

Silicified angiosperm wood from the Middle Miocene of Poland: *Ulmoxylon* in the Neogene cover of the Holy Cross Mountains, southern Poland

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Received 26 April 2012; accepted for publication 29 October 2012

ABSTRACT. In this article silicified trunk fragments originating from the Middle Miocene of the Holy Cross Mountains, Poland, are described. The fossil shows great similarity to the morphospecies *Ulmoxylon marchesonii* Biondi. Characteristic features of this taxon include its ring porous nature, vessel arrangement in tangential or oblique bands, simple perforation plates, spiral thickening in narrow pores, chambered crystalliferous axial parenchyma, uniseriate and multiseriate rays. All available references of petrified elm woods, literature (1842–2008), have been critically reviewed and compared with the anatomical structure of the trunk fragments from Holy Cross Mountains. The present record of 22 silicified specimens is remarkable because up to date, only few samples of angiosperm petrified wood from Poland are identified. The paper gives also an overview of this fossil angiosperm wood record.

KEY WORDS: *Ulmoxylon*, fossil angiosperm wood, wood anatomy, Middle Miocene, Poland

INTRODUCTION

This paper presents the first noted occurrence of a fossil angiosperm wood in the area of Holy Cross Mountains. The study material is also one of a few examples of the presence of angiosperm fossil wood in the area of Poland. The majority of Palaeogene and Neogene xylofloras described so far from this territory contain exclusively gymnosperm species. They are known, first of all, from the Miocene lignites, originating from Turów and Konin brown coal mines (e.g. Zalewska 1953, 1955, Grabowska 1956, Kostyniuk 1967). Gymnosperm woods were also noted from other localities that are comparatively numerous in the area of the whole country. Among these one can recall the presence of fossil wood in Mazovia region (Kostyniuk 1938), Dobrzyń on the Vistula River (Kownas 1951), Gliwice locality (Reyman 1956) as well as in the Krościenko

area (Kostyniuk 1950). The studies concerning fossil wood of gymnosperms dominate also in older scientific literature. They can be found in reports of such authors as Raciborski (1889), Lilpop (1917, 1924), Rubczyńska & Zabłocki (1924) and Zabłocki (1935). Rare descriptions of angiosperm woods appear in the works of Unger, Caspary, Conwentz, Felix and Kräusel. Therefore each described angiosperm wood gives important palaeoxylological information about composition and arrangement of fossil plant assemblages.

Unger was the first author to analyse angiosperm fossil woods from Poland. He described *Betulinium parisiense* Unger, *Fegonium salinarum* Unger, and *Fegonium vasculosum* Unger, all from Wieliczka salt mine (Unger 1849). The latter two taxa were afterwards reclassified as *Plataninium salinarum* (Unger)

Vater and *Plataninium vasculosum* (Unger) Vater, respectively (Vater 1884). Unger (1845) defined also *Charpentiera nivium* Unger from the Galicia region. Similarly, as in the previous cases, the systematic classification of this species was revised by Edwards (1931) and finally the wood was determined as *Dryoxylon nivium* (Unger) Edwards. From the area of Galicia (Winniki village) Unger (1850) distinguished also Miocene wood *Petzholdia polonica* Unger. Moreover, Unger (1850) analysed specimens from Głogów, Zielona Góra, Legnica and Poznań. These fossils were attributed to *Quercinium sabulosum* Unger (Unger 1850).

At a later time, Conwentz (1880) presented fossil wood from Karolin near Sobótka as *Rhizoalnoxylon inclusum* Conwentz. The usage of the prefix *Rhizo-* in the genus name emphasized that this specimen constituted the root. However, the division applied by Conwentz that assumed different prefixes for wood belonging to various organs of the plant, was not widely accepted, because of the difficulty to differentiate these wood types based on its anatomical structure (Seward 1919).

Angiosperm woods from the area of Poland can be also found in few studies of Felix. This author analysed specimens from the area of Kraków. One of them had been initially classified by Felix (1882) as *Betulinium diluviale* (Unger) Felix. This name referred to *Ulmium diluviale* Unger that was thought by Felix to be equivalent to the analysed specimen. As the result of further research, however, the lauraceous affinity of *Ulmium diluviale* was discovered and the wood from Kraków was named as *Betulinium* sp. only (Felix 1883). From Kraków vicinity Felix (1882) described also *Ornoxylon fraxinoides* Felix species, as well as some material of uncertain taxonomical position, defined as *Stephanoxylon dubium* Felix.

A relatively big number of angiosperm woods were presented by Caspary (1888) from the Pomerania and Warmia-Masuria regions. Among analysed material, that was originating from different sites, he distinguished the following species: *Acer borussicum* Caspary, *Juglans triebelii* Caspary, *Laurus biseriata* Caspary, *Laurus triseriata* Caspary, *Platanus borealis* Caspary, *Schinus primaevum* Caspary, and *Magnolia laxa* Caspary. Subsequently, *Schinus primaevum* was reclassified as *Rhamnacinium primaevum* (Caspary)

Felix (Felix 1894), whereas *Magnolia laxa* was finally assigned to *Dryoxylon laxum* (Caspary) Edwards (Edwards 1931).

Also, one of the greatest palaeoxyzilologist, that was Kräusel, studied the fossil wood material from the area of Poland. Kräusel (1920) described from the Miocene of Silesia, three wood taxa belonging to deciduous trees: *Betula* sp. from Węgliniec and Bytom, *Carpinus* sp. from Zgorzelec and *Populus* sp. from Knurów. From Lower Silesia originates also the only one contemporary designation of angiosperm fossil wood. Namely, it is *Quercoxylon* sp. from the Pliocene deposits of Gozdnica region (Pyszyński 1992).

The objective of this paper is to further our understanding of the Miocene arboreal vegetation that grew along or near to the northern margins of the Central Paratethys Sea, by providing detailed anatomical analysis and taxonomic classification of Miocene angiosperm wood from the area of the Holy Cross Mountains.

MATERIAL AND METHODS

Material was gathered in 2006 year by the author and by Jerzy Jędrychowski. Petrified woods were collected from the Włoszczowice site. No other types of fossils were found at this locality (Fig. 1). Włoszczowice village is situated in the southern part of the Holy Cross Mountains. Holy Cross Mountains are one of the oldest mountain ranges in Europe. They were formed during the Caledonian orogenesis and then rejuvenated in the Variscan and Alpine cycles. In this territory layers and fossils of all geological periods are present (Mizerski 2004). Across the area of the sampled locality occur clays, sands and marls of Badenian and Sarmatian age (16.4–11.5 Ma) (Filonowicz 1973). Presumably they were the source rocks for analysed wood. The origin of these deposits is related to the marine transgression of Paratethys Sea (Filonowicz 1973). Paratethys stretched from the region north of the Alps over Central Europe to the Aral Sea in Central Asia. During the Middle Miocene also the southern slopes of the Holy Cross Mountains was flooded by this warm sea of epicontinental characteristics. Central Paratethys had the form of relatively narrow, brackish or freshwater basin which was filled with coarse clastic sediments derived mainly from the emergent front of the Carpathians and from the Holy Cross Mountains (Rögl 1999).

Discussed woods are characterized by a low degree of rounding of the surface and insignificant level of abrasion. This indicates that specimens were not exposed to intense erosion or weathering. Therefore, it should be inferred that the fossils were not transported long distance after their mineralisation. Most probably they were moved by the waters flowing from

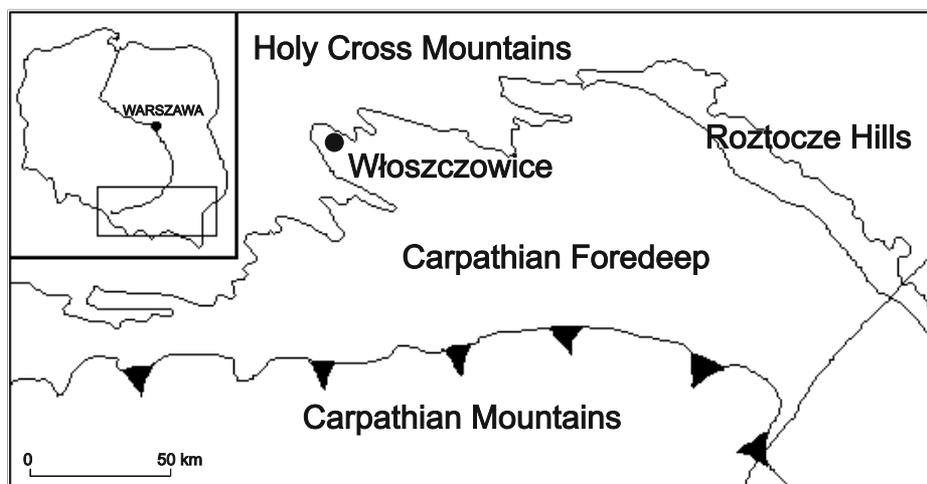


Fig. 1. Map showing location of the Włoszczowice site, and the extent of Middle Miocene (Badenian) transgressive deposits in the northern periphery of Central Paratethys

the neighbouring area and then deposited in a sedimentary basin at the foothill of the mountains.

In total, twenty two specimens of silicified wood were collected from the Włoszczowice site. Fossils were taken from a layer of modern soil. All of the specimens have been found in a small area of about 1000 m². This may suggest that they could be the splinters of one or two mineralized trunks. Fossils are beige and orange in colour. The samples range from 5 to 22 cm in length and from 3 to 9 cm in diameter. The number of existing growth rings within a single trunk fragment varies from 6 to 18 rings. Woods are marked by an excellent state of anatomical preservation. On the basis of sample size and anatomy, ring curvature and the divergence of rays it was determined that these woods are the fragments of large diameter branches or trunks.

All twenty two samples were subjected to anatomical analysis. For this purpose, standard petrographic thin sections were used. They were prepared at the Institute of Applied Geology of the Silesian University of Technology. The thin slides were made in three planes of a trunk, perpendicular to each other: transverse (TS), radial longitudinal (RLS) and tangential longitudinal (TLS). Sectional area of these slides was between 1.9×2.3 cm² and 3.3×4.9 cm². Microscopic observation and photographic documentation of wood were carried out using an Olympus BX51 transmission light microscope. Applied anatomical terminology follows the IAWA recommendation (Wheeler et al. 1989). Samples are housed in the Museum of the Earth (Polish Academy of Science) in Warsaw.

SYSTEMATIC DESCRIPTION

Family: Ulmaceae de Mirbel

Organ genus: *Ulmoxyton* Kaiser

Type species: according to Index Nominum Genericorum not designated

Morphospecies

Ulmoxyton marchesonii Biondi

Fig. 2a–f

- 1981 *Ulmoxyton marchesonii* Biondi, p. 77–91, pl. 1, figs 1–3, pl. 2, figs 1–6, pl. 3, figs 1–5, text-figs 2–4
- 2002 *Ulmoxyton marchesonii* Biondi, Sakala, p. 161–166, fig. 2a–h

Material. Twenty two silicified woods from Włoszczowice site. Specimens are labelled from GS1 to GS22. Description is based on specimen GS1. The slides prepared from this specimen are marked as GS1-C, GS1-R and GS1-T respectively.

Description. Wood ring porous, with 2–3 tangential rows of earlywood pores. Growth rings visible to the naked eye, ring boundaries distinct. Ring width amounts to 1.5–4.4 mm (mean 3.0 mm). Earlywood vessels arranged mostly solitary or in short radial multiples. Latewood vessels grouped in radial multiples and clusters, aligned in tangential or oblique bands (Fig. 2:a). Vessels are round to oval in cross-section. Mean tangential diameters of earlywood vessels vary from 198 μm (standard deviation 31 μm) to 214 μm (standard deviation 31 μm), with a total range of variation of 145–348 μm. All vessels filled with thin-walled tyloses (Fig. 2:b).

Intervessel pits bordered, circular to polygonal in outline, with oval or slit-like apertures, crowded and alternately arranged (Fig. 2:c). Fine spiral thickenings distinctly visible in narrow pores. Perforation plates simple (Fig. 2:e).

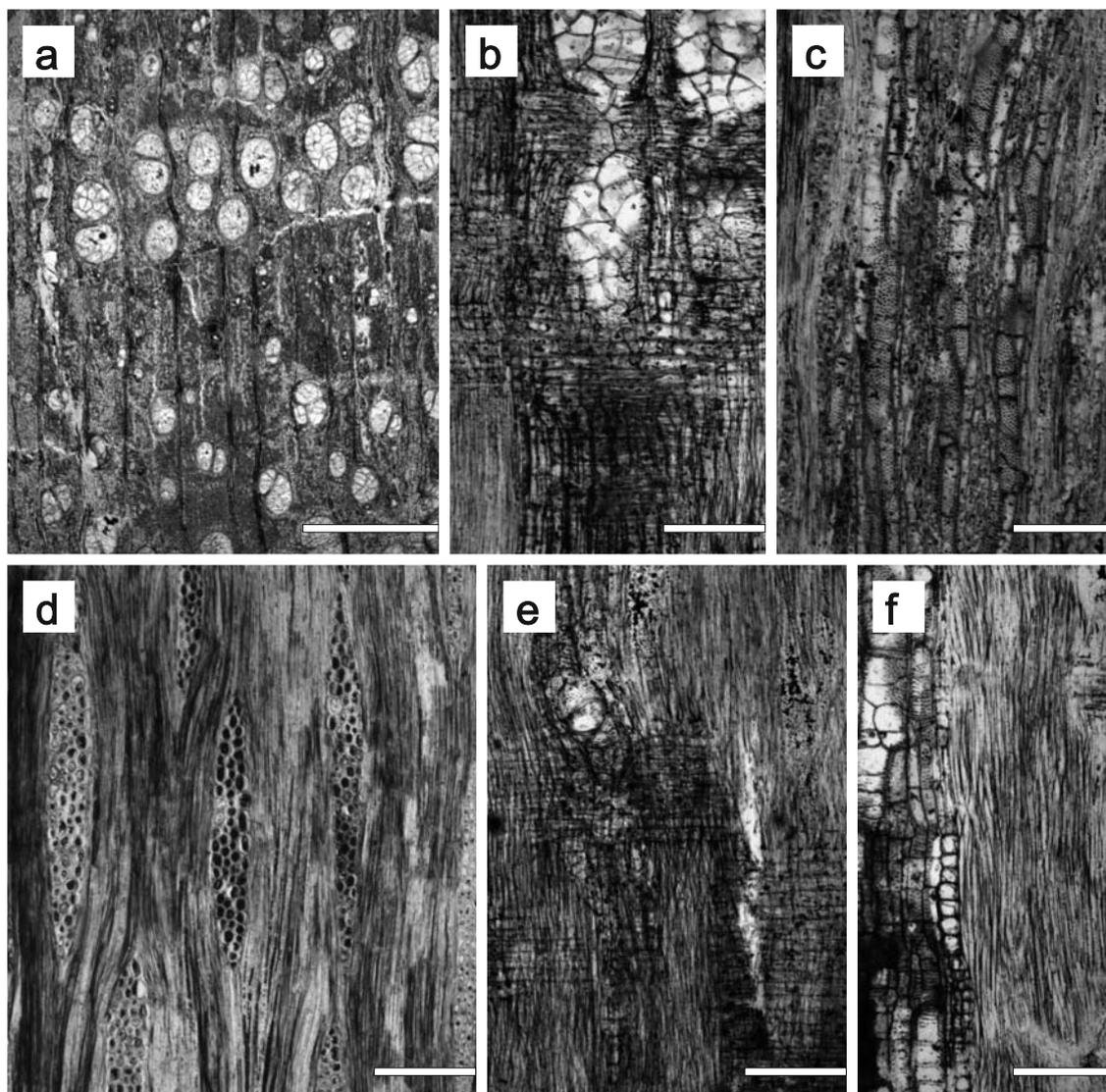


Fig. 2. *Ulmoxylon marchesonii* Biondi, from Miocene of Włoszczowice, specimen GS1, slides GS1-C, GS1-R and GS1-T: **a** – ring porous wood with latewood vessels arranged in tangential bands (TS), **b** – vessels filled with thin-walled tyloses and homocellular rays composed of procumbent cells (RLS), **c** – narrow vessels with fine spiral thickenings and alternate, bordered pits (TLS), **d** – multiseriate rays (TLS), **e** – simple perforation plate (RLS), **f** – chambered parenchyma with crystals and libriform fibres (RLS). Scale bar = 1000 μm in (a) and 200 μm in (b – f)

Vessels intermixed with vascular tracheids. Vascular tracheids with uniseriate up to triseriate crowded pits. Pits circular or oval in shape, possessing elliptical apertures. Fibre tracheids present. In latewood commonly occur 3–7 layers of flattened tracheids. Ground tissue formed by thick-walled libriform fibres (Fig. 2:f). Fibres are polygonal or rounded in cross-sectional outline, with no obvious pits in longitudinal section. Axial parenchyma is abundant in earlywood and also among vessel groups in latewood. Paratracheal parenchyma vasicentric. Crystals, when present, appear in chambered axial parenchyma strands (Fig. 2:f). Rays uniseriate and multiseriate (Fig. 2:d), mostly 2–4-seriate, occasionally wider. Rays

generally homogeneous, composed of procumbent cells (Fig. 2:b) or slightly heterogeneous, with one row of square marginal cells. Ray height varies from 15 to 60 cells, usually 25–45 cells. Vessel-ray parenchyma pits are similar to intervessel ones.

DISCUSSION

The results of microscopic observations showed all the analysed specimens of Miocene woods from the Holy Cross Mountain to represent the same type of anatomical structure. The anatomy has shown closest similarity to the wood of extant *Ulmus* L. The characteristic

features of this genus are: ulmiform distribution of latewood pores which are grouped in clusters forming tangential, oblique or sinuous bands, simple perforation plates, helical thickenings along latewood vessels, alternate intervessel pits, thin-walled tyloses, vascular tracheids intermixed with vessel clusters, non-septate fibres without obvious pits, paratracheal axial parenchyma, homocellular, uniseriate and multiseriate rays and the presence of chambered axial parenchyma strands (Metcalfe & Chalk 1989, Schweingruber 1990, Wheeler & Manchester 2007).

In the palaeontological literature fossil elm woods have been classified as *Ulminium*, *Ulmoxylon* or *Ulmus*. *Ulminium* was first introduced by Unger (1842) based on the species *U. diluviale* from the Oligocene-Lower Miocene volcanic deposits in Jáchymov (Dupéron et al. 2008). However, this wood was later re-examined by Felix (1883) and assigned to *Laurinoxylon*.

To date, about twenty species of fossil elm woods are known to originate from the deposits of Europe, Asia and North America (Gregory et al. 2009). However, many are considered to be synonyms (Privé & Brousse 1969, Privé-Gill et al. 2008, Gregory et al. 2009). A comparison of the anatomy of published fossil *Ulmoxylon* woods with that of specimens from the Holy Cross Mountains is summarised in Table 1. Differences are more or less significant and are as follows.

Ulminium protoracemosum (Penhallow) Nagalhard and *Ulminium protoamericanum* (Penhallow) Nagalhard, defined on the basis of Oligocene wood from British Columbia, possess at least 4-seriate rays (Penhallow 1907, Nagalhard 1922). Moreover, *U. protoracemosum* differs in having a smaller number and more scattered arrangement of vessels in the earlywood zone and also by the lack of tyloses.

Ulminium columbianum (Penhallow) Nagalhard, also found within Oligocene sediments of British Columbia, is characterised by a more scattered arrangement of vessels in earlywood. Additionally, in the earlywood zone there are radial multiples of vessels which are up to 5 cells long (Penhallow 1907, Nagalhard 1922).

Ulminium simrothi (Platen) Edwards, described for the first time from the Pliocene of California, has one row of small, radially elongated and mostly isolated earlywood vessels. Rays are usually 5–6 cells wide and often weakly heterogeneous (Platen 1908, Edwards 1931).

Ulminium hungaricum (Lingelsheim) Edwards, originating from Miocene strata of Hungary, has slightly larger rays, 3–6 cells wide. Vessels in the earlywood zone are arranged in one, sometimes two rows (Lingelsheim 1917, Edwards 1931).

Ulmoxylon lapidariorum (Unger) Felix, from Neogene deposits of Gleichenberg in Austria, has one tangentially discontinuous row of vessels in the earlywood zone. Vessels are solitary or rarely tangentially or radially grouped by two. Rays are 1–7 cells wide, and usually about 40 cells high (Unger 1842, Felix 1883).

Pliocene wood from Piedmont, referred by Charrier (1951) to the species *Ulmus campestris* L., possesses one row of scattered earlywood vessels and medullary rays of 7–8 cell width.

Ulmus crystallophora Watari, a species determined from Miocene strata of Japan, has 2–4 rows of earlywood pores, rays mostly 4–6 cells wide and very abundant chambered parenchyma cells (Watari 1952).

Ulmoxylon sp. ex aff. *Ulmus campestris* L. classified by Sacchi-Vialli (1958) from the Pliocene of Italy, differs from the Holy Cross Mountains wood in the presence of scattered vessels in earlywood, arranged in one or, rarely in two rows. Moreover, the rays of this wood are at least 5–6 cells wide.

Ulmus miocenica Prakash & Barghoorn, from the Miocene of Central Washington, has vessels in the earlywood zone arranged in one row, and rays up to 4 cells wide (Prakash & Barghoorn 1961a).

Ulmus pacifica Prakash & Barghoorn, also from the Miocene of Central Washington, is semi-ring porous and possesses one row of earlywood vessels. Latewood vessels are arranged in irregular clusters and very rarely form wing- or festoon-like oblique bands. Rays are 1–8 cells wide (Prakash & Barghoorn 1961a).

Ulmus baileyana Prakash & Barghoorn, the next Miocene species from Central Washington, has solitary earlywood vessels that are usually arranged in 1 to 4 rows. Rays are mostly 4–5 cells wide (Prakash & Barghoorn 1961b).

Ulmoxylon kersonianum Starostin & Trelea, Miocene wood from Moldavia, is distinguished from the analysed specimens by the presence of single vessels in earlywood and by wider, usually 6-seriate rays (Starostin & Trelea 1969).

Table 1. Differences between analysed wood and selected fossil elm taxa

Taxon	Publication	Age and origin	Earlywood	Ray width	Other important differences
<i>Ulmium protoracemosum</i>	Penhallow (1907); Nagalhard (1922)	Oligocene, British Columbia	no differences	at least 4-cell	
<i>Ulmium protoamericanum</i>	Penhallow (1907); Nagalhard (1922)	Oligocene, British Columbia	smaller number and more scattered arrangement of vessels in the earlywood zone	at least 4-cell	lack of thyloses
<i>Ulmium columbianum</i>	Penhallow (1907); Nagalhard (1922)	Oligocene, British Columbia	more scattered arrangement of vessels in earlywood zone	no differences	radial multiples of vessels which are up to 5 cells long
<i>Ulmium simrothi</i>	Platen (1908); Edwards (1931)	Pliocene, California	one row of small, radially elongated and mostly isolated earlywood vessels	usually 5–6 cells	
<i>Ulmium hungaricum</i>	Lingelsheim (1917); Edwards (1931)	Miocene, Hungary	vessels in the earlywood zone arranged usually in one row	3–6 cells	
<i>Ulmoxylon lapidariorum</i>	Unger (1842); Felix (1883)	Neogene, Gleichenberg (Styrie, Austria)	one tangentially discontinuous row of earlywood vessels	1–7 cells	rays about 40 cells high
<i>Ulmus campestris</i>	Charrier (1951)	Pliocene, Piedmont, Italy	one row of scattered earlywood vessels	7–8 cells	
<i>Ulmus crystallophora</i>	Watari (1952)	Miocene, Japan	2–4 rows of earlywood pores	4–6 cells	very abundant chambered parenchyma
<i>Ulmoxylon</i> sp. ex aff. <i>Ulmus campestris</i>	Sacchi Vialli (1958)	Pliocene, Italy	scattered vessels in earlywood zone, arranged in one or, rarely, two rows	at least 5–6 cells	
<i>Ulmus miocenica</i>	Prakash & Barghoorn (1961a)	Miocene, Central Washington	vessels in the earlywood zone arranged in one row	maximum of 4 cells	
<i>Ulmus pacifica</i>	Prakash & Barghoorn (1961a)	Miocene, Central Washington	semi-ring porous, one row of earlywood vessels	1–8 cells	latewood vessels clustered in irregular groups and very rarely arranged in wing- or festoon-like oblique bands
<i>Ulmus baileyana</i>	Prakash & Barghoorn (1961b)	Miocene, Central Washington	solitary earlywood vessels, usually arranged in 1 to 4 rows	mostly 4–5 cells	
<i>Ulmoxylon kersonianum</i>	Starostin & Trelea (1969)	Miocene, Moldavia	single vessels in earlywood	usually 6 cells	
<i>Ulmoxylon</i> cf. <i>carpinifolia</i>	Greguss (1969)	Miocene, Hungary	no differences	up to 8 cells	rays up to 80 cells high
<i>Ulmoxylon scabroides</i>	Greguss (1969)	Miocene, Hungary	no differences	no differences	rays 3–25–30 cells high
<i>Ulmoxylon</i> sp. (cf. <i>Ulmus scabra</i> Mill.)	Greguss (1969)	Miocene, Hungary	no differences	no differences	
<i>Ulmoxylon</i> sp.	Greguss (1969)	Miocene, Hungary	no differences	from 3 to 8 cells	
<i>Ulmus woodii</i>	Wheeler & Manchester (2002)	Eocene, Oregon	semi-ring porous, broad zone of earlywood, more than 2–3 vessels deep	usually 35 cells	
<i>Ulmus danielii</i>	Wheeler & Manchester (2002)	Eocene, Oregon	semi-ring porous	usually 3–5 cells	

Ulmoxylon wood from Miocene deposits of Hungary, studied and named by Greguss (1969) as *Ulmoxylon* cf. *carpinifolia* Gled., has wider, up to 8 cells, and higher rays – up to 80 cells.

Ulmoxylon scabroides, *Ulmoxylon* sp. (cf.

Ulmus scabra Mill.) and *Ulmoxylon* sp., also specified by Greguss (1969) from the Miocene of Hungary, are all very similar to the specimens from the Holy Cross Mountains. The only features that distinguish them are lower rays, 3–25(–30) cells high, in the first of the

mentioned species and greater width of rays, from 3 to 8 cells, in the last one.

Ulmus woodii and *Ulmus danielii* created by Wheeler & Manchester (2002) and collected from the Eocene strata of Oregon, differ significantly from the analysed wood because they are semi-ring porous and have usually 3–5-seriate rays.

Among the fossil taxa, the wood from Holy Cross Mountains is the most similar to *Ulmoxylon marchesonii* Biondi, defined on the basis of a Miocene silicified wood from the Apennines. *U. marchesonii* has its earlywood vessels aligned in 2–3 rows. The latewood pores of this species form ulmiform aggregates composed of 10–60 elements. These aggregates also consist of tracheids and parenchyma cells. The subtle thickenings on vessel walls are most visible in latewood (Biondi 1981). According to the original designation, the width of rays varies from 1 to 6(–7) cells; however, the photos presented with the species description show the rays to be a maximum of 4 cells wide. This fact suggests that the wider rays appear sporadically. The wood possesses homocellular rays, composed of procumbent cells. The parenchyma is paratracheal and occurs as numerous strands in earlywood zone. In latewood the parenchyma is discontinuous, associated with vessels. A characteristic feature of *Ulmoxylon marchesonii* is a chambered parenchyma particularly rich in crystals (Biondi 1981). Chambered axial parenchyma also occurs in the wood from Holy Cross Mountains, but it is difficult to observe the presence of crystals in it. However, this disappearance of crystals may be the result of remobilisation during the wood silicification process (Buurman 1972).

CONCLUSION

This paper presents the first noted occurrence of a fossil *Ulmoxylon* wood in the area of Poland, documented so far. Nevertheless, the appearance of fossil elm woods is known in other areas in the close neighbourhood. One sample of *Ulmoxylon* sp. has been collected in Bonfol, Switzerland, two were found in the northalpine Molasse Foreland in southern Germany (Bavaria). Unfortunately, they specific affinity has not been accurately determined (Selmeier 2002). Similarly, two specimens of Pleistocene wood originating from

Czech Republic area have been classified to the *Ulmoxylon* genus, without their precise names being given (Fietz 1926). From Czech Republic an early Miocene wood belonging to *Ulmoxylon marchesonii* Biondi has been also mentioned (Sakala 2002).

According to Sakala (2002), *Ulmoxylon marchesonii* wood from Bílina locality is certainly related to the elm foliage and samara belonged to *Ulmus pyramidalis* Göppert. In the area of the North-Bohemian brown-coal basin, *Ulmus pyramidalis* grew in stands along the river banks, a characteristic of riparian forest (Bůžek et al. 1992). Similar environmental conditions presumably prevailed also in the Holy Cross Mountains when the ancient trees were alive. During the Badenian and Sarmatian stages the southern foothills of the Holy Cross Mountains were the zone delimiting from the north the range of the Central Paratethys sea transgression (Oszczypko 1998). At that time, land areas situated on the northern edge of Central Paratethys were covered with temperate and warm temperate floras (Bruch et al. 2007). The composition of Miocene plant assemblages of this region is documented, among other things, by leaf imprints described from the Chmielnik locality. Most taxa identified within the Badenian foliage flora from Chmielnik represented forest communities of alluvial plants of coastal zones and/ or seasonally flooded river banks. *Ulmus* was the one of the most common genera in this forest (Zastawniak 1980, 1995).

ACKNOWLEDGEMENTS

I would like to thank Jerzy Jędrychowski from Kielce for donating the specimens of fossil wood and for indicating the sites of their occurrence in the area of Holy Cross Mountains. I thank the reviewers, Alfred Selmeier (Ludwig Maximilian University of Munich, Germany), Jakub Sakala (Charles University in Prague, Czech Republic) and an anonymous reviewer, for the detailed proofreading and constructive comments.

REFERENCES

- BIONDI E. 1981. *Ulmoxylon marchesonii* n. sp. di legno fossile rinvenuta sui Monti Sibillini (Appennino Centrale). Stud. Trent. Sci. Nat., Acta Biol., 58: 77–91.
- BRUCH A.A., UHL D. & MOSBRUGGER V. 2007. Miocene climate in Europe – Patterns and evolution.

- A first synthesis of NECLIME. *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 253: 1–7.
- BUURMAN P. 1972. Mineralization of fossil wood. *Scripta Geol.*, 13: 1–43.
- BŮŽEK Č., DVOŘÁK Z., KVAČEK Z. & PROKŠ M. 1992. Tertiary vegetation and depositional environments of the 'Bílina delta' in the North-Bohemian brown-coal basin. *Časopis Mineral. Geol.*, 37: 117–134.
- CASPARY R. 1888. Einige fossile Hölzer Preussens. *Schriften Phys.-Ökon. Ges. Königsberg*, 28: 27–45.
- CHARRIER G. 1951. Primo contributo di paleoxilologia pedemontana. *Arch. Bot.*, 27: 194–206.
- CONWENTZ H. 1880. Die fossilen Hölzer von Karlsdorf am Zobten. *Schrif. Naturforsch. Ges. Danzig, Neue Folge*, 4(4): 1–48.
- DUPÉRON J., DUPÉRON-LAUDOUENEIX M., SAKALA J. & DE FRANCESCHI D. 2008. *Ulmium diluviale* Unger: Historical data on the discovery and new study. *Ann. Paléontol.*, 94: 1–12.
- EDWARDS W.N. 1931. Dicotyledones (Ligna), *Fossilium Catalogus II: Plantae, Pars 17*. W. Junk, Berlin.
- FELIX J. 1882. Studien über fossile Hölzer. Inaugural Dissertation, Leipzig.
- FELIX J. 1883. Untersuchungen über fossile Hölzer. 1 Stuck. *Zeitschr. Deutsch. Geol. Ges.*, 35: 59–91.
- FELIX J. 1894. Untersuchungen über fossile Hölzer. 4 Stuck. *Zeitschr. Deutsch. Geol. Ges.*, 46: 79–110.
- FIETZ A. 1926. Fossile Hölzer aus Schlesien. *Jahrb. Geol. Bundesanst.*, 76: 217–244.
- FILONOWICZ P. 1973. Szczegółowa mapa geologiczna Polski. Arkusz Kielce (815) w skali 1: 50 000 wraz z objaśnieniami. Wydawnictwa Geologiczne, Warszawa.
- GRABOWSKA I. 1956. Przewodnie lignity węgla brunatnego z obszaru Konina (summary: Index lignites of brown-coal from the area of Konin (Central Poland)). *Prace Inst. Geol.*, 15: 201–258.
- GREGORY M., POOLE I. & WHEELER E.A. 2009. Fossil dicot wood names – an annotated list with full bibliography. *IAWA. Journal Supplement*, 6: 1–220.
- GREGUSS P. 1969. Tertiary angiosperm wood in Hungary. *Akademiai Kiado, Budapest*.
- KOSTYNIUK M. 1938. Trzeciorzędowe drewna i pyłki z Mazowsza i Wołynia (summary: Ueber die tertiären Pollen und Koniferenhölzer von einigen Gegenden Polens). *Kosmos (Lwów)*, 63: 1–33.
- KOSTYNIUK M. 1950. Szczątki drewna szpilkowych flory pliocenkiej z Krościenka. *Prace Wrocł. Tow. Nauk.*, B, 22: 5–57.
- KOSTYNIUK M. 1967. Pnie drzew iglastych z górnego pokładu węgla brunatnego w Turowie (summary: Coniferous stumps from the brown coal deposit of Turów near Bogatynia, SW Poland). *Prace Muz. Ziemi*, 10: 3–96.
- KOWNAS S. 1951. Trzeciorzędowe drewna z Dobrzynia nad Wisłą (summary: Fossil Tertiary woods from Dobrzyń). *Stud. Soc. Sci. Toruniensis*, 1: 67–121.
- KRÄUSEL R. 1920. Nachträge zur Tertiärflora Schlesiens II. Braunkohlenhölzer. *Jahrb. Preuss. Geol. Landesanst.*, 39: 418–460.
- LILPOP J. 1917. Mikroskopisch-anatomische Untersuchungen der Mineralkohlen. *Bull. Intern. l'Acad. Sci. de Cracovie (B)*, 1(3): 6–24.
- LILPOP J. 1924. Materiały do flory drzew lignitowych Polski (summary: Materials to the knowledge of the lignites in Poland). *Sprawozd. Pol. Inst. Geol.*, 2(3,4): 387–401.
- LINGELSHEIM A. 1917. Ein Beitrag zur fossilen Flora Ungarns. *Jahrb. König. Ungar. Geol. Reichsanstalt*, 1915: 545–563.
- METCALFE C.R. & CHALK L. 1989. *Anatomy of the Dicotyledons. Second Edition, vol. 2*. Clarendon Press, Oxford.
- MIZERSKI W. 2004. Holy Cross Mountains in the Caledonian, Variscan and Alpine cycles – major problems, open questions. *Prz. Geol.*, 52: 774–779.
- NAGALHARD K. 1922. *Ulmaceae, Fossilium Catalogus II: Plantae, Pars 10*. W. Junk, Berlin.
- OSZCZYPKO N. 1998. The Western Carpathian Foredeep – development of the foreland basin in front of the accretionary wedge and its burial history (Poland). *Geol. Carpath.*, 49: 415–431.
- PENHALLOW D.P. 1907. A report on fossil plants from the international boundary survey for 1903–1905. *Trans. Royal Soc. Canada*, III, 1(4): 287–351.
- PLATEN P. 1908. Untersuchungen fossiler Hölzer aus dem Westen der Vereinigten Staaten von Nordamerika. *Sitzungsber. Naturf. Ges. Leipzig*, 34: 1–155.
- PRAKASH U. & BARGHOORN E.S. 1961a. Miocene fossil woods from the Columbia Basalts of Central Washington. *J. Arnold Arbor.*, 42: 165–203.
- PRAKASH U. & BARGHOORN E.S. 1961b. Miocene fossil woods from the Columbia Basalts of Central Washington. II. *J. Arnold Arbor.*, 42: 347–362.
- PRIVÉ C. & BROUSSE R. 1969. Bois fossiles de la nappe de ponces villafranchienne à La Bastide-du-Fau (Cantal): 233–263. In: Ters M. (ed.), 8e Congrès INQUA, Etudes sur le Quaternaire dans le monde. Centre National de la Recherche Scientifique, Paris.
- PRIVÉ-GILL C., CAO N. & LEGRAND P. 2008. Fossil wood from alluvial deposits (reworked Oligocene) of Limagne at Bussières (Puy-de-Dôme, France). *Rev. Palaeobot. Palynol.*, 149: 73–84.
- PYSZYŃSKI W. 1992. Remains of wood from Gozdnicca–Stanisław profile 2. In: Zastawniak E. (ed.), The younger Tertiary deposits in the Gozdnicca Region (SW Poland) in the light of recent palaeobotanical research. *Pol. Bot. Stud.*, 3: 46–48.
- RACIBORSKI M. 1889. O niektórych skamieniałych drzewach okolicy Krakowa. *Sprawozd. Kom. Fizjogr. Akad. Umiejęt. Krak.*, 23: 170–181.

- REYMAN M. 1956. O drewnach kopalnych ze śląskiego miocenu (summary: Fossil woods from Silesian Miocene). *Acta Soc. Bot. Poloniae*, 25: 517–527.
- RÖGL F. 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). *Geol. Carpath.*, 50: 339–349.
- RUBCZYŃSKA M. & ZABŁOCKI M. 1924. Über zwei fossile Koniferenhölzer von Pośadza. *Bull. Acad. Polon. Sci.*, (B): 433–436.
- SACCHI-VIALLI G. 1958. Flora fossile della fontana di Annibale (Casteggio) IV, *Ulmoxylon* sp. ex aff. *Ulmus campestris* L. *Atti dell' Istituto Geologico della Università di Pavia*, 8: 111–123.
- SAKALA J. 2002. First record of fossil angiosperm wood (*Ulmoxylon*, Ulmaceae) from the famous locality of Bílina (Czech Republic, Early Miocene). *C. R. Palévol.*, 1: 161–166.
- SCHWEINGRUBER F.H. 1990. *Anatomy of European woods*. Paul Haupt Publishers, Berne, Stuttgart.
- SELMEIER A. 2002. Streufunde verkieselter Hölzer in der Bayerischen Staatssammlung für Paläontologie und Geologie. *Mitt. Bayer. Staatssamml. Paläontol.*, 42: 155–185.
- SEWARD A.C. 1919. *Fossil Plants*, vol. IV. Cambridge University Press, England.
- STAROSTIN G. & TRELEA N. 1969. Studiu paleoecologic al florei din Miocenul Moldovei (Paleoecologic study of flora from the Pliocene of Moldova). *An. Stiintif. Univers. Alexandru Ioan Cuza din Iasi (serie noua)*. IIA Biologie, 15: 447–451. (in Romanian).
- UNGER F. 1842. Synopsis Lignorum fossilium Plantarum Acramphibryarum: 100–102. In: Endlicher S. (ed.), *Genera Plantarum secundum ordines naturales disposita*, Suppl. II, Appendix. Mantissa, Wien.
- UNGER F. 1845. *Synopsis Plantarum fossilium*. Voss, Leipzig.
- UNGER F. 1849. Die Pflanzenreste im Salzstocke von Wieliczka. *Denkschr. Akad. Wiss. Wien, Math.-Naturwiss. Kl.*, 1: 311–322.
- UNGER F. 1850. *Genera et Species Plantarum Fossilium*. Wilhelmum Braumüller, Vindobonae.
- VATER H. 1884. Die fossilen Hölzer der Phosphoritlager des Herzogthums Braunschweig. *Zeitschr. Deutsch. Geol. Ges.*, 36: 783–853.
- WATARI S. 1952. Dicotyledonous Woods from the Miocene along the Japan Sea side of Honsyu. *Jour. Fac. Sci., Univ. Tokyo, Section III Botany*, 6: 97–134.
- WHEELER E.A., BAAS P. & GASSON P.E. (eds.), 1989. IAWA list of microscopic features for hardwood identification. *IAWA Bull. N. S.*, 10: 219–332.
- WHEELER E.A. & MANCHESTER S.R. 2002. Woods of the Middle Eocene Nut Beds Flora, Clarno Formation, Oregon, USA. *IAWA Journal Supplement*, 3: 1–188.
- WHEELER E.A. & MANCHESTER S.R. 2007. Review of the wood anatomy of extant *Ulmaceae* as context for new reports of late Eocene *Ulmus* woods. *Bull. Geosci.*, 82: 329–342.
- ZABŁOCKI J. 1935. Dotychczasowe wyniki badań nad trzeciorzędową florą Chłapowa na Pomorzu. *Ref. Pol. Tow. Bot.*, Kraków: 14–16.
- ZALEWSKA Z. 1953. Trzeciorzędowe szczątki drewna z Turowa nad Nysą Łużycką, część I (summary: Tertiary remains of fossil wood from Turów near Lusatian Neisse). *Acta Geol. Pol.*, 3(4): 481–543.
- ZALEWSKA Z. 1955. Trzeciorzędowe szczątki drewna z Turowa nad Nysą Łużycką, część II (summary: Tertiary remains of fossil wood from Turów near Lusatian Neisse). *Acta Geol. Pol.*, 5(2): 277–304.
- ZASTAWNIAK E. 1980. Sarmatian leaf flora from the southern margin of the Holy Cross Mts. (South Poland). *Prace Muz. Ziemi*, 33: 39–107.
- ZASTAWNIAK E. 1995. New data about plant macrofossils in the Middle Miocene limestone at Młyny near Chmielnik (Central Poland). *Acta Palaeobot.*, 35: 237–242.

