Anatomy and taphonomy of a coniferous wood from the Zechstein (Upper Permian) of NW-Hesse (Germany)

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ABSTRACT
The anatomy of a coniferous wood, originating from a small trunk or a branch, from the Zechstein (Upper Permian) of NW-Hesse (Germany) is described. Though permineralized wood has been known from this locality at least since the end of the 18th century, this is the first specimen of trunk or branch wood described in anatomical detail from this locality. The wood has no visible growth-rings, rays are rare. Tracheids show uniseriate bordered pits of the "mixed" type, which are often contiguous and sometimes spaced more than one pit diameter apart. Cross-field pitting is probably araucarioid. It shows great similarities to the protopinacean form-genus *Brachyoxylon* Hollick & Jeffrey. However, due to the poor preservation of the cross-field pitting, a definite determination of this wood is not possible. Because of the lack of sterile foliage in organic connection, this specimen could not be assigned to any conifer taxon known from the Zechstein. The poor preservation of this specimen is probably due to desiccation, followed by mechanical stress during transport and microbiological decay. The latter process may have also played an important role for the permineralization of parts of this specimen with pyrite/chalcopyrite. Similar microbiological processes may have been involved during the permineralization of other plant material known from this locality (the so-called "Frankenberger-Kornähren").

KEY WORDS
Upper Permian,
Zechstein,
permineralization,
pyritization,
wood anatomy,
taphonomy.

RÉSUMÉ

Anatomie et taphonomie d'un bois de conifère du Zechstein (Permien supérieur) du NW de la Hesse (Allemagne).

L'anatomie d'un bois de conifère, d'après de petits fragments de tronc ou de branche, du Zechstein (Permien supérieur) du NW de la Hesse (Allemagne) est décrite. Bien que du bois minéralisé soit connu de cette localité au moins depuis la fin du XVIII[e] siècle, c'est la première analyse anatomique précise de bois de tronc ou de branche de cette localité. Le bois ne présente pas d'anneaux de croissance, les rayons sont rares. Les trachéides sont entourées de ponctuations unisériées de type mixte, qui sont souvent proches et parfois distantes d'une valeur supérieure à leur diamètre. Les ponctuations des champs de croisement sont probalement de type araucarioide. Il présente de grandes similitudes avec les formes protopinacées comme le genre *Brachyoxylon* Hollick & Jeffrey. Cependant, à cause de la mauvaise conservation de ces ponctuations de champs de croisement, il n'est pas possible de déterminer ce bois avec certitude. À cause de l'absence de feuillage stérile en position anatomique, ce spécimen ne peut pas être rapporté à un quelconque taxon de conifère connu dans le Zechstein. Ce sont la desiccation et les stress mécaniques associés pendant le transport ainsi que la dégradation microbiologique qui sont responsables du mauvais état de conservation de ce spécimen. Le rôle joué par ce dernier processus est important pour la minéralisation de certaines régions du spécimen par de la pyrite et de la chalcopyrite. Des processus microbiologiques comparables ont pu intervenir pendant la phase de minéralisation d'autres plantes connues dans cette localité (« Frankenberger-Kornähren »).

MOTS CLÉS
Permien supérieur, Zechstein, minéralisation, pyritisation, anatomie du bois, taphonomie.

INTRODUCTION

During the Upper Permian most terrestrial ecosystems on the Northern Hemisphere were dominated by conifers (e.g., Kerp 1996, 2000). Unfortunately, there are only a few plant bearing localities from this period, especially in the euramerican floral-province. In Northern America there are no plant bearing localities from this period at all, and in Europe plant bearing localities are restricted to the fully marine English and German Kupferschiefer (e.g., Weigelt 1928; Stoneley 1956, 1958; Schweitzer 1962, 1968, 1986; Ullrich 1964), some marginal-marine localities (e.g., Ullmann 1803; Bronn 1828; Göppert 1850; Poort & Kerp 1990), and a few terrestrial localities in the southern alps (e.g., Clement-Westerhoff 1984, 1987; Poort & Kerp 1990; Visscher *et al.* 2001), as well as in Thuringia (e.g., Ullrich 1964; Uhl & Kerp 2002a).

A number of plant bearing deposits from the Upper Permian Zechstein, which have been known for more than 200 years (e.g., Waldin 1778; Ullmann 1803), can be found near Frankenberg in NW-Hesse (Germany). In this area the Zechstein is developed in a marginal marine facies and these sediments, often containing abundant plant remains, have been deposited in an embayment of the Central European Zechstein Sea (e.g., Paul 1982; Kulick & Richter-Bernburg 1987). The first publications on fossil plants from this area appeared in the late 18th and early 19th centuries (e.g., Waldin 1778; Ullmann 1803) and even these early authors mentioned the occurrence of abundant permineralized wood remains. In subsequent years, several authors investigated individual taxa from this area (e.g., Bronn 1828; Althaus 1846; Göppert 1850, 1864-1865; Gothan & Nagalhard 1922; Florin 1931; Poort & Kerp 1990), but only a few included anatomically preserved plant remains, which occur frequently at the locality Frankenberg-Geismar (Solms-Laubach 1884;

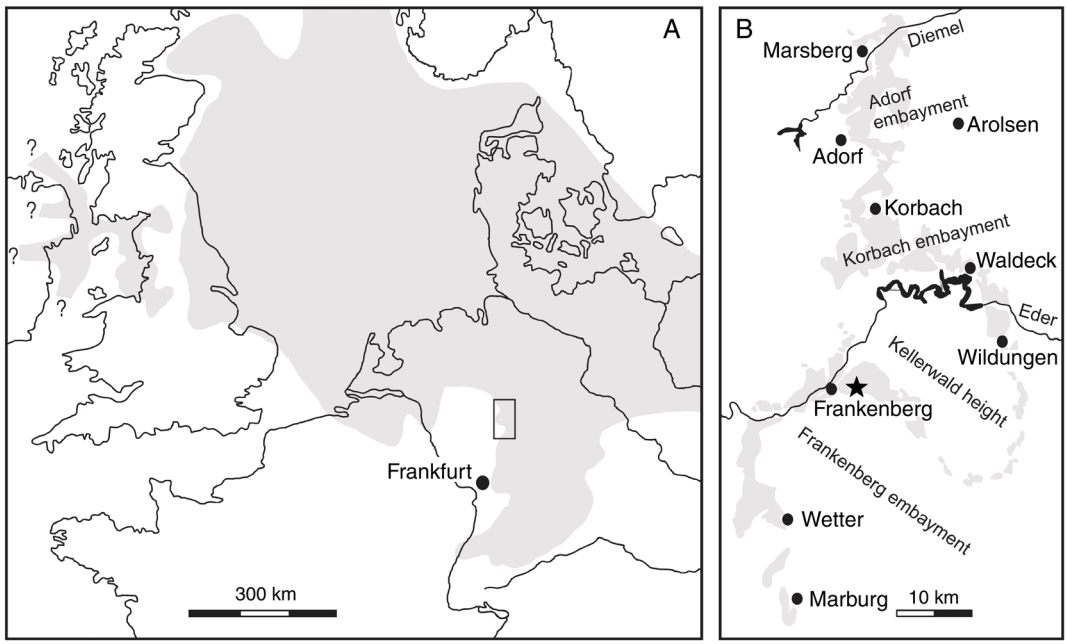

FIG. 1. — Map indicating the position of the locality Frankenberg-Geismar; **A**, schematic map of the geographic extent of the Zechstein Sea (in grey) in Western and Central Europe; **B**, map indicating the outcrops of Zechstein-sediments (grey) in NW-Hesse and the locality Frankenberg-Geismar (★).

Lemoigne & Schaarschmidt 1968; Uhl & Kerp 2002b). Most of these particular plant remains are permineralized with pyrite and/or chalcopyrite (e.g., Uhl & Kerp 2002b) and are widely known among palaeobotanists as "Frankenberger Kornähren". However, the degree to which the internal anatomy of these plant remains is preserved varies greatly, and in most specimens only small parts of the internal tissues have been preserved (e.g., Solms-Laubach 1884; Uhl & Kerp 2002b). Although relatively large wood fragments (up to 10 cm in diameter and more than 20 cm long) are very common at the locality Frankenberg-Geismar (e.g., Ullmann 1803), this material has not attracted much scientific interest yet. Solms-Laubach (1884) described some thin sections from three unidentified wood specimens from this locality, but only very small parts of the internal anatomy had been preserved in these specimens. Therefore no detailed descriptions of these woods have been given by this author. The most complete anatomically preserved specimen described so far is a fragment of a woody shoot of probably ultimate order, belonging to the conifer *Ullmannia bronnii* Göppert (Lemoigne & Schaarschmidt 1968).

Here a relatively large specimen of partly pyritized wood from this locality is described. Additionally some taphonomical observations are presented, which shed some light on the permineralization processes involved in the formation of the pyritized plant remains from the locality Frankenberg-Geismar ("Frankenberger Kornähren").

MATERIAL AND METHODS

The specimen described here was collected during field work in summer 2000, at an old spoil tip of a former copper mine, about 1.5 km SW from Frankenberg-Geismar in NW-Hesse (Fig. 1). The fragment (*c.* 7 × 3 × 2 cm) seems to belong to the central part of a larger twig or smaller branch. According to Kulick (1987), the

sediments belong to the top part of Zechstein Z1, transitional zone to Zechstein Z2, the so-called "Geismarer Kupferletten-Flöz". The sediments, which yield abundant plant remains in different modes of preservation (Uhl & Kerp 2002b), represent a marginal marine facies (Kulick 1987). The geology and stratigraphy of this area were discussed in detail by Richter-Bernburg (1955), Sauer (1964), Kulick & Richter-Bernburg (1987) and Kulick (1987). Palaeogeographically, the Frankenberg area represents an embayment of the Central European Zechstein Basin (Fig. 1). A review of the facies development of this and adjacent embayments along the margins of the Central European Zechstein Basin was given by Paul (1982).

The surface of the specimen described here was originally completely covered with marly sediments, which were partly removed with dilluted acetic acid (10-25%). After acid treatment, the specimen was photographed with a Nikon F-90 camera on AGFAPAN 25 film. The specimen was subsequently embedded in resin (Castolite, Buehler) to stabilize it during thin-sectioning. Thin sections of the specimen here described are stored in the collection of the Forschungsstelle für Paläobotanik, Universität Münster; accession-numbers Pb-WB-H-1/a-f. They were photographed with the aid of a Wild M400 Macrobinocular (reflecting light) and a Leitz Diaplan Microscope (transmitting light) on AGFAPAN 25 film.

SYSTEMATICS

Genus *Brachyoxylon* Hollick & Jeffrey, 1909

?***Brachyoxylon*** sp.
(Figs 2; 3; 4A-E)

DESCRIPTION

A fragment of partly pyritized wood, possibly originating from a small trunk or a branch, without cortex. In radial longitudinal view tracheids are 20-30 µm wide. Tracheids exhibit uniseriate bordered pits on the radial walls. Pits circular (to elliptical) (18-25 µm diameter) with circular or oval apertures and often contiguous (then flattened) and sometimes spaced more than one pit diameter apart. In some areas, tracheids occur which seem to have spirally thickened cell walls. Rays very scarce and composed of parenchymatous cells, 25-35 µm long and 20-30(50) µm high. Rays uniseriate and 2-4 cells high. Cross-field pitting very badly preserved, but probably araucarioid consisting of 1-4(?) alternately arranged circular pits per field. No growth rings visible. Pith of a twig or small branch(?) 200-250 µm wide, consisting of parenchymatous cells, 20-80 µm wide. In an area, probably representing a small branch or a leaf trace, tracheids and rays are arranged irregularly. In this area, bordered pits occur on tangential tracheid walls and rays can be seen in tangential view.

REMARKS

This is the first record of a wood with a "mixed" type of pitting (araucarioid and abietoid) from the Upper Permian of the euramerican floral province. This type of pitting is diagnostic of woods of the Protopinaceae (e.g., Vogellehner 1967, 1968; Müller-Stoll & Schultze-Motel 1989), a phylogenetically artificial group with mainly Mesozoic occurrence. Taken all characters together, the wood described here shows great similarities to the protopinacean form-genus *Brachyoxylon* (cf. Bamford & Philippe 2001). However, an important character for such an assignation is the type of cross-field pitting (cf. Bamford & Philippe 2001). Although the cross-field pitting is very poorly preserved in this specimen it seems to be of the araucarioid type. Therefore this wood is here only provisionally identified as ?*Brachyoxylon* sp.

Despite the type of pitting on the radial tracheid walls, the wood described here shows great similarities with the wood of the conifer *Pseudovoltzia liebeana* (Geinitz) Florin, which has been described by Schweitzer (1962) based on a 2 mm thick axis from the Zechstein of the Lower Rhine (W-Germany). Unfortunately, Schweitzer (1962) gave no quantitative data concerning the measurement of the individual anatomical details. The only measurements given by Schweitzer (1963)

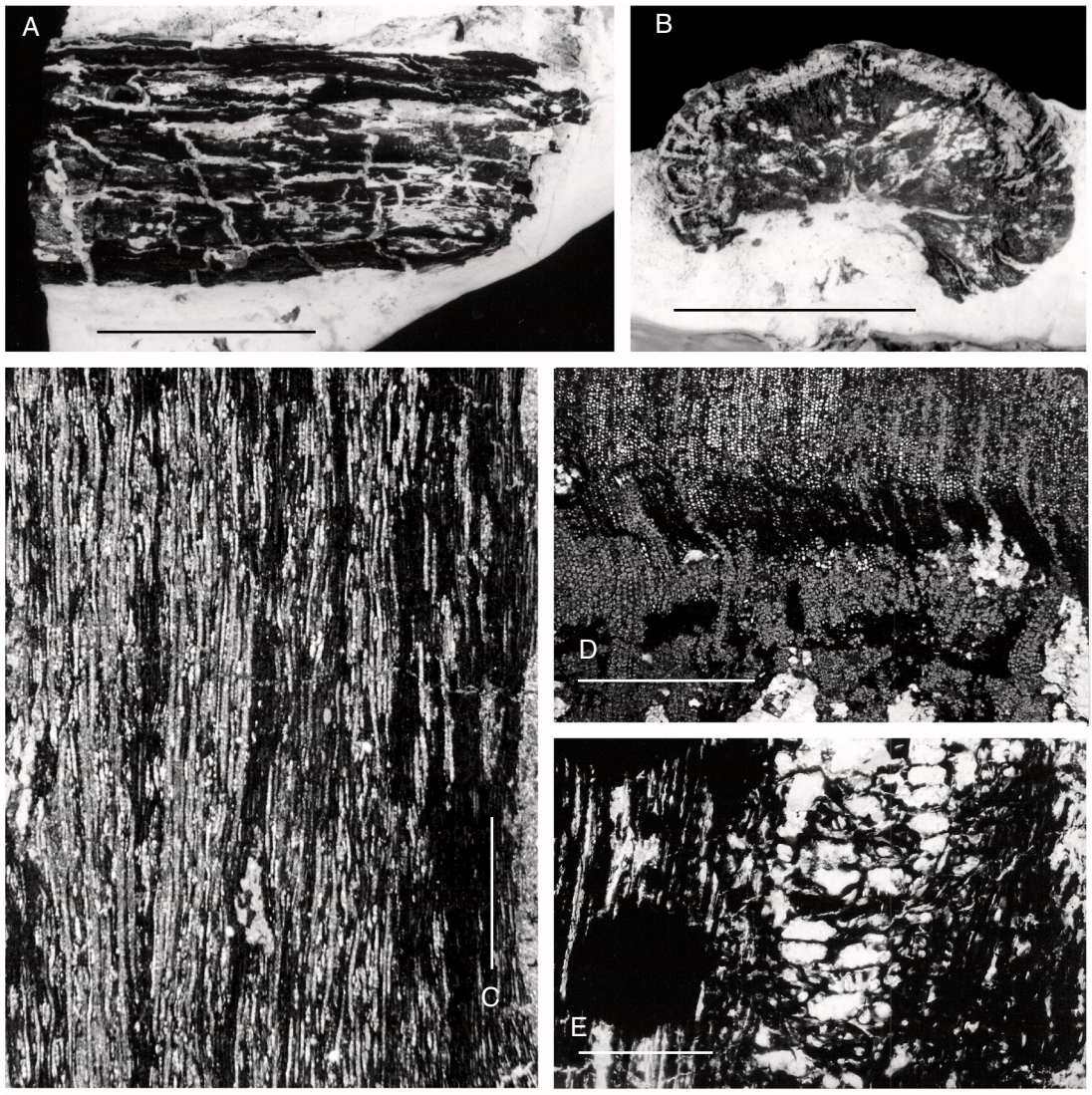

FIG. 2. — ?*Brachyoxylon* sp. from the Zechstein (Upper Permian) of Frankenberg-Geismar (NW-Hesse); **A**, complete specimen in tangential view; **B**, complete specimen in perpendicular view; **C**, radial section, showing pyritized and non-pyritized areas with anatomical preservation (Pb-WB-H-1/d); **D**, cross-section, showing pyritized and non-pyritized areas with anatomical preservation (Pb-WB-H-1/a); **E**, radial section, showing details of the central pith (Pb-WB-H-1/b). Scale bars: A, 3 cm; B, 2 cm; C, D, 1 mm; E, 200 µm.

come from a cone axis of *Pseudovoltzia liebeana* and can probably not be compared with wood originating from a stem or even large twig. However, Schweitzer (1962) could not find any significant differences between the wood of this taxon and other Upper Permian conifer taxa from the same area (see also Table 1). Due to the poor preservation and scarcity of fossil woods from the Zechstein of the Lower Rhine area, Schweitzer (1962) could not describe these woods in great detail and several important characteristics are still not known for most of the woods described by this author (Table 1). Therefore it is not yet possible to assign the wood

TABLE 1. — Comparison of some anatomical characteristics of woods from the Zechstein (Upper Permian).

	?Brachyoxylon sp.	*Ullmannia bronnii* Göppert	*Ullmannia bronnii* Göppert	*Ullmannia frumentaria* (Schlotheim) Göppert	*Pseudovoltzia liebeana* (Geinitz) Florin	*Quadrocladus solmsii* (Gothan & Nagalhard) Schweitzer
Author(s)	This work	Lemoigne & Schaarschmidt 1968	Schweitzer 1962	Schweitzer 1962	Schweitzer 1962, 1963	Schweitzer 1962
Source locality	Frankenberg-Geismar, NW-Hesse	Frankenberg-Geismar, NW-Hesse	Lower Rhine, North Rhine Westfalia	Lower Rhine, North Rhine Westfalia	Lower Rhine, North Rhine Westfalia	Lower Rhine, North Rhine Westfalia
Growth rings	No	Yes, inconspicuous	No	Yes, conspicuous	No	Yes, conspicuous
Tracheid diameter	20-30 µm	Wide	-	-	-	-
Tracheid radial pitting	Uniseriate, protopinoid	Uni- and partly biseriate, araucarioid	Uniseriate	Uniseriate	Uniseriate	Uniseriate
Covering of pitting	Complete	Complete	Complete	Complete	Complete	Complete
Pit aperture	Circular	Circular	Circular to elliptical	Circular to elliptical	Circular to elliptical	Circular to elliptical
Cross field pits	1-4 (araucarioid?)	2-4-6 araucarioid	-	-	-	-
Ray width (cells)	Uniseriate	Uniseriate	Uniseriate	Uniseriate	Uniseriate	Uniseriate
Ray height (cells)	2-4	1-2-5-10	-	-	2-3-6	-
Ray frequency	Rare	Frequent	-	-	-	-
Pith	Parenchymatous	-	-	Parenchymatous	Parenchymatous	-

described here to any of the known conifer taxa from the Zechstein. Lemoigne & Schaarschmidt (1968) were able to give a more detailed description of the wood of the conifer *Ulmannia bronnii* Göppert than Schweitzer (1962). Their description, which was based on the wood of a small, partly pyritized shoot with attached needles from Frankenberg-Geismar, does not match this wood. In contrast to the wood described here, these authors observed abundant rays and they reported that the always contiguous, bordered pits were not only arranged uniseriately, but also biseriately. Though we cannot exclude that these differences are due to positional variations within a single plant, a unification of the wood described here with this taxon is absolutely not justified. However, some details (scarcity of rays, dimensions of tracheids, uniseriate arrangement of pits) of this wood are similar to "woodtype 5", described by Uhl & Kerp (2003) based on charcoalified material from the same locality. However, both modes of preservation differ too much to allow a certain unification of both types of wood.

TAPHONOMICAL OBSERVATIONS AND INTERPRETATIONS

Like many other plant remains from the locality Frankenberg-Geismar described by previous authors (e.g., Göppert 1850; Solms-Laubach 1884; Lemoigne & Schaarschmidt 1968; Poort & Kerp 1990), this specimen is permineralized with pyrite/chalcopyrite. However, when we have

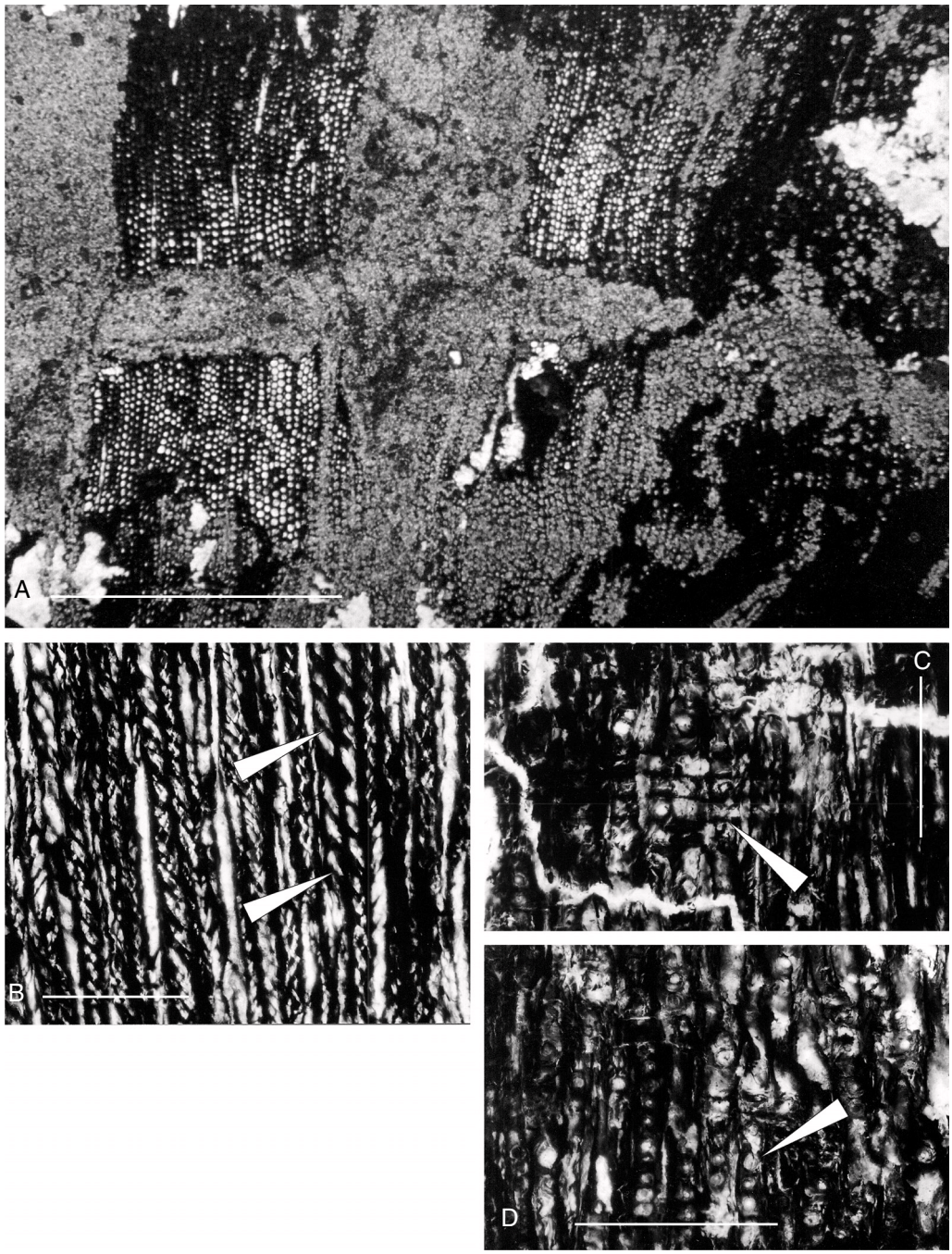

FIG. 3. — ?*Brachyoxylon* sp. from the Zechstein (Upper Permian) of Frankenberg-Geismar (NW-Hesse); **A**, cross-section, showing cracks filled with pyrite (Pb-WB-H-1/a); **B**, radial section, showing "spirally thickened" (probably checked during desiccation) tracheid walls (arrows) (Pb-WB-H-1/d); **C**, radial section, showing remains of a ray (arrow) with very poorly preserved cross-field pitting (Pb-WB-H-1/d); **D**, radial section, showing uniseriate, circular bordered pits (arrow) (Pb-WB-H-1/d). Scale bars: A, 1 mm; B, 150 µm; C, D, 100 µm.

a closer look at this specimen we can see, that not the entire specimen is permineralized, but only some areas within the wood (e.g., Figs 2C, D; 3A). Pyritization of plant remains is generally mediated by microbial action under anaerobic conditions (e.g., Grimes *et al.* 2001, 2002) and it is very likely that also in this case bacterial decay has played an important role during pyritization.
But how can the observed pyritization patterns be explained? There are obviously some areas which were more affected by this permineralization process than others. On the other hand, the overall preservation of anatomical details is not very good (e.g., Figs 2E; 3B, C; 4A-C), probably indicating microbial decay also in parts which were not pyritized. A closer inspection of the specimen reveals that there are numerous cracks within this specimen which are filled with sediment (Fig. 4D, E) or pyrite (Figs 2D; 3A). Especially in the marginal areas, the wood is torn apart and sometimes individual tracheid rows have been partly separated from the wood (Fig. 4D). These observations may indicate that this specimen has experienced severe desiccation, sometime prior to burial (e.g., Schweingruber 2001). Such an assumption also facilitates an interpretation of the observation, that in some areas, tracheids occur which seem to have spirally thickened cell walls. These supposed spiral thickenings may be artifacts, caused by diagonal checking of the cell walls during desiccation (cf. Jones 1993). The same phenomenon can be observed in some charcoals from the same locality (Fig. 4F, G), also indicating desication of these woods prior to charring.
Microbial activities depend on the presence of water and therefore it is not very likely that massive decay occurred during this phase of the taphonomic history of this specimen. Due to some unknown process (most likely involving fluvial transport), the specimen must then have been transported in the marginal marine area, where it has been buried. It can be assumed that the wood experienced at least some mechanical stress during transport. Such stress may have increased the damage already induced by desiccation. Microbial activity may have started (again?) as soon as the (desiccated) wood entered the water column. In this phase the cracks may have acted as important entryways not only for the water, but also for the penetration of microbial organisms. In such a scenario the cracks could have been the initial areas of microbial decay and associated pyritization. This is in accordance with the observation that many of the cracks are filled with pyrite. Though it is difficult to prove in every single case (due to the three-dimensional structure of the wood), it is highly probable that all areas with pyritized tissues are in close proximity to such cracks. In some cases, damaged tracheids may act as pathways from the cracks into undamaged areas of the wood, leading to cell lumina filled with pyrite. Microbial decay must have stopped before the cell walls were completely decayed in this areas. As shown by previous authors, the cellulose contents of the cell walls is more easily decayed than the lignin contents (e.g., Kenrick & Edwards 1988), often leading to a permineralization of lignified tissues, with more or less intact cell walls.
The question remains, why some cracks show no sign of pyritization. As demonstrated by Grimes *et al.* (2001) pyritization of plants requires very special conditions and it is very likely that the particular environmental variables involved in this process may vary even within an individual piece of wood, lying on the sediment-surface or being (partly) buried within the sediment.

CONCLUSIONS

Though overall preservation of individual specimens may be unfavourable for taxonomic investigations (Solms-Laubach 1884), the protopinacean wood presented in this study demonstrates that woods from the Zechstein (Upper Permian) of NW-Hesse represent a hitherto largely neglected source of information on Late Palaeozoic terrestrial biodiversity. Knowledge about this diversity is crucial for understanding terrestrial ecosystems from this period, especially in the light of the global mass extinction, which took place at the Permian-Triassic boundary (Erwin 1993).

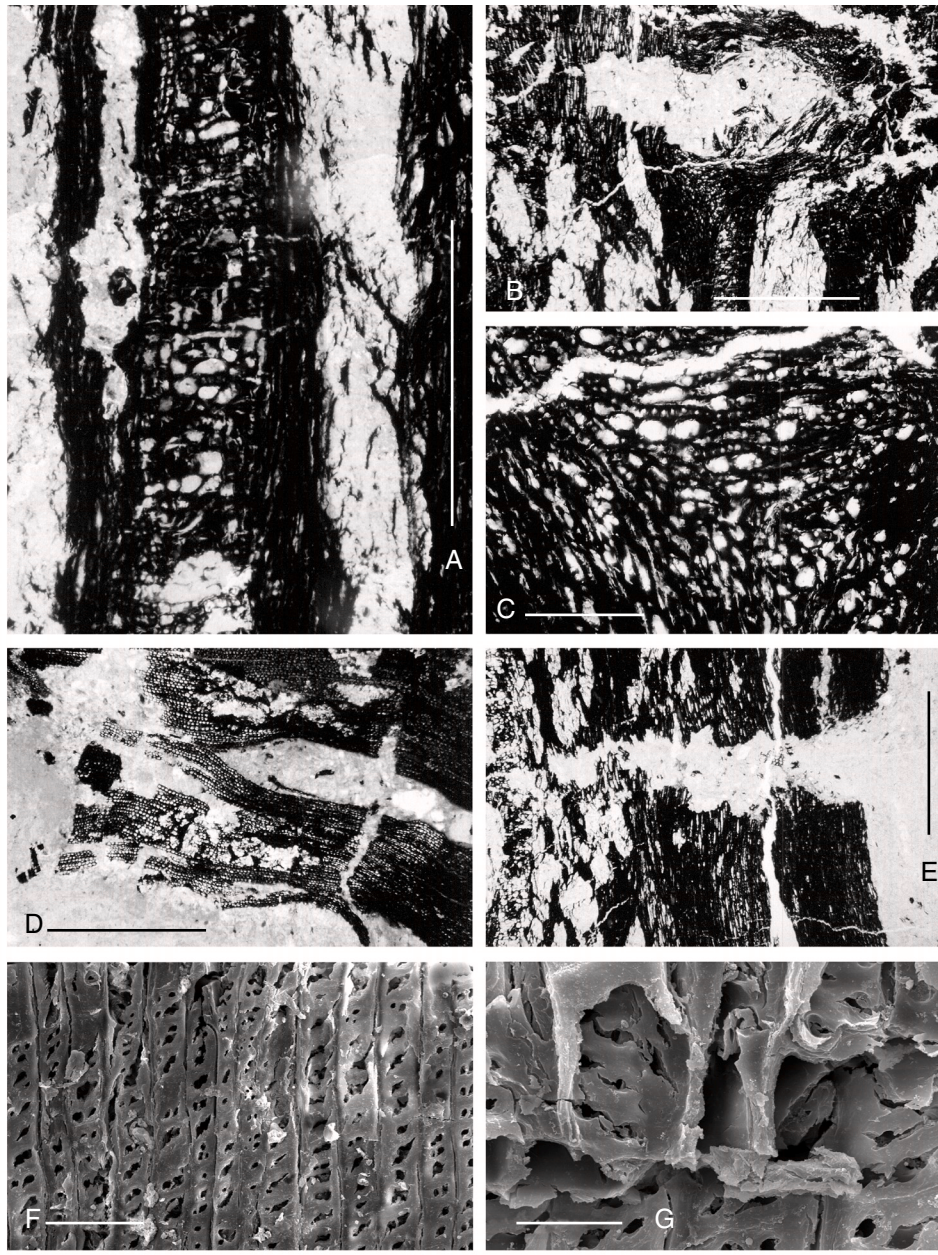

FIG. 4. — **A**-**E**, ?*Brachyoxylon* sp. from the Zechstein (Upper Permian) of Frankenberg-Geismar (NW-Hesse); **A**, radial section, showing the central pith, flanked by cracks filled with sediment (Pb-WB-H-1/b); **B**, radial section, showing remains of a branch(?) (Pb-WB-H-1/b); **C**, detail of B, showing tracheids and rays adjacent to the branch(?) (Pb-WB-H-1/b); **D**, cross-section, showing cracks filled with sediment (Pb-WB-H-1/a); **E**, radial section, showing cracks filled with sediment (Pb-WB-H-1/b); **F**, **G**, charcoal from the Zechstein (Upper Permian) of Frankenberg-Geismar (NW-Hesse), exhibiting checked cell-walls, resulting from desiccation prior to charring. Scale bars: A, 500 µm; B, 1 mm; C, 100 µm; D, E, 1 mm; F, 90 µm; G, 30 µm.

Additional to the information on biodiversity, an analysis of such wood remains can also give new information about local or regional environmental and climatic conditions. Investigations on the less abundant wood remains from the Zechstein of the Lower Rhine (Germany) indicated seasonality (e.g., Schweitzer 1962, 1986). The abundant wood remains from the Zechstein of NW-Hesse have undoubtably a great potential to refine such interpretations which have so far been preliminary due to the small number of woods investigated by Schweitzer (1962, 1986). Further investigations on pyritized woods, as well as other plant remains, from Frankenberg-Geismar may also provide a more solid base to understand the processes involved in the formation of pyritized plant remains from this and other localities.

Acknowledgements
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