First wood with anatomically preserved details from the Middle Eocene oilshale of Messel (Hesse, Germany)

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ABSTRACT. For the first time fragments of a lignitic trunk were saved from the Middle Eocene organic-rich clay ("oilshale") of Messel near Darmstadt (Hesse, Germany). The organic material of the trunk is highly compressed but still showing some details under SEM. The matrix of the wood is indistinguishably collapsed, but the rays are three-dimensionally preserved and clearly showing disjunctive cell walls of the ray parenchyma. This wood-anatomical character is today rare and restricted to some genera of few families of angiosperms. The fossil wood proved to be most similar to the conditions in an extant species of *Buxus* (Buxaceae). This is probably the oldest record of the genus from macroscopic remains.

KEY WORDS: fossil wood, disjunctive cell walls, ray parenchyma, Buxus, Buxaceae, Middle Eocene, Messel, Germany

INTRODUCTION

The organic-rich clay ("oilshale") of Messel near Darmstadt (Hesse, Germany) was mined for almost a century until commercial activities ceased in 1972 and exploitation for scientific purposes increased exponentially (Schaal & Schneider 1995, Klausewitz 2000). The respective pit is now a famous locality for a wide range of vertebrates, plants and insects which was consequently declared as World Heritage Site by UNESCO in 1995 (Schaal 1996). According to the occurrence of stratigraphically significant vertebrates (Franzen & Haubold 1986) and confirmed by palynological data (Thiele-Pfeiffer 1988), the oilshale is of lower Middle Eocene age (Lower Geiseltalian; Franzen & Haubold 1986). It is filling the largest of several more or less contemporaneous isolated structures of tectonic and/or volcanic origin northeast of Darmstadt (Hessisches Landesamt für Bodenforschung 1999).

Each of the different modes of preservation known for fossil wood requires appropriate methods for preparation and study (e. g. Kräusel 1950, several papers in Jones & Rowe 1999). Most studies of fossil wood are traditionally devoted to permineralized material which is studied in thin sections, acetate peels or polished slabs depending on the mineral(s) forming the matrix. Another kind of preservation in wood is charcoalification. Because of its fragility and intransparency microscopic study of charcoal for a long time was difficult. But fossil charcoal considerably gained importance in palaeobotanical studies when scanning electron microscopy (SEM) became available as a routine tool. Lignitic wood sometimes also preserves characters of systematic significance and may be studied either by thin sectioning or SEM.

Permineralized material was obviously not yet recovered from the oilshale of Messel. Few fragments existing in old collections are most probably erroneously labelled "Messel", but have possibly been derived from "Grube Prinz von Hessen", another nearby isolated occurrence of Middle Eocene sediments including browncoal and oilshale with intercalated quartzitic horizons containing silicified plant remains (Müller-Stoll 1935). Previously there were only few oral records of tree-trunks which had been noted in the oilshale of Messel but obviously no material was preserved in any of the public collections. The present paper is dealing with the first reliable evidence of wood anatomical structures from the Middle Eocene oilshale of Messel.

THE PLANT TAPHOCOENOSE OF MESSEL

The Middle Eocene plant taphocoenose of Messel is known for a long time and has been studied in considerable detail (Schaarschmidt 1988). The composition of the association is influenced by a number of taphonomic factors, including filtering effects of marginal herbaceous and aquatic vegetation. There are dispersed pollen and spores (Thiele-Pfeiffer 1987), numerous leaves (Engelhardt 1922, Sturm 1971, Wilde 1989) and fruits/seeds (Collinson 1988, Schaarschmidt 1988), a considerable number of flowers (Schaarschmidt 1984, 1988), and few fragments of wood.

One of the factors causing the rarity of wood in the oilshale surely was intense degradation of terrestrial organic material under a paratropical climate. This is nicely reflected in the preponderance of structureless matrix in almost contemporaneous coals of central Germany which is most probably mainly representing degraded woody material (W. Riegel, pers. comm. 2000). Rapid degradation was primarily limiting the availability of woody material for potential transport. On the other hand, transport of logs and larger wood fragments into the Messel-lake was prevented by a fringing belt of herbaceous and aquatic vegetation which was favored by an inconspicuous relief. This is additionally supported by the taphoflora of the slightly younger Eckfeld maar which is in contrary comprising a lot of woody material but few evidence of a marginal herbaceous vegetation due to the instability of comparatively steep slopes (Wilde & Frankenhäuser 1998).

MATERIAL AND METHODS

The material for the present study is derived from a compressed trunk (SMB ME 14229) which was discovered in 1999. Incomplete homogenisation of the wood was indicated by a fibrous structure on broken fragments which could be observed by naked eyes. One of the larger pieces recovered from the field was therefore air-dried in the laboratory while the remaining material is routinely preserved and stored by immersion in glycerol. As expected the wood disintegrated into fragments of cm-size upon drying. A selection of those fragments was manually split or broken to reveal surfaces approximately representing the three directions conventionally needed for wood anatomical studies. They were mounted on stubs accordingly, sputter coated with Au/Pd, and studied by SEM.

DESCRIPTION

The originally preserved length of the trunk which was compressed with diagenetic settling of the enclosing sediment is unknown. The fragments at hand are representing only a part of it which is less than one meter in length, about 16 cm wide, and 5 cm thick. The cellular framework of the wood is in fact incompletely compressed (Pl. 1 figs 1, 3) and only in places incipiently homogenized (Pl. 1 fig. 2). Most prominent in more or less tangential view are homogeneous parenchymatous rays interspersed in a matrix of almost completely and indistinguishably collapsed vertical elements like wood parenchyma, fibres and potential vessels (Pl. 1 figs 3, 4) Because of the collapsed matrix the rays appear quite close to each other (Pl. 1 fig. 3). Individual rays are up to about 10 cells high (Pl. 1 figs 3, 5) and 1-2 (sometimes 3) cells wide with a diameter of the respective cells of about 12-20 µm (Pl. 1 figs 3, 4). Following Record (1934: p. 15, fig. 6), the cell walls of the ray parenchyma are disjunctive (="partially disjoined but with contacts maintained through tubular or complex wall processes"; Wheeler et al. 1989: p. 294, fig. 133) (see Pl. 1 figs 6-8 of the present paper).

INTERPRETATION

The prominent rays of the present material (Pl. 1 fig. 3) immediately indicate angiospermous affinities. Most distinctive are the disjunctive cell walls of the ray parenchyma (Pl. 1 figs 7, 8) which have previously only once been found in fossil wood (Selmeier 1998). According to Wheeler et al. (1989: p. 294) they are today only known from certain species of the Apocynaceae, Buxaceae, Euphorbiaceae, Malpighiaceae and Rubiaceae. A combination of

disjunctive cell walls of the ray parenchyma with homogeneous rays up to about 10 cells high and 1-2 (rarely 3) cells wide, and a diameter of the individual ray cells of about 12–20 µm as observed in the fossil material is restricted to some species of Aspidosperma C. Martius & Zucc., Geissospermum Allemao (both Apocynaceae) and Buxus L. (Buxaceae) (Metcalfe & Chalk 1950). Disjunctive cell walls of the ray parenchyma can not be confirmed for those species of Aspidosperma which were studied for comparison by the second author. (A. excelsum Benth., A. macrocarpum Mart., A. olivaceum Muell. Arg., A. polyneuron Muell. Arg., A. quebracho-blanco Schlecht.), and Geissospermum was not represented in the comparative collections at hand. Buxus sempervirens L. and B. macowani Oliv. clearly showed disjunctive cell walls of the ray parenchyma which turned out to be quite similar to those of the fossil material in the latter species. Further species of *Buxus* (*B. acuminata* (Griseb.) Muell. Arg., B. aneura Urb., B. brevipes (Muell. Arg.) Urb., B. crassifoila (Britt.) Urb., B. ekmannii Urb., B. foliosa (Britt.) Urb., B. glomerata Muell. Arg., B. gonoclada Muell. Arg., B. marginalis (Britt.) Urb., B. muelleriana Urb., B. shaferi (Britt.) Urb., B. wrightii Muell. Arg.) did not show disjunctive cell walls of the ray parenchyma.

All of the families in which disjunctive cell walls of the ray parenchyma are known to occur have hitherto no unequivocal record from the Middle Eocene of Messel. None of them has been recognized in the pollen flora (Thiele-Pfeiffer 1988). Engelhardt (1922) described several species of Apocynaceae, Malpighiaceae and Rubiaceae from leaves, but like most of his leaf determinations they are far from being reliable. Apocynaceous affinities of those leaves which were later assigned or compared to species of Apocynophyllum Heer have not been proven (Wilde 1989). Euphorbiaceae and Malpighiaceae have been mentioned in a preliminary report of the fruits/seeds from Messel by Collinson (1988) with one species each. The four-winged fruits tentatively determined as Tetrapterys Cav. (Malpighiaceae) have later been assigned to an extinct genus of Juglandaceae (Cruciptera Manchester; Manchester et al. 1994), and the affinities of the potential euphorbiaceous fruits still need to be confirmed by detailed studies (repeated pers. comm. by M. Collinson and K. Goth).

CONCLUSIONS

The present study is nicely showing the potential for the preservation of wood anatomical structures even in considerably compressed material without permineralisation. It may easily be prepared for SEM-studies by controlled fracturing of dried fragments. As evident from the present example such material may even add new taxa to the taphoflora. Therefore more attention should be paid to wood fragments from the oilshale of Messel and at least any large trunk should be checked for the preservation of systematically significant structures.

The Buxaceae have a long fossil record starting with flowers from the mid-Cretaceous Potomac-Flora of eastern North America showing clear affinities to the family (Drinnan et al. 1991). Dispersed pollen which is similar to pollen of some species of extant Buxus is occuring almost contemporaneously on the Southern Hemisphere (Hexaporotricolpites Boltenhagen; Drinnan et al. 1991). Later, Buxus is well documented by dispersed pollen since the Lower Eocene (Bessedik 1983). Leaves of Buxus have been described repeatedly from the Miocene and Pliocene of Europe and Asia (e.g. Straus 1969, Givulescu 1971, Uemura 1979, Kvaček et al. 1982). The present trunk from Messel may thus represent the oldest macro-record of the genus.

Today *Buxus* is preferrably growing under more or less equable tropical to warm and mild temperate (including mediterraneantype) climates (Kvaček et al. 1982). It is distributed in a belt stretching from East-Asia to the Mediterranean (with northernmost populations in southern England) and Central America as well as in East and southern Afrika (e.g. Köhler & Brückner 1989, 1990). Present distribution and climatic requirements of the genus are therefore well in accordance with *Buxus* occuring in the Middle Eocene of Messel under paratropical conditions as suggested from the respective taphocoenosis by e.g. Wilde (1989).

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PLATE

Plate 1

Details of a lignitic trunk from the Middle Eocene "oilshale" of Messel (cf. Buxus sp., Buxaceae), SEM

- 1. Fragment of heavily compressed wood with collapsed rays and an interspersed network of homogenized layers corresponding to the matrix of vertical elements. Tangential section; scale 200 μm
- 2. Detail from fig. 1 showing almost homogenized layers between collapsed ray structures; scale 100 μm
- 3. Slightly oblique tangential section of a better preserved wood fragment with ray structures separated by layers of collapsed tissue; scale 200 μm
- 4. Detail from fig. 3 showing details of the rays in cross section and fibrous layers representing the collapsed matrix of vertical structures; scale 50 μm
- 5. Radial section showing several rays, overview; scale 200 μm
- 6. Part of the ray parenchyma in lateral view (corresponding to a radial section); scale 50 μ m
- 7. Ray parenchyma with disjunctive cell walls; scale $50 \ \mu m$
- 8. Detail of the ray parenchyma showing a disjunctive cell wall with connecting projections; scale 10 µm



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