangential section) of *Taxodioxylon gypsaceum* (Goeppert) Kraeusel showing rays, axial parenchyma with smooth thin end walls, and tangential pits, ×400.

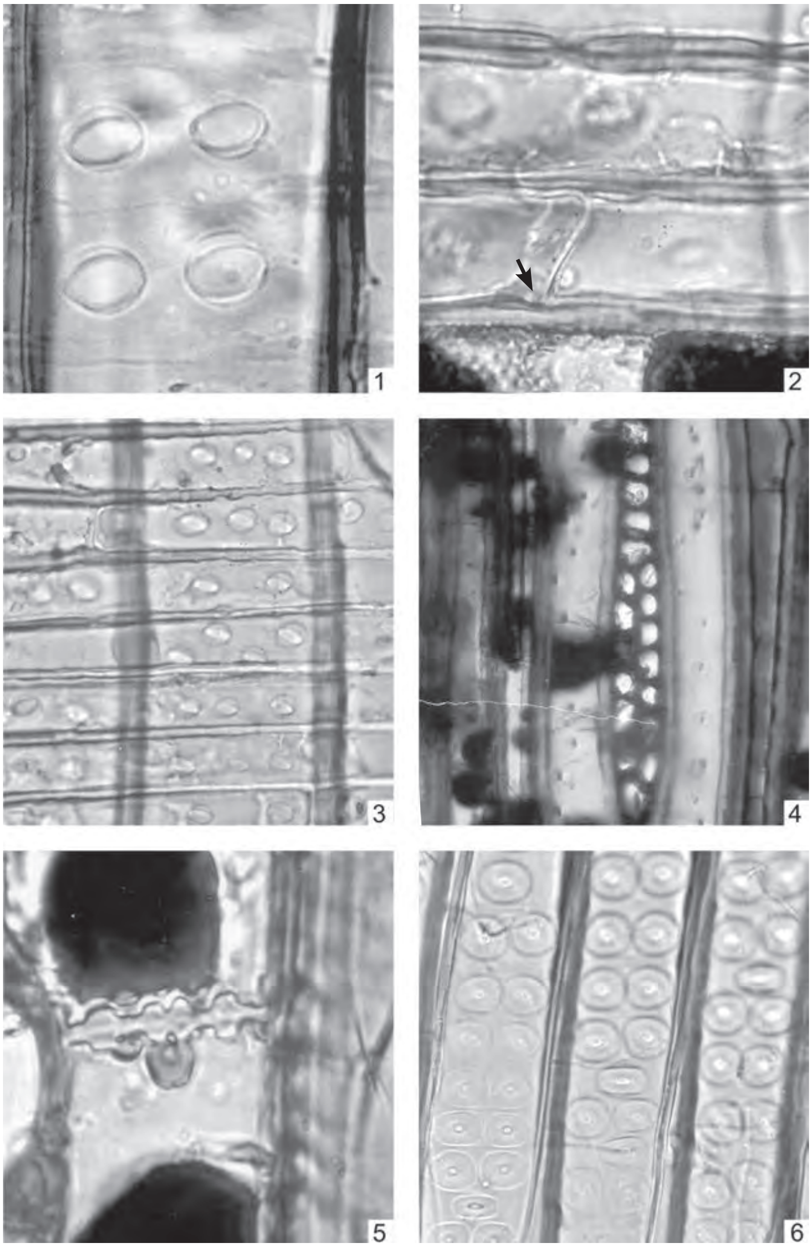

Plate I Woods of *Taxodioxylon gypsaceum* (Goeppert) Kraeusel (1–2), *Taxodioxylon germanicum* (Greguss) Van der Burgh (3–4), and *Taxodioxylon taxodii* Gothan (5–6). — 1: RS of *T. gypsaceum* with taxodioid cross-field pits, opencast mine at Berzdorf, prep. 080300/3, ×630. — 2: RS of *T. gypsaceum* with horizontal and tangential ray cell walls and indentures (arrow), clay pit at Wetro, prep. 250800/05, ×400. — 3: RS of *T. germanicum* with taxodioid cross-field pits, opencast mine at Jänschwalde, prep. 301001/236, ×400. — 4: TLS of *T. germanicum* with a biseriate ray and tangential pits, opencast mine at Jänschwalde, prep. 301001/236, ×200. — 5: TLS of *T. taxodii* with nodular transverse parenchyma wall, opencast mine at Meuro, prep. 230800/16, ×630. — 6: RS of *T. taxodii* with opposite bordered pits and crassulae, opencast mine at Meuro, prep. 230800/16, ×400.

in one cross-field.

Origin of samples

Clay pit at Wetro, Saxony (Fig. 1), Clay horizon below the Second Lusatian Seam.

Samples: 250800/01, 250800/02, 250800/04, 250800/ 05, 250800/07-10.

Opencast mine at Berzdorf, Saxony (Fig. 1), Middle Miocene brown coal

Samples: Bank 10: 230600/19, 230600/20, 230600/21, 230600/22; Bank 99: 080300/3.

Taxodioxylon germanicum (Greguss) Van der Burgh 1973

Description: (Plate I, 3–4; Figs. 7–8)

Growth rings: The transition from early- to latewood gradual, tending to be abrupt. Growth rings variable in width.

Tracheids: The lumina are polygonal in cross section.

Bordered pits: Bordered pits on the radial walls of the tracheids are in two or three vertical rows (Fig. 7). They attain a diameter of up to 18 µm. Crassulae are abundant. Many small pits are present in the tangential walls of the tracheids; their diameter is 8–9 µm (Fig. 8).

Axial parenchyma: Parenchyma is concentrated in several tangential zones in both early- and latewood. The longitudinal walls bear many pits with a diameter of up to 8 µm (Fig. 8). The horizontal walls are up to 5 µm thick and pitted (Fig. 8).

Rays: Rays are uniseriate, occasionally biseriate, and homocellular (Plate I, 4; Fig. 8). The average height is 10 cells with a maximum of 20 cells. The cells are ca. 20 µm high. The tangential walls are smooth and quite thin, up to 3 µm thick. Indentures are present. The horizontal walls, with a thickness of up to 5 µm, are pitted (Plate I, 3; Fig. 7). The cross-fields have 1–3 taxodioid pits and rarely cupressoid pits (Plate I, 3; Fig. 7). In the marginal cells up to six pits per cross-field can be found. The average diameter is around 10 µm, but occasionally pits up to 18 µm diameter are found.

Identification

The predominance of taxodioid cross-field pits together with the occurrence of axial parenchyma indicates this wood is *Taxodioxylon* (Kräusel, 1949, p. 168). However, the wood differs in some characters from the *Taxodioxylon* species listed by Kräusel. It differs from *Taxodioxylon gypsaceum* in having thick ray cell walls and smaller cross-field and bordered pits, but the differences with this species are minor. *Taxodioxylon taxodii* differs in its thick horizontal walls of axial parenchyma. The above described wood is similar to *Taxodioxylon germanicum* from the Lower Rhine Embayment (Van der Burgh, 1973, 1978). However, in contrast to the latter wood, the Lusatian material frequently has more than two pits per cross-field. Despite this minor difference, the wood seems best assigned to *T. germanicum*.

Greguss (1959) described *Sequoioxylon germanicum* Greguss (basionym of *Taxodioxylon germanicum*) from Rozewie (Poland, formerly Rixhöft in Germany) on the Baltic Sea. Another specimen of this species from the Miocene of Pôtor near Modrý Kameň in the South Slovakian Basin was described by Brezinová & Kourimský (1974). Greguss (1967) reports that this same wood also occurs in the Lower Palaeocene and Upper Oligocene of Hungary. *Taxodioxylon germanicum* is not comparable to the wood of any living species of the Cupressaceae *s.l.*, excepting those of *Sequoia sempervirens* (D. Don) Endlicher. However, in the extant wood of *S. sempervirens* (Universiteit Utrecht, Laboratory of Palaeobotany and Palynology No. 04), the horizontal ray cell walls are thin and not pitted, and the horizontal walls in the wood parenchyma are smooth. As the distribution of the living *S. sempervirens* is a relict of a much wider Palaeo-/Neogene range, spreading over the entire Northern hemisphere (Mai, 1995), it is conceivable that the variability of the species in its relictual range would be less than in its ear-

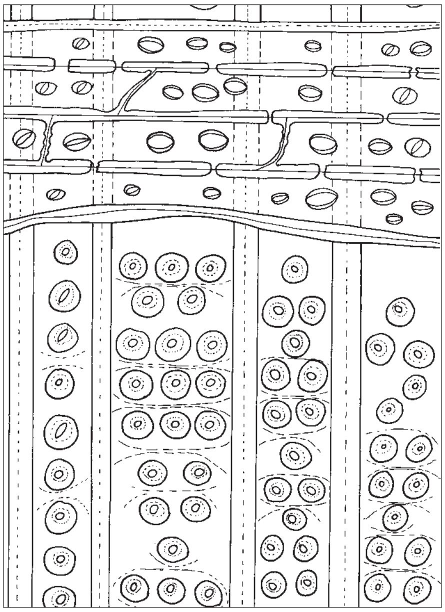

Fig. 7 RS of *Taxodioxylon germanicum* (Greguss) Van der Burgh showing longitudinal tracheids with one to three rows of pits, crassulae, and ray parenchyma with thick horizontal and thin tangential walls, taxodioid to cupressoid cross-field pits, and indentures, ×400.

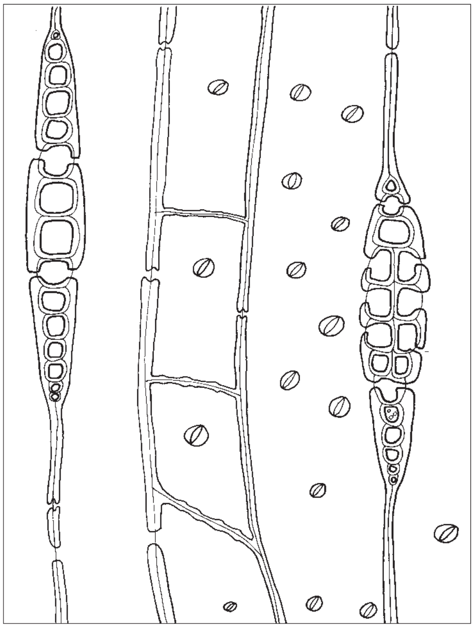

Fig. 8 TLS of *Taxodioxylon germanicum* (Greguss) Van der Burgh showing uniseriate and biseriate rays, tracheids, axial parenchyma, and tangential pits, ×400.

lier Palaeo-/Neogene range. Thus, a relation of *Taxodioxylon germanicum* with the extant species cannot be excluded. Nonetheless, there is a possibility that the morphospecies is an extinct species of *Sequoia*.

Origin of samples

Opencast mine at Jänschwalde, Brandenburg (Fig. 1), Second Lusatian Seam.

Samples: Bank 1/K7–facies: 291001/134, 291001/149; Bank 2/K6–facies: 291001/87; Bank 2/K5–facies: 301001/179, 301001/194, 301001/236; Bank 3/K1–facies: 301001/221, 301001/234, 301001/262, 301001/265, 301001/286.

Taxodioxylon cryptomerioides Schoenfeld 1953

Description: (Plate II, 1–2; Fig. 9)

Growth rings: The transition from early- to latewood gradual, tending to be abrupt. Growth rings variable in width.

Tracheids: The lumina are polygonal in cross section.

Bordered pits: Bordered pits in the radial walls of the tracheids are mostly in one row. Crassulae are not commonly observed. The diameter of the bordered pits is 12–18 µm.

Axial parenchyma: Parenchyma occurs in several scattered tangential lines. Pits occur in the longitudinal walls with a size of up to 8 µm. The horizontal walls are irregularly thickened (Plate II, 2; Fig. 9).

Rays: Rays are uniseriate, occasionally biseriate, and homocellular. Rays are low, mostly 2–4 cells, occasionally up to 12 cells. The average height of the middle cells is ca. 12 µm. The horizontal walls are up to 6 µm thick and are slightly pitted, occasionally also smooth (Plate II, 1). The tangential walls are mostly smooth. Indentures are not observed. There are mostly one or two, sometimes up to four, taxodioid pits per cross-field with a diameter of 7 to 8 µm (Plate II, 1).

Identification

The predominance of taxodioid cross-field pits together with the occurrence of axial parenchyma indicates that this wood belongs to the morphogenus *Taxodioxylon* (Kräusel, 1949, p. 168). Further, because of the combination of narrow tracheids, short rays, small taxodioid cross-field pits, and mostly uniseriate radial bordered pits, this fossil belongs to *Taxodioxylon cryptomerioides* Schoenfeld (Schönfeld, 1953, pp. 198–201, fig. 19–22) described from the Palaeogene Middle German Brown Coal. Van der Burgh (1973) described this morphospecies from the Rhineland Miocene in Germany. *Taxodioxylon cryptomerioides* is most similar to the wood of living species *Cryptomeria japonica* (Thunb. ex L. f.) D. Don, because it has relativly narrow tracheids, taxodioid cross-field pits, uniseriate bordered pits, and thick-walled axial parenchyma.

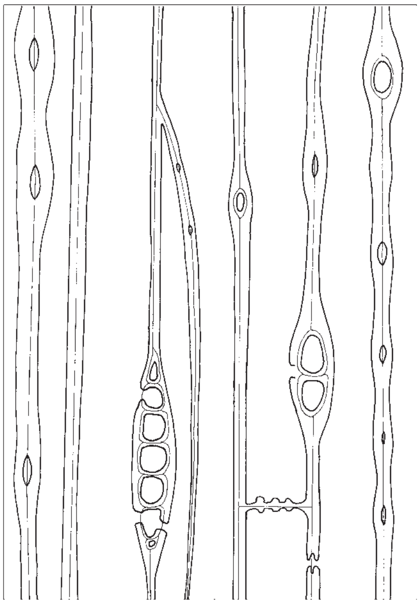

Fig. 9 TLS of *Taxodioxylon cryptomerioides* Schoenfeld showing short uniseriate rays and axial parenchyma with nodular end walls, ×400.

Origin of samples

Opencast mine at Klettwitz, Brandenburg (Fig. 1), Second Lusatian Seam.

Sample: 080704/01.

Opencast mine at Welzow, Brandenburg (Fig. 1), Second Lusatian Seam

Samples: Bank 0/A–facies: 120701/3; Bank 1/M–facies: 31795, 280502/12, 280502/27, 280502/28, 120701/83, 120701/84, 120701/86, 050302/6, 050302/7, 050302/68, 070302/19, 130302/33, 130302/34, 130302/100, 130302/101, 130302/156, 130302/158, 130302/159, 130302/161, 270504/46, 270504/47, 270504/49-53, 270504/59-61, 270504/64, 270504/66, 270504/74, 270504/75, 270504/78, 270504/80, 270504/84-86, 270504/89, 270504/92, 270504/95; Bank 2/K–facies: 30939, 30203, 120701/47, 120701/48.

Taxodioxylon taxodii Gothan 1906

Description: (Plate I, 5–6; Fig. 10–11)

Growth rings: The transition from early- to latewood gradual, tending to be abrupt. The latewood zone is relatively narrow.

Tracheids: The lumina are polygonal in cross section.

Bordered pits: In the radial walls the bordered pits are mostly biseriate (Plate I, 6; Fig. 10). They reach a diameter of up to 20 μm, on average 17 μm. Crassulae are often present (Fig. 10). Numerous pits occur in the tangential walls with a diameter of ca. 10 μm (Fig. 11).

Axial parenchyma: The parenchyma is scattered, often throughout the growth rings, in one or several zones. The horizontal walls are up to 5 to 8 μm thick and nodular (Plate I, 5; Fig. 11).

Rays: The rays are homocellular, uniseriate (occasionally biseriate), and up to 22 cells high (Fig. 11). The horizontal walls are up to 5 to 6 μm thick and pitted (Fig. 10). On the other hand, the tangential walls are thinner (3 μm) and smooth. Indentures are present. The cross-field pits occur mostly in pairs, sometimes up to three, in one cross-field and are mostly taxodioid, but sometimes cupressoid or even glyptostroboid (Fig. 10). Their diameter ranges between 7 and 13 μm.

Identification

Based on its characteristics of smooth ray walls, thick-walled tracheids, cross-field pits mostly taxodioid, and axial parenchyma frequently present with nodular transverse walls, this wood belongs to *Taxodioxylon taxodii* Gothan 1906. The wood differs in its anatomical characters from the *Taxodioxylon* species of the European Tertiary listed by Kräusel (1949), such as *T. gypsaceum* (Goeppert) Kraeusel, *T. germanicum* (Greguss) Van der Burgh, and *T. cryptomerioides* Schoenfeld, and from a new one, *T. vanderburghii* (Dolezych et al., 2011). It is similar to *Taxodium* Richard. There are three extant *Taxodium* species: *Taxodium distichum* (L.) Richard, *T. mucronatum* Tenore, and *T. ascendens* Brongniart (Van Gelderen & Van Hoey Smith, 1996, pp. 25, 26). According to Farjon (2001, pp. 98–100), *Taxodium distichum* (L.) Richard var. *imbricatum* (Nuttal) Croom is synonymous with *Taxodium ascendens* Brongniart. Based on the examination of three modern wood specimens, the species *Taxodium distichum* is not identical with *Taxodioxylon taxodii,* because it has cupressoid cross-field pits in addition to taxodioid cross-field pits (prep. UN 320/*T. distichum*, Universiteit Utrecht). *Taxodium mucronatum* comes closest as a living comparative to the fossil *Taxodioxylon taxodii*. This species from the North of Mexico needs a drier habitat than *Taxodium distichum,* and its habitat is more comparable with the ecological picture of the Cenozoic brown coal moorland.

Origin of samples

Opencast mine at Meuro, Brandenburg (Fig. 1), Second Lusatian Seam.

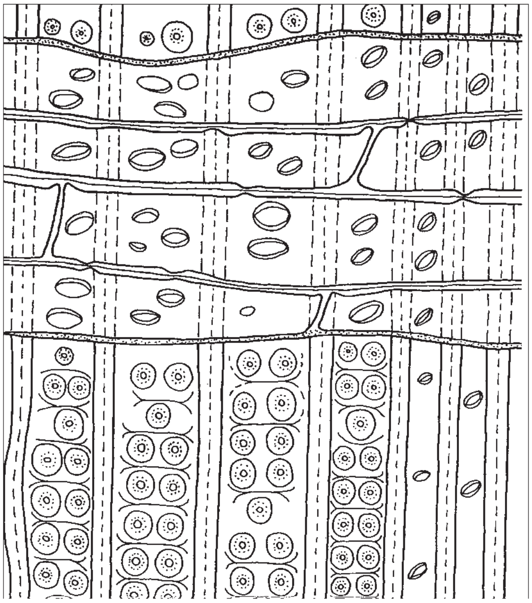

Fig. 10 RS of *Taxodioxylon taxodii* Gothan showing longitudinal tracheids with two rows of pits, crassulae, and smooth walled ray parenchyma with taxodioid cross-field pits and indentures, ×400.

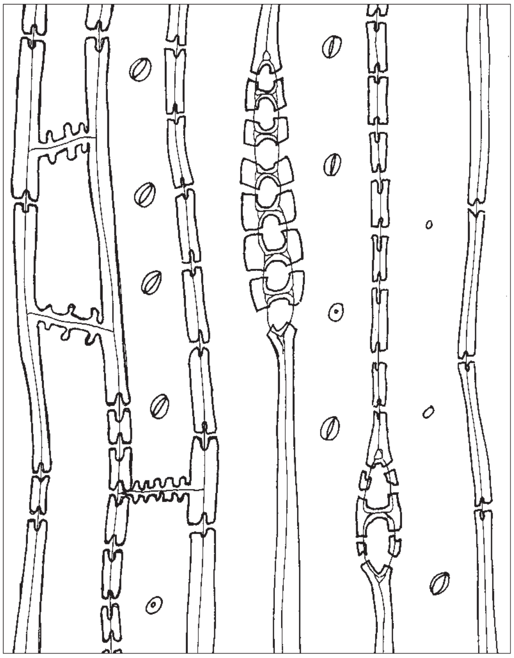

Fig. 11 TLS of *Taxodioxylon taxodii* Gothan showing uniseriate uniseriate rays, tracheids, axial parenchyma with nodular end walls, and tangential pits, ×400.

Samples: Bank 3/M3–facies: 230816, 2308017, 230818, 230819, 070202/17, 070202/19, 070202/20, 070202/46, 070202/63, 070202/64, 070202/65.

2. *Glyptostroboxylon* woods

Conifers

Cupressaceae Li *sensu lato* (i.e., incl. Taxodiaceae)

Glyptostroboxylon Conwentz 1884 emend. Dolezych & Van der Burgh 2004

Glyptostroboxylon Dolezych & Van der Burgh 2004

Glyptostroboxylon rudolphii Dolezych & Van der Burgh 2004

Description: (Plate II, 3–4; Figs. 12, 13)

Growth rings: The transition from early- to latewood is gradual. Growth rings are of variable width.

Tracheids: The lumina are polygonal in cross section.

Bordered pits: The bordered pits in the radial walls of the tracheids are in one to three vertical adjacent rows, mostly biseriate (Plate II, 4; Fig. 12). Crassulae are present. The diameter of the pits varies between 12 and 20 µm. Pits are also in the tangential walls of the tracheids (Fig. 13), ca. 8 µm in diameter.

Axial parenchyma: The parenchyma is diffuse or occurs concentrated in tangential zones. The horizontal walls are thin, weakly nodular. The vertical walls are smooth to moderately pitted (Fig. 13).

Rays: The rays are homocellular, mostly uniseriate, sometimes biseriate, and up to 20 cells high (Fig. 13). Intercellular spaces occur. The horizontal and tangential walls are thin and simply pitted (Plate II, 3; Fig. 12). In the cross-fields there are one to four pits which are mostly glyptostroboid, less frequently taxodioid, and even sometimes cupressoid (Plate II, 3; Fig. 12). Their diameter can be up to 8 µm. The average height of the middle cells is ca. 20 µm. The peripheral cells are somewhat higher.

Identification

Kräusel's key (1949, S. 173) leads via the descripter "like *Taxodioxylon* but with glyptostroboid cross-field pits" to *Glyptostroboxylon tenerum* (Kraus) Conwentz. Rediscovery of the original preparation of *Glyptostrobus tener* Kraus, the basionym for *Glyptostroboxylon tenerum* (Kraus) Conwentz, enabled a detailed re-assessment of this taxon and formulation of an emended diagnosis for the genus *Glyptostroboxylon* (Dolezych & Van der Burgh, 2004). The type material of Kraus (1864) from the Miocene of Wetterau/Germany as well as samples from Lusatia turned out to be comparable with the wood of modern *Cunninghamia*. As a consequence, *G. rudolphii* (Dolezych & Van der Burgh, 2004) was proposed for *Glyptostroboxylon* wood similar to that of modern *Glyptostrobus*. *Glyptostroboxylon rudolphii* is named after the palaeobotanist K. Rudolph, who described a Pliocene *Glyptostrobus*-like fossil wood of a clay pit at Neudorf from the basin of Eger (Bohemia) in detail and compared it with modern *Glyptostrobus* (1935, pp. 262–265, Taf. II). Because this is the first authentic reliable description of a fossil *Glyptostrobus* wood, the authors adopted "*rudolphii*" as the epithet.

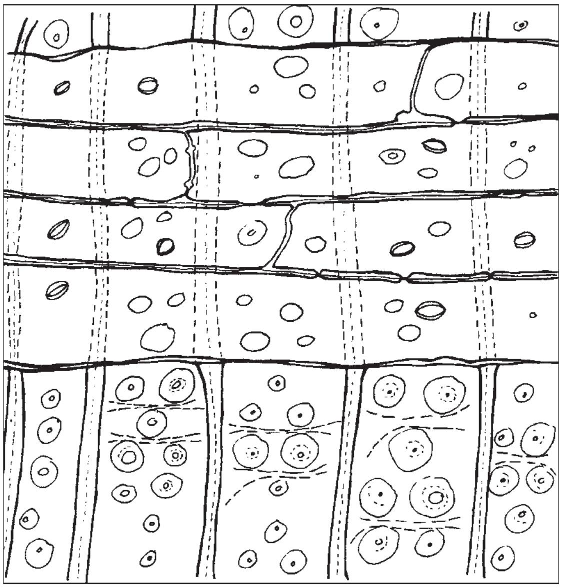

Fig. 12 RS of *Glyptostroboxylon rudolphii* Dolezych & Van der Burgh showing longitudinal tracheids with oner or two rows of pits, crassulae, and thin walled ray parenchyma with glyptostroboid cross-field pits, ×400.

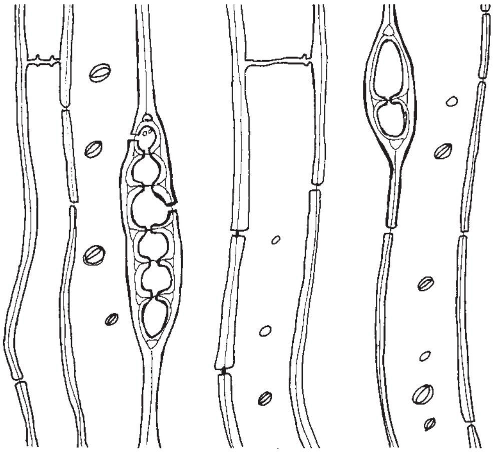

Fig. 13 TLS of *Glyptostroboxylon rudolphii* Dolezych & Van der Burgh showing uniseriate rays, tracheids, axial parenchyma with weakly nodular, and tangential pits, ×400.

Origin of samples

Opencast mine at Berzdorf, Saxony (Fig. 1), Middle

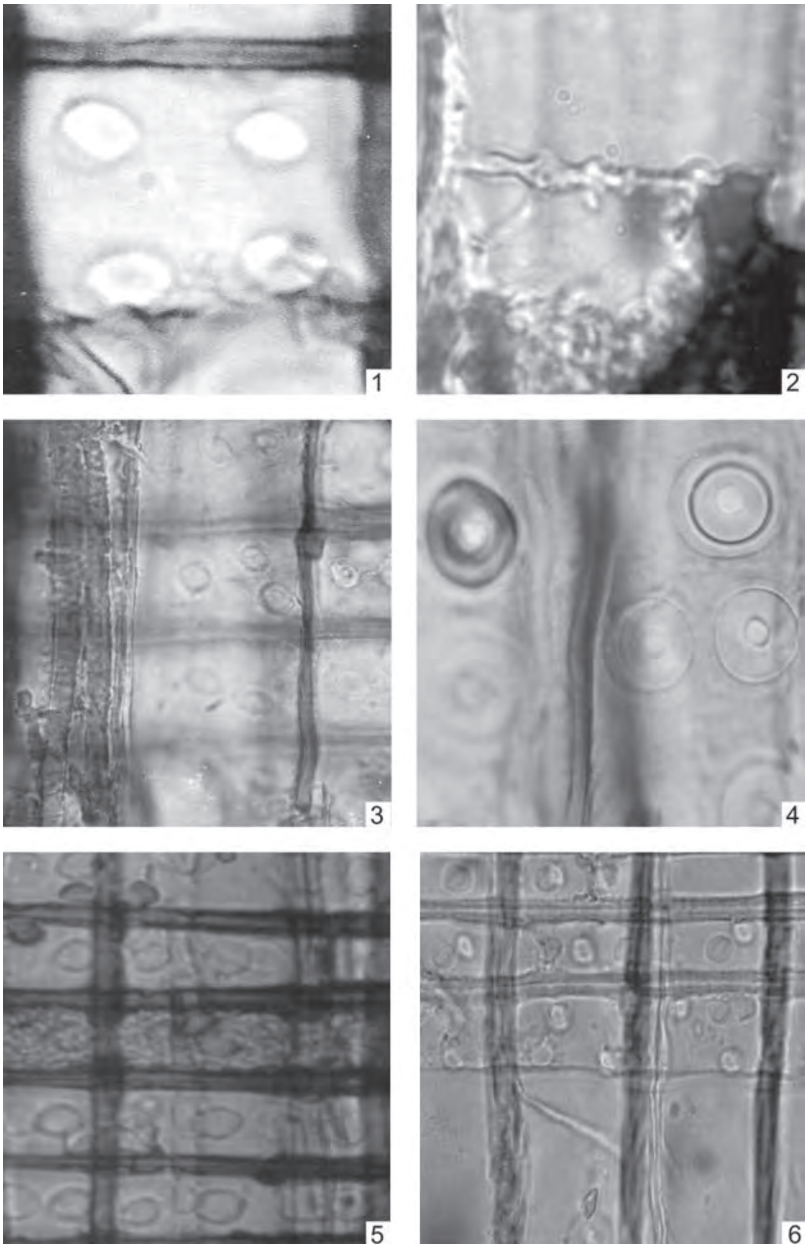

Plate II Woods of *Taxodioxylon cryptomerioides* Schoenfeld (1–2), *Glyptostroboxylon rudolphii* Dolezych & Van der Burgh (3–4), *Glyptostroboxylon tenerum* (Kraus) Conwentz (5–6). — 1: RS of *T. cryptomerioides* with taxodioid cross-field pits, opencast mine at Welzow, prep. 130302/33, ×630. — 2: TLS of *T. cryptomerioides* with smooth pitted transverse parenchyma wall, opencast mine at Welzow, prep. 270504/61, ×630. — 3: RS of *G. rudolphii* with a ray and glyptostroboid cross-field pits, opencast mine at Berzdorf, prep. 101001/25, ×400. — 4: RS of *G. rudolphii* with uni- and biseriate bordered pits, opencast mine at Berzdorf, prep. 101001/33, ×630. — 5: RS of *G. tenerum* with a ray and glyptostroboid cross-field pits, opencast mine at Berzdorf, prep. 101201/22, ×400. — 6: RS of *G. tenerum* with a ray, glyptostroboid cross-field pits and radial tracheids, opencast mine at Berzdorf, prep. 080300/8, ×400.

Miocene brown coal.

Samples: Bank 8: 200400/1, 200400/2, 200400/3, 200400/4, 200400/6, 200400/8, 200400/25, 200400/28, 200400/29, 230600/1, 230600/2, 230600/3, 230600/4, 230600/5, 101201/14, 101201/15, 101201/19, 101201/25, 101201/26, 101201/27, 101201/28; Bank 9.1: 120100/6, 120100/14, 120100/15, 120100/16, 120100/17, 120100/18, 120100/19, 120100/20, 120100/21, 120100/22, 120100/24, 120100/25.

Glyptostroboxylon tenerum (Kraus) Conwentz 1884

Description: (Plate II, 5–6; Figs. 14–16)

Growth rings: The transition from early- to latewoods gradual. Growth rings are all wide although the latewood rings are somewhat narrow.

Tracheids: The lumina are round to polygonal in cross section.

Bordered pits: Bordered pits in the radial walls occur in a single row, very seldom in two rows and are loosely arranged; they touch each other only occasionally

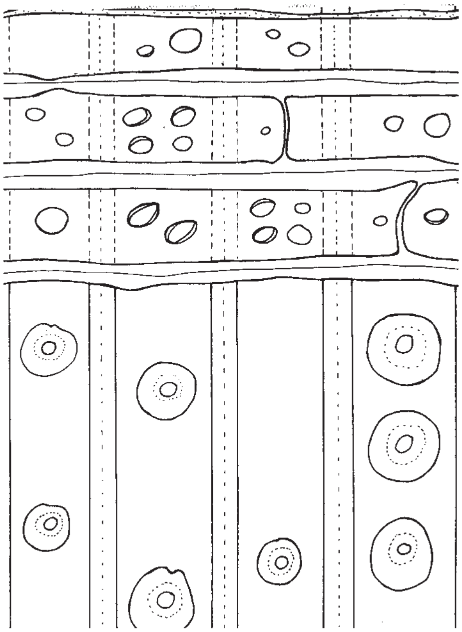

Fig. 14 RS of *Glyptostroboxylon tenerum* (Kraus) Conwentz showing longitudinal tracheids with one row of pits, and smooth walled ray parenchyma with glyptostroboid to taxodioid cross-field pits and indentures, ×400.

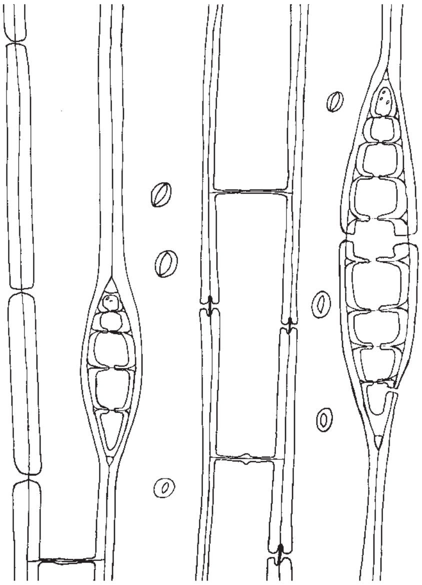

Fig. 15 TLS of *Glyptostroboxylon tenerum* (Kraus) Conwentz showing uniseriate rays, tracheids, axial parenchyma, and tangential pits, ×400.

(Fig. 14, 16). Crassulae seldom occur. The diameter of the bordered pits are ca. 8–20 µm. The pits are sometimes notched (Fig. 14). Pits occur in the tangential walls of the tracheids as well, ca. 8 µm in diameter (Fig. 15).

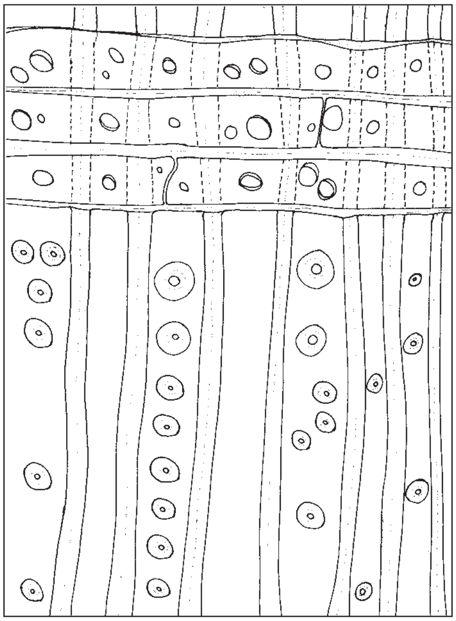

Fig. 16 RS of *Glyptostroboxylon tenerum* (Kraus) Conwentz showing ray, tracheids, cross-field pits, tangential walls in the ray, and radial bordered pits, ×400 (drawing from the type material of *Glyptostrobus tener* Kraus, No. 59 repository in the Senckenberg Naturhistorische Sammlungen Dresden).

Axial parenchyma: The parenchyma is diffuse and tangentially concentrated in zones. The vertical walls are thin. The horizontal walls are mostly smooth, up to 5 µm thick, and heavily pitted (Fig. 15).

Rays: The rays are homocellular, uniseriate, seldom biseriate, and up to 11 cells high (Fig. 15). The horizontal and tangential walls are thin and simply pitted (Plate II, 5, 6; Fig. 14, 16). Indentures occur sparingly. Cross-fields usually have one or two pits, up to four. These are generally glyptostroboid, but can be also taxodioid (Plate II, 5, 6; Fig. 14, 16). Their diameter can be ca. 10 µm. The average height of the middle cells is 14 µm. The marginal cells are higher.

Identification

This wood with *Taxodioxylon*-structure with predominantly glyptostroboid cross-field pits is assigned to *Glyptostroboxylon tenerum* (Kraus) Conwentz (see Kräusel, 1949, p. 173).

The wood resembles the living genus *Cunninghamia* R. Brown. ex A. Richard (*Cunninghamia lanceolata* (Lambert) Hooker, *Cunninghamia konishii* Hayata), because it has taxodioid cross-field pits, low rays, mostly uniseriate, sometimes biseriate rays, vesicular ray cells, mostly uniseriate bordered pits, and mostly smooth horizontal wassl of axial parenchyma. Examination of the wood of a fossil twig assigned to *Cunninghima miocenica* Ettinghausen (Natural History Museum, Berlin – Collection Number 441, 152/21L; Dolezych & Schneider 2007, Textfig. 12) showed its wood to have characteristics of *Glyptostroboxylon* (prep. 111202/1). And so the *Glyptostroboxylon* wood in the Second Coal Seam of the Lusatian Tertiary can be assigned to *Cunninghamia miocenica* Ettingshausen. Additional study of the type of *Glyptostroboxylon tenerum* (Kraus) Conwentz supported the affinity of this fossil to *Cunninghamia,* not to *Glyptostrobus*.

Origin of the samples

Formerly opencast mine at "Friedrich Ernst" Senftenberg, nearby the opencast mine at Meuro, Brandenburg (Fig. 1), Second Lusatian Seam.

Collections of the Natural History Museum at Berlin: 441, 152/21L, 111202/1.

Opencast mine at Meuro, Brandenburg (Fig. 1), Second Lusatian Seam.

Samples: Bank 2/A6–facies: 070202/118, 130404/12.

Opencast mine at Berzdorf, Saxony (Fig. 1), Middle Miocene brown coal.

Samples: Bank 8: 120100/34, 120100/35, 120100/36, 080300/8, 080300/9, 080300/10, 080300/13, 101201/20, 101201/21, 101201/22, 101201/23, 101201/24.

3. *Cupressinoxylon* wood

Conifers

Cupressaceae Li *sensu lato* (i.e., incl. Taxodiaceae)

Cupressinoxylon Goeppert 1850 emend. Dolezych 2005

Cupressinoxylon cupressoides Kraeusel 1920c

Description: (Plate III, 1–2; Fig. 17, 18)

Growth rings: Growth rings are distinct. The transition from early- to latewood is gradual, tending to be abrupt. Only a narrow zone of latewood is present.

Tracheids: The lumina are circular and polygonal in cross section.

Bordered pits: In the radial walls the bordered pits are uniseriate, rarely biseriate (Fig. 17). Crassulae are sometimes present. Diameter of the pits is ca. 13–15 µm. Pits in the tangential walls of the tracheids are observed (Fig. 18). Their size is ca. 8 µm.

Axial parenchyma: Axial parenchyma is not common and concentrated in zones. The horizontal walls are mostly smooth and up to 3 µm thick (Fig. 18).

Rays: The rays are homocellular and mostly uniseriate, occasionally biseriate, reaching a maximum of 12 cells high (Plate III, 2; Fig. 18). The horizontal and tangential walls have simple pits (Plate III, 1; Fig. 17). Indentures are absent. One to two, rarely three, cupressoid pits are present in the cross-fields (Plate III, 1; Fig. 17). The average height of the central inner cells is ca. 18 µm. The marginal cells are somewhat higher.

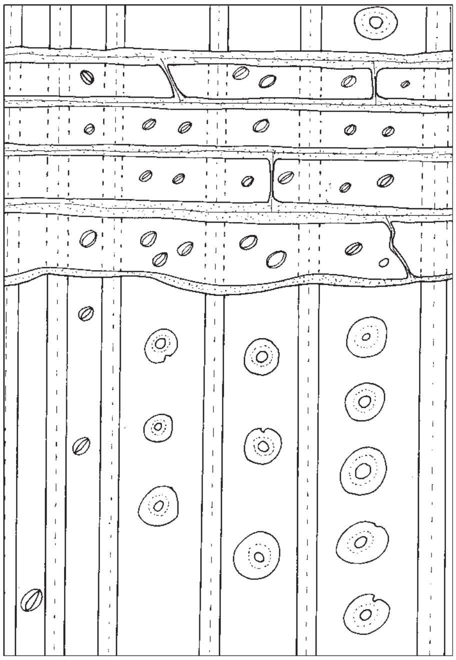

Fig. 17 RS of *Cupressinoxylon cupressoides* Kraeusel showing longitudinal tracheids with one row of pits, and smooth walled ray parenchyma with cupressoid cross-field pits, ×400.

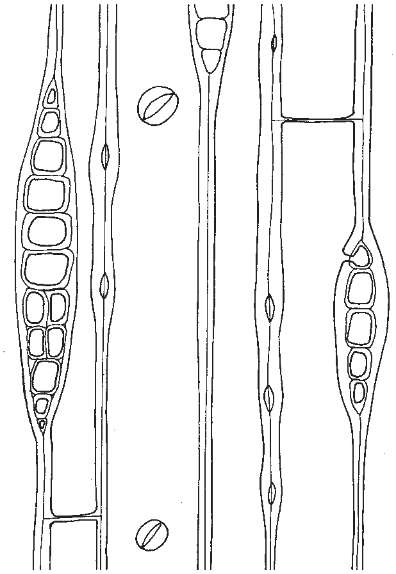

Fig. 18 TLS of *Cupressinoxylon cupressoides* Kraeusel showing occasionally biseriate rays, tracheids, axial parenchyma with smooth end walls, and tangential pits, ×400.

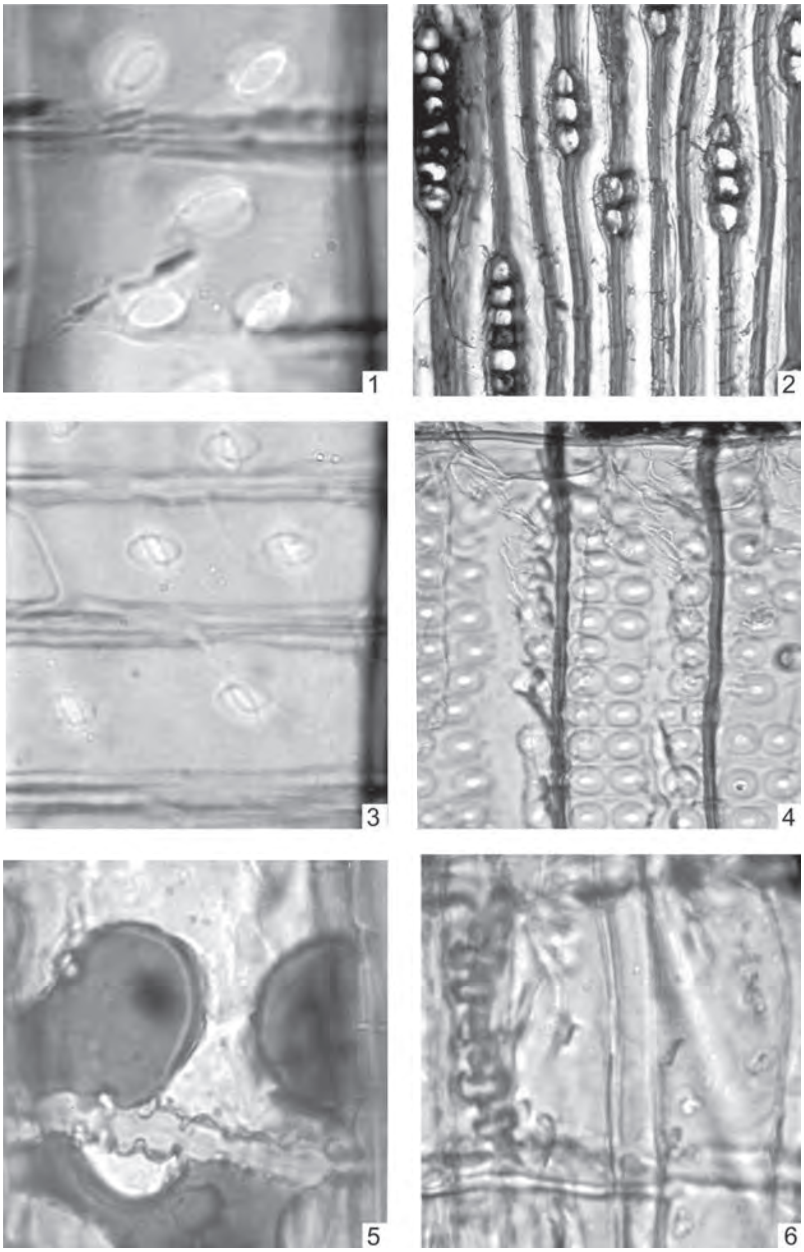

Plate III Woods of *Cupressinoxylon cupressoides* Kraeusel (1–2), *Quasisequoioxylon piskowitzense* Dolezych & Van der Burgh (3–4), and *Juniperoxylon pachyderma* (Goeppert) Kraeusel (5–6). — 1: RS of *C. cupressoides* with cupressoid cross-field pits, opencast mine at Welzow, prep. 270504/35, ×630. — 2: TLS of *C. cupressoides* with uni- and biseriate rays, opencast mine at Welzow, prep. 050302/101, ×200. — 3: RS of *Q. piskowitzense* with a ray cell walls and cupressoid cross-field pits, opencast mine at Piskowitz, prep. 171101/1, Holotypus, ×630. — 4: RS of *Q. piskowitzense* with multiseriate bordered pits, opencast mine at Piskowitz, prep. 171101/1, Holotypus, ×400. — 5: RS of *J. pachyderma* with knotted transverse parenchyma wall, opencast mine at Nochten, prep. 270803/2, ×630. — 6: RS of *J. pachyderma* with juniperoid tangential ray cell wall, opencast mine at Nochten, prep. 270803/3, ×630.

Identification

The combination of cupressoid cross-field pits, smooth ray cell walls, and the occurrence of axial parenchyma indicates *Cupressinoxylon* Goeppert 1850 emend. Dolezych (see also the Kräusel's key, 1949, p. 174). The small cupressoid cross-field pits, one to two in one cross-field, smooth transverse wall of axial parenchyma, mostly uniseriate rays, and uniseriate radial bordered pits lead to the morphospecies *Cupressinoxylon cupressoides* Kraeusel 1920, originally described from the Silesian Tertiary (Kräusel, 1920c, p. 427–429).

Comparison with recent conifer wood indicates that *C. cupressoides* is similar to the wood of extant *Taiwania cryptomerioides* Hayata. Both are characterised by cupressoid cross-field pits, one or two in one cross-field, smooth ray cell walls, relatively wide tracheids, the occurrence of axial parenchyma, smooth horizontal walls of axial parenchyma, mostly uniseriate and rarely biseriate rays, and uniseriate borederd pits. Applying the whole-plant concept—where a fossil plant is reconstructed from different organs of a fossil plant—to this fossil wood supports the wood-anatomical evidence of

Taiwania as a living relative, because *Cupressinoxylon cupressoides* Kraeusel co-occurs with remains that were identified as *Taiwania schaeferi* Schloemer-Jaeger (cuticles of fossil *Taiwania*) and *Enormicutis ovalicavata* Schneider (dispersed cuticles of fossil *Taiwania*) in the brown coal.

Origin of the samples

Opencast mine at Welzow, Brandenburg (Fig. 1), Second Lusatian Seam.

Samples: Bank 0/A–facies: 050302/101; Bank 1/A–facies: 130302/168; Bank 1/K–facies: 130302/107, 130302/108; Bank 2/K14–facies: 120701/202, 120701/203, 31760, 270504/35.

Cupressinoxylon cupressoides Kraeusel—A fossil taxodiaceous wood

Cupressinoxylon cupressoides is a remarkable, intriguing fossil. This wood has characteristics of *Cupressinoxylon*, but it has anatomy of the extant *Taiwania*. Gothan (1905, p. 48) wrote: “Eine Frage von großer Schwierigkeit bietet die Abtrennung der Taxodieen von den Cupressinoxyla” (“One question of great difficulty is the separation between Taxodiaceae and *Cupressinoxylon*)”.

4. *Quasisequoioxylon* wood

Conifers

Cupressaceae Li *sensu lato* (i.e., incl. Taxodiaceae)

Quasisequoioxylon Dolezych & Van der Burgh 2005

Quasisequoioxylon piskowitzense Dolezych & Van der Burgh 2005

Description: (Plate III, 3–4; Figs. 19, 20)

Growth rings: The transition from early- to latewood is gradual, tending to be abrupt. Growth rings are of variable width.

Tracheids: The lumina are polygonal in cross section.

Bordered pits: The bordered pits in the radial walls of the tracheids are biseriate or triseriate (Plate III, 4; Fig. 19). Some pits are irregularly arranged and flattened when touching with each other (Fig. 19). The pits are up to 18 μm in diameter. Crassulae are often present. The pits in the tangential walls are significantly smaller and round in shape, ca. 9 μm in diameter (Fig. 20).

Axial parenchyma: Axial parenchyma is diffuse, but tangentially zonate. The horizontal walls of the parenchyma are smooth, and occasionally some pits, up to 3 μm in diameter, are present (Fig. 20).

Rays: The rays are uniseriate and homocellular, up to 20 cells high (Fig. 20). The horizontal and tangential walls are thin and simply pitted (Plate III, 3, 4 and; Fig. 19). Indentures are not observed. The pits in the cross-fields are small and mostly cupressoid (Plate III, 3; Fig. 19). They occur singly or in pairs, rarely more. The cross-field pits are irregularly spaced; sometimes

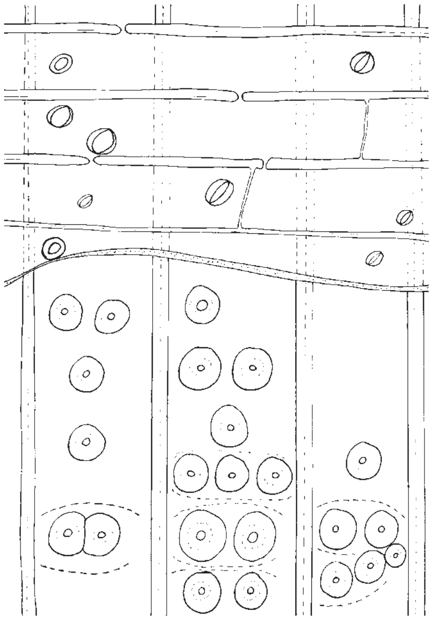

Fig. 19 RS of *Quasisequoioxylon piskowitzense* Dolezych & Van der Burgh showing longitudinal tracheids with one to three rows of pits, crassulae, and smooth walled ray parenchyma with cupressoid cross-field pits, ×400.

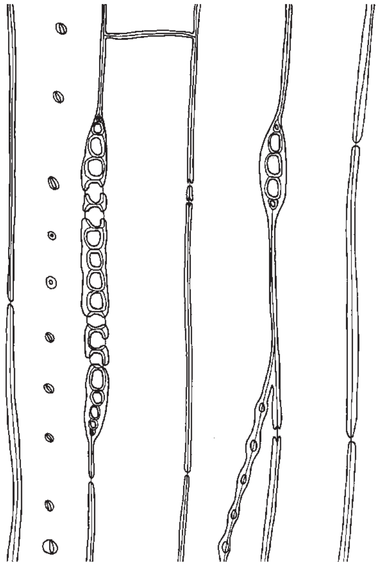

Fig. 20 TLS of *Quasisequoioxylon piskowitzense* Dolezych & Van der Burgh showing uniseriate rays, tracheids, axial parenchyma with smooth end walls, and tangential pits, ×400.

they are concentrated, sometimes altogether lacking (Fig. 19). Their diameter can be up to 10 µm, with the majority around 6 µm. The average height of the central cells is ca. 22 µm. The marginal cells are somewhat higher.

Identification

The predominately cupressoid cross-field pits, the smooth ray cell walls, and the almost smooth horizontal walls in the axial parenchyma are characteristic of *Cupressinoxylon*. The frequent occurrence of biseriate and triseriate bordered pits is not a characteristic of *Cupressinoxylon*. However, this morphogenus does not have predominantly cupressoid cross-field pits. Therefore, the fossil is considered to represent a distinctive cupressaceous morphogenus, described here under the name *Quasisequoioxylon*.

A comparison of the present material with wood from the Tertiary of Silesia, Poland, indicates a strong resemblance with *Cupressinoxylon wellingtonioides* (Prill) Kraeusel described from Opole (formerly Oppeln) (Kräusel, 1920b, pp. 293–297). According to Kräusel, the partial biseriate radial wall pitting is not typical of cupressaceous affinity. Yet, the presence of cupressoid cross-field pits indicates affinity with *Cupressinoxylon*. In the Lusatian material, cross-field pits occur more sparsely and very rarely with three together in a cross-field; this is only a small difference with the Silesian wood. However, Kräusel used only a small (thumb-thick) branch to describe the species *C. wellingtonioides*, and one cannot be sure about the structure of the wood of the corresponding mature stem. Therefore, we do not use the epithet *wellingtonioides* for classifying the *Cupressinoxylon* wood from Piskowitz at a morphospecies level. Comparisons with the wood of recent Cupressaceae indicate that the anatomical features of *Q. piskowitzense* are similar, but not identical, to those of *Sequoia gigantea* (Lindley) Buchholz. Living *Sequoia gigantea* has significantly larger cross-field pits, up to 20 µm in diameter, which are predominantly taxodioid and only occasionally glyptostroboid. Furthermore, no ray tracheids are observed in our wood.

Already Schenk (1869) and Kräusel (1920b) considered the possibility that fossil wood from Saxony and Silesia, identified as *Cupressinoxylon*, could correspond to *Sequoia couttsiae* Heer. Represented by leafy shoots, cones, and seeds, this supposed extinct species of *Sequoia* is particularly widespread in the Paleocene of Europe (Heer, 1862; Gardner, 1883; Dorofeev & Sveshnikova, 1963). The species has also been attributed to *Athrotaxis* (*Athrotaxis couttsiae* (Heer) Gardner). More recently Kunzmann (1999) has transferred the species to *Quasisequoia* Srinivasan & Friis emend. Kunzmann, an extinct conifer genus, already present in the late Cretaceous, which differs from *Sequoia* in vegetative organs as well as in female cones and seeds (Srinivasan & Friis, 1989; Kunzmann, 1999). Mai (1964, p. 57) reported the presence of seeds of *Sequoia couttsiae* in the upper horizon of Piskowitz coal from which our wood originated (cf. Rathner et al., 1995). In the Rhenish brown coal, Pingen (1994) recorded abundant remains of *Quasisequoia couttsiae* (Heer) Kunzmann from the opencast mine at Hambach. For comparison with *Quasisequoioxylon piskowitzense* from Lusatia, we studied a wood sample from Hambach (sample 190703/1), collected from a horizon in which twigs of *Q. couttsiae* are the only other plant mega fossils present. This wood is conspecific with the material described from Piskowitz. Because of its association with *Quasisequoia couttsiae* in Hambach, *Quasisequoioxylon piskowitzense* is likely to represent the wood of this extinct conifer species.

Origin of the samples

Opencast mine at Piskowitz, Saxony (Fig. 1), First Seam- and Second Lusatian Seam.

Sample: 171101/1.

Opencast mine at Hambach, Rhineland, Miocene brown coal.

Sample: 190703/1.

5. *Juniperoxylon* wood

Conifers

Cupressaceae Li *sensu lato* (i.e., incl. Taxodiaceae)

Juniperoxylon Gothan emend. Van der Burgh 1973

Juniperoxylon pachyderma (Goeppert) Kraeusel 1949

Description: (Plate III, 5–6; Figs. 21, 22)

Growth rings: The transition from early- to latewood gradual.

Tracheids: The lumina is polygonal in cross section. Resin particles are abundant.

Bordered pits: The bordered pits in the radial walls of the tracheids occur in single or double rows and are mostly loosely arranged (Fig. 21). Crassulae are present. The diameter of the bordered pits ranges from 11 to 18 µm. In the tangential walls pits are usually present (Fig. 22). Their diameter is ca. 10 µm.

Axial parenchyma: The parenchyma, occurring in abundance, is found in several tangential bands as well as scattered (Fig. 22). The pits in the longitudinal walls are similar to those in the cross-fields and have a diam-

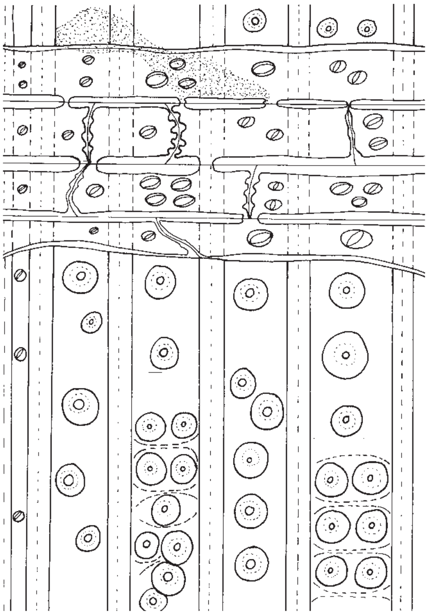

Fig. 21 RS of *Juniperoxylon pachyderma* (Goeppert) Kraeusel showing longitudinal tracheids with one or two rows of pits, crassulae, ray parenchyma with juniperoid pitted end walls and taxodioid to cupressoid cross-field pits, and resin, ×400.

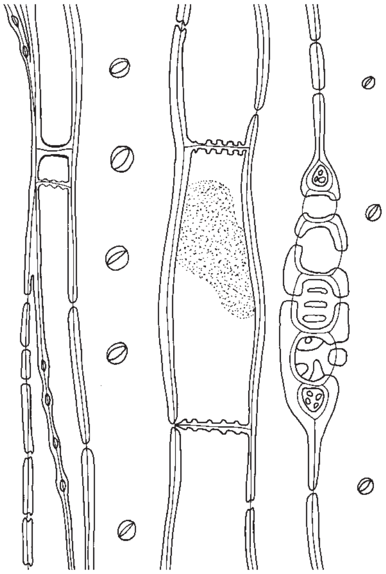

Fig. 22 TLS of *Juniperoxylon pachyderma* (Goeppert) Kraeusel showing a uniseriate ray, tracheids, axial parenchyma with nodular end walls and resin, and tangential pits, ×400.

eter of ca. 9 μm. The transverse walls are up to 7–8 μm thick and nodular (Plate III, 5; Fig. 21). Resin particles are abundant (Fig. 21, 22).

Rays: Rays are homocellular, generally uniseriate, occasionally biseriate (Fig. 22), and are 2 to 7 cells high. The average height of the middle cells is 22 μm. The marginal cells are somewhat higher. The horizontal walls are up to 5 μm thick (Plate III, 6; Fig. 21). The tangential walls are thicker, up to 7 μm, and by characteristic juniperoid pitted (Plate III, 6; Fig. 21). The cross-field pits in the trunk wood are more akin to the taxodioid type (Fig. 21), and those in the root wood are rather akin to the cupressoid type. Usually 2 to 4 pits with a diameter of ca. 8–9 μm are to be found in each cross-field (Fig. 21).

Identification

The particular combination of pitted horizontal ray cell walls, juniperoid pitting of tangential ray cell walls, predominantly taxodioid cross-field pits, and pitted axial parenchyma cell walls corresponds to *Juniperoxylon* emended by Van der Burgh (1973), in which he brings together into a single morphogenus wood with both cupressoid and taxodioid cross-field pitting and juniperoid pitting of the tangential walls. The Lusatian material is identical to *Juniperoxylon pachyderma* as described from the Rhenish brown coal (Van der Burgh, 1973). *Juniperoxylon juniperoides* (Kownas) Huard 1966 mentioned by Schneider (2004) should be included in *J. pachyderma* following the definition of this morphospecies by Van der Burgh (1973).

The term "Juniperustüpfelung" goes back to Gothan (1905), who used this term to describe the type of ray cell pitting consisting of only slightly pitted horizontal ray walls, while the tangential ray cell walls are heavily pitted. He categorized such wood within the morphogenus *Cupressinoxylon*. Wood-anatomical characters of *Juniperoxylon pachyderma* clearly support relationship with the Cupressaceae *s.l.* However, there is no close correspondence with the wood of any extant genus of the Cupressaceae.

The characteristic juniperoid pitting occurs in the wood of *Juniperus* L. Yet, because of some variability in the juniperoid pitting and the wide tracheids with often biseriate bordered pits, the morphogenus *Juniperoxylon* does not necessarily represent *Juniperus*. It is likely, therefore, that *Juniperoxylon pachyderma* may be an extinct taxon. *Juniperoxylon pachyderma* does not occur wtih other wood types, but with seeds and twigs described as *Cupressospermum saxonicum* Mai (Mai & Schneider, 1988). The genus *Cupressospermum* was established by Mai (1960) and emended by Kunzmann (1999)—and its corresponding cuticles is known as *Enormicutis saxonica* described by Schneider (Mai & Schneider, 1988; Schneider, 2004; Plate I, 2 and 3; Fig. 45). This association indicates that *J. pachyderma* ex parte could well represent the wood of this

Taxodiaceous morphotaxa comparable with extant taxa

- *Taxodioxylon*-woods*:*
- *Taxodioxylon gypsaceum* – aff. *Sequoia*
- *Taxodioxylon germanicum* – ? aff. *Sequoia*
- *Taxodioxylon taxodii* – aff. *Taxodium*
- *Glyptostroboxylon*-woods:
- *Glyptostroboxylon rudolphii*– aff. *Glyptostrobus*
- *Glyptostroboxylon tenerum* – aff. *Cunninghamia*
- *Cupressinoxylon*-wood:
- *Cupressinoxylon cupressoides* – aff. *Taiwania*

Taxodiaceous morphotaxa without comparable extant taxa

- *Taxodioxylon*-wood*:*
- *Taxodioxylon germanicum* – ? aff.
- *Juniperoxylon*-wood:
- ? *Juniperoxylon pachyderma - ex parte* – aff. *Cupressospermum saxonicum*
- *Quasisequoioxylon*-wood:
- *Quasisequoioxylon piskowitzense* – aff. *Quasisequoia*

Fig. 23 Overview of Lusatian taxodiaceous woods with their affinities.

extinct conifer species. Interestingly, Kunzmann (1999) assigned the morphogenus *Cupressospermum* to another family, the extinct Geinitziaceae Kunzmann.

Origin of the samples

Opencast mine at Nochten, Saxony (Fig. 1), Second Lusatian Seam.

Samples: Bank 2/X–facies: 270803/1, 270803/2, 270803/3, 270803/4, 270803/5, 270803/6, 270803/7a, 270803/7b.

Nomenclatural and taxonomical treatment of taxodiaceous wood genera

1. History of *Taxodioxylon* Gothan 1905

Taxodioxylon is one of the most investigated morphogenus in the European, as well as in the Lusatian, Cenozoic. Despite this conifer genus being known since Hartig (1848), there is confusion about it, mostly concerning the affinities. Hartig (1848) erected the genus *Taxodioxylon* with the type species *Taxodioxylon goeppertii,* but unfortunately this Triassic wood was not well described.

Later, on the basis of his research on the Lusatian brown coal, Gothan (1905, p. 49) emended *Taxodioxylon* and described it with the original German words: “die auf Grund von Holzresten bestimmten Taxodiaceen werde ich als *Taxodioxylon* bezeichnen” (“I will name Taxodiaceae determined on the basis of wood remains as *Taxodioxylon*”). Additionally he gave a key (Gothan, 1905, pp. 101–103), and valid and more detailed definition for the morphogenus *Taxodioxylon* Gothan with:

- Gymnospermaeous woods,
- Bordered pits round, large, solitary and if they are multiseriate, they are standing at the same level (“gleichhochstehend”),
- Tracheids without helical thickenings,
- Abietineous pitting are not present,
- Axial parenchyma regularly present,
- Cross-field pits between cupressoid and glyptostroboid and in a great number (often more than six).

On the basis of investigations in Lusatian brown coal, Gothan (1906) described two morphospecies in an identification key, *T. taxodii* and *T. sequoianum.* Later Kräusel (1949) in his key added information to the list of morphospecies of *Taxodioxylon.* Here are the words of the key:

- Radial tracheid pits round, if they are multiseriate they are opposite and separated by “SANIO”-strips,
- Normal wood without resin ducts, only sometimes in wounded wood,
- Ray cell walls predominately smooth,
- Cross-field pits taxodioid (apertures in the earlywood horizontal and wide).

It seems appropriate to conserve the name *Taxodioxylon* sensu Gothan rather than use *Taxodioxylon* Hartig with a conserved type from Lusatian Tertiary material. And I suggest to keep *Taxodioxylon* as a *nomen conservandum* and to send a report to the ICBN committee.

2. Discussion of taxodiaceous wood nomenclature and taxonomy

In Lusatia different taxodiaceous wood species are described. They are customarily assigned to the morphogenera: *Taxodioxylon*, *Glyptostroboxylon*, *Cupressinoxylon*, *Quasisequoioxylon*, and *Juniperoxylon*. The investigated taxodiaceous woods have affinities to either extant or extinct genera (Fig. 23).

When one compares the morphospecies names described here with their affinities, some inconsistencies in taxonomy and nomenclature become apparent (Fig. 23):

1. *Glyptostroboxylon* includes two morphospecies that have living relatives in two different living taxodiaceous genera, *Cunninghamia* and *Glyptostrobus*.
2. One of the *Cupressinoxylon* wood is *C. cupressoides* with affinity to *Taiwania* of Taxodiaceae and not to a living wood of Cupressaceae *s.s.*
3. *Juniperoxylon pachyderma* ex parte has an affinity to the fossil genus *Cupressospermum*. Firstly, *Juniperoxylon pachyderma* has no attribution with the living genus *Juniperus* of Cupressaceae *s.s.* Secondly, according to Kunzmann (1999), *Cupressospermum* belongs to another family, the extinct Geinitziaceae.

In nomenclature and taxonomy, the same root-word is often applied to different plants. This is the result of the historical development of the nomenclature. However, for both nomenclature and taxonomy, it is important to provide detailed descriptions of the features of the plant organs.

3. Proposal for a revision of the morphogenus *Taxodioxylon*

1. Some authors used to establish a morphogenus for every living genus; for example, Greguss (1967) and Blokhina (1986) used the *Sequoioxylon* as well as *Metasequoioxylon*. These morphotaxa, however, fit under the broadly defined morphogenus *Taxodioxylon*. We should follow the rule of priority for plant names, and the impartiality must be maintained. We must take into consideration earlier palaeobotanical works.
2. All fossil woods of the Taxodiaceae (Cupressaceae) fit the diagnosis of *Taxodioxylon* by Gothan (1905, p. 49). However, it is possible to distinguish woods of Cupressaceae *s.s.* from Taxodiaceae by several xylotomical features: the *Taxodioxylon* woods differ in its characters from the *Cupressinoxylon* woods in having mostly biseriate bordered pits, sometimes biseriate rays, and predominately taxodioid cross-field pits (Phillips, 1948; Kräusel, 1949; Dolezych, 2005, see above).
3. The proposal is that a revision of *Taxodioxylon* should be made. Süss proposed a diagnosis (in Süss & Velitzelos, 1997), but did it without an emendation. I would propose continued use of the term *Taxodioxylon,* but with a more precise description. This taxon should be characterized by the following features:

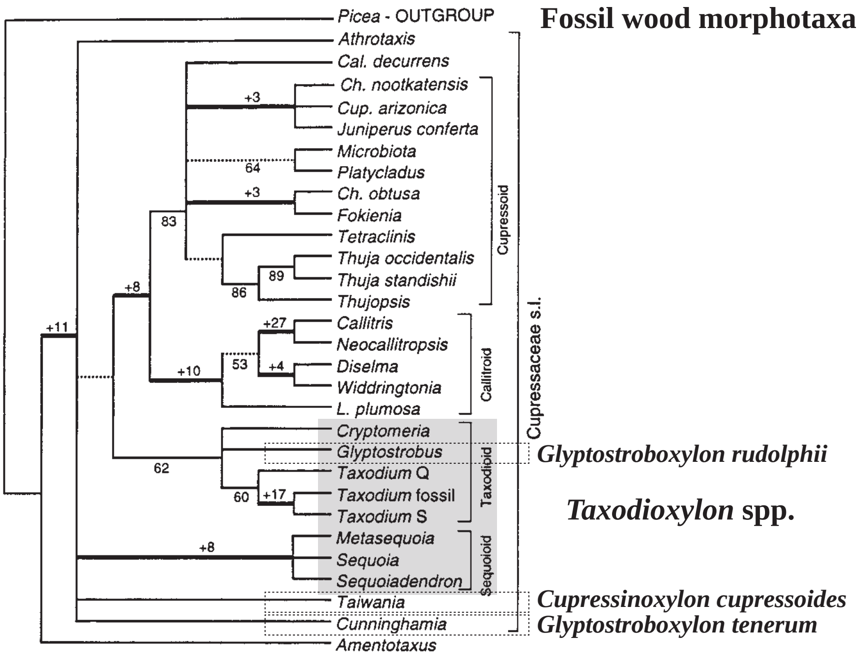

Fig. 24 Distribution of Lusatian taxodiaceous fossil wood morphotaxa on a molecular phylogenetic tree of the Cupressaceae *s.l.* (Gadek et al., 2000).

Table 2 Morphospecies described in this paper and with their botanical affinities

Botanical genus or extinct genus	Related fossil wood
Sequoia Endlicher	*Taxodioxylon germanicum* (Greguss) Van der Burgh, *Taxodioxylon gypsaceum* Kraeusel
Taxodium (L.) Rich.	*Taxodioxylon taxodii* Gothan
Cryptomeria D. Don	*Taxodioxylon cryptomerioides* Schoenfeld
Glyptostrobus Endlicher	*Glyptostroboxylon rudolphii* Dolezych et Van der Burgh
Taiwania Hayata	*Cupressinoxylon cupressoides* Kraeusel
Cunninghamia R. Br. et A. Richard	*Glyptostroboxylon tenerum* (Kraus) Conwentz
Cupressospermum Mai emend. Kunzmann	*Juniperoxylon pachyderma* ex parte Kraeusel emend. Van der Burgh
Quasisequoia Srinivasan et Friis	*Quasisequoioxylon piskowitzense* Dolezych et Van der Burgh

- Distinct growth rings,
- Ray cell walls predominately smooth,
- Abietinean pitting in radial walls mostly biseriate,
- Predominately taxodioid cross-field pits,
- Wood parenchyma present.

Comparison between palaeoxylotomy and molecular phylogeny

A new way of looking at taxodiaceous woods is in the context of the recent phylogenetic analyses of living plants. In the combined molecular genetic and morphological analyses of Gadek et al. (2000, Fig. 2) for the living woods of Cupressaceae *s.l.*, the *Taxodioxylon* woods (*Taxodioxylon* spp.) are included in the taxodioid and sequoioid clades of the phylogenetic tree (Fig. 24).

Glyptostroboxylon Conwentz emend. Van der Burgh & Dolezych includes *Glyptroboxylon rudolphii* Van der Burgh & Dolezych and *Glyptostroboxylon tenerum* (Kraus) Conwentz which are suggested to have characteristics seen in the extant *Glyptostrobus* and *Cunninghamia*. These genera belong to different clades (Fig. 24).

Furthermore, *Cupressinoxylon cupressoides* Kraeusel is suggested to have features of *Taiwania*, which is included in a separate phylogenetic clade of Cupressaceae *s.l.* (Fig. 24).

Conclusions

The systematic collection and anatomical analysis of taxodiaceous woods from various opencast mines in Lusatia has resulted in a representative record of autochthonous wood from the paralic Second Lusatian Seam (Dolezych, 2005; Dolezych & Schneider, 2006, 2007), as well as the approximately time-equivalent brown coal deposits of the limnic Berzdorf Basin (Dolezych & Van der Burgh, 2004).

At the family level, the Lusatian wood flora in this paper is notably characterized by its wide variety of representatives of the Cupressaceae *s.l.* (Cupressaceae *s.s.* + Taxodiaceae). The majority of the wood types have features seen in genera of extant conifers and in a few cases with extinct natural conifer genera. Taxodiaceous woods in Lusatia are diverse with these genera present: *Glyptostrobus*, *Taxodium*, *Sequoia*, *Taxodioxylon*, *Cunninghamia*, *Taiwania*, as well as the extinct genera *Cupressospermum* and *Quasisequoia* (Table 2). These were the dominant trees responsible for peat/brown coal formation.

Rediscovery of the original preparation of *Glyptostrobus tener* Kraus, the basionym for *Glyptostroboxylon tenerum*, enabled a detailed re-assessment of this taxon and formulation of an emended diagnosis for the genus *Glyptostroboxylon* (Dolezych & Van der Burgh, 2004). Wood-analytical analysis from Lusatia also led to an emended diagnosis for *Cupressinoxylon* (Dolezych, 2005). The original description of the morphogenus by Goeppert (1850, pp. 196–200) is too general and can be applied to very different types of fossil wood. Furthermore, Lusatian materials justified the establishment of *Quasisequoioxylon* (Dolezych, 2005), a new morphogenus considered to constitute the wood of the extinct cupressaceous genus *Quasisequoia*. Wood identified as *Juniperoxylon pachyderma* ex parte is likely to represent the extinct genus *Cupressospermum*.

It was possible to recognize differences in the composition of various plant assemblages of the bog in the xylotomic inventory. This succession, taking place in several facies stages, is reflected in wood content: from an eutrophic stage with *Taxodioxylon taxodii*, *Glyptostroboxylon rudolphii,* and *Juniperoxylon pachyderma,* via the mesotrophic succession with *Taxodioxylon gypsaceum*, *T. germanicum*, *Glyptostroboxylon tenerum,* and *Cupressinoxylon cupressoides,* to the oligotroph extremely poor in nutrients facies with, e.g., *Taxodioxylon cryptomerioides*.

A proposal for a new, more precise diagnosis for *Taxodioxylon* is given. Furthermore, it is suggested to conserve the name *Taxodioxylon* sensu Gothan against the *Taxodioxylon* Hartig with a conserved type from Lusatian Tertiary material.

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