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Source: *Acta Palaeontologica Polonica*, 59(3) : 697-708

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: <https://doi.org/10.4202/app.2011.0158>

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Miocene coniferous woods of the Polish Carpathian Foredeep

MARZENA KLUSEK



Klusek, M. 2014. Miocene coniferous woods of the Polish Carpathian Foredeep. *Acta Palaeontologica Polonica* 59 (3): 697–708.

This paper presents the results of analysis of the Miocene woods collected from three sampling sites in the Polish part of the Carpathian Foredeep. The location in the stratigraphic profile and the state of fossil preservation indicate that the woods were transported by waters flowing from highland or from mountainous regions and then deposited and fossilised in delta areas. Fragments of 16 lignified or silicified woods were collected for anatomical research. The fossil woods were classified as *Piceoxylon piceae*, *Juniperoxylon pachyderma*, *Cupressinoxylon canadense* and *Cupressinoxylon polonicum*. Disturbance zones observed in *Cupressinoxylon polonicum* are interpreted as frost rings. Frost rings suggest that despite the documented existence of warm and humid climatic conditions during the Miocene period, the temperatures in mountainous areas could temporarily drop below freezing point.

Key words: Coniferophyta, fossil woods, palaeoecology, wood anatomy, Miocene, Poland.

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Received 12 October 2011, accepted 29 October 2012, available online 7 November 2012.

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Introduction

This article presents the results of studies of Miocene wood collected from the area of the Carpathian Foredeep. The research undertaken involved their anatomical analysis and taxonomic classification. Taxonomic identification of fossil woods contributes to the knowledge of assemblage composition of fossil plants. It provides information about biogeography, biodiversity, and floral dynamics in geological time. Fossil wood classification can also be employed in the study of morphological and anatomical changes of trees, their phylogeny and evolution. Determination of fossil wood taxa is often used to reconstruct palaeoenvironmental conditions that prevailed while the ancient trees were alive. Moreover, woods provide also opportunity for the examination of their growth rings (Chaloner and Creber 1973; Creber and Chaloner 1984). The presence of growth rings, ring width, the ratio of early and latewood zones and the occurrence of any disturbances within the wood structure can be useful in identifying the environmental factors affecting tree growth (Francis and Poole 2002; Falcon-Lang 2005; Vaganov et al. 2011; Olano et al. 2012). In the present paper the analysed woods, particularly the observations made on their growth rings were useful to conclude about the palaeoenvironmental

conditions prevailing during the Miocene in the area of the Carpathian Foredeep.

Institutional abbreviations.—MZ, Museum of the Earth, Warsaw, Poland.

Other abbreviations.—RLS, radial longitudinal plane; TLS, tangential longitudinal plane; TS, transverse plane.

Geological setting

The fossil woods which are the subject of this study came from three sampling sites situated in the Polish Carpathian Foredeep (Fig. 1), which is a part of a large sedimentary basin that stretches from the Danube in Vienna to the Southern Carpathians in Romania. The Early Miocene to Middle Miocene Carpathian Foredeep developed as a peripheral foreland basin and its genesis is related to the advancing Carpathian Front. The progressive subsidence, accompanied by the Early Badenian transgression, flooded the foredeep and the marginal part of the Carpathian Mountains (Oszczypko 1998). As a result during the Middle Miocene the area of the Carpathian Foredeep was the northern part of the Central Paratethys, which was a warm sea of epicontinental characteristics. This relatively narrow brackish or freshwater basin was filled with

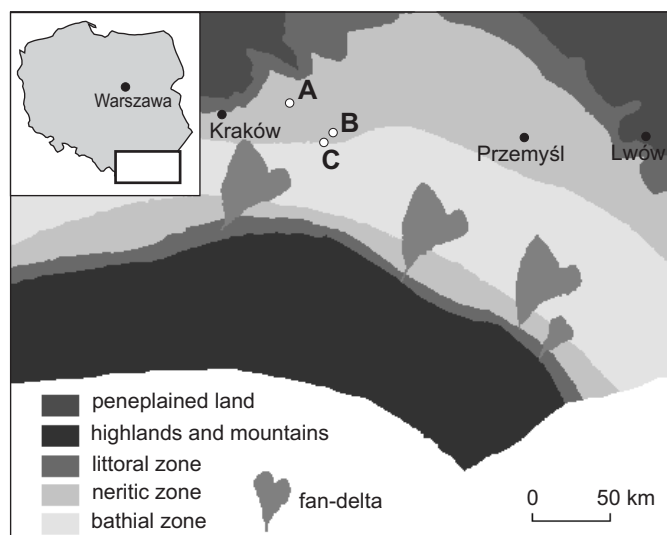


Fig. 1. Early Badenian palinspastic paleogeography map of the Polish Carpathian Foredeep (after Oszczypko 2006, simplified). A. Hebdów locality. B. Tarnów-Gumniska locality. C. Zgłobice locality.

coarse clastic sediments derived from the emergent front of the Carpathians and from the platform area (Rögl 1999; Rögl et al. 2008). The analysed woods were deposited in layers of clay, silt, and sand of deltaic origin. The beds from which the fossil wood was taken formed proximal mouth bars, delta-fed marine fans and submarine landslides lithofacies. The mineral and petrographic composition of sediments indicates that they had been transported by the waters flowing from the Carpathian area and then deposited in a sedimentary basin at the foothill of the mountains. Especially the petrographic composition of gravel particles shows predominance of Carpathian-derived sandstone and granitoid rocks (Brud 2002). The wood-containing strata belong to Skawia and Grabowiec Beds and also to Machów Formation. They were dated using microfossils as Middle Miocene (16.4–11.5 Ma) (Otfinowski 1973; Porębski 1999).

Material and methods

In total, 16 specimens of wood were collected from the Tarnów-Gumniska, Zgłobice, and Hebdów localities (Fig. 1). The size of the analysed specimens varied from several to twenty centimetres in length.

The small size of specimens, the absence of bark and the abrasion of the wood surface confirm the assumption that woods were moved by rivers from highland or mountainous areas. Simultaneously, the low degree of roundness of specimen's surfaces indicates that transport of the material took place before they fossilisation process.

The material was preserved in the form of coalified or silicified fragments of trunks and branches. Their origin from specific morphological organs of plants was established on the basis of wood size and anatomy, ring curvature and the divergence of rays.

For the purposes of anatomical analysis, standard petrographic thin sections were used. Sections were prepared for both coalified and silicified specimens along three perpendicular planes: transverse (TS), radial longitudinal (RLS) and tangential longitudinal (TLS). Microscopic observation and photographic documentation of wood was carried out using an Olympus BX51 transmission light microscope. Samples were deposited in the Museum of the Earth (Polish Academy of Science) in Warsaw.

At the request of the Editors, both fossil and extant plant taxa and higher units of the botanic system are cited with fully spelt authors' names and the year of publication, according to the zoological usage.

Systematic paleontology

Order Pinales Dumortier, 1829

Family Pinaceae Lindley, 1836

Morphogenus *Piceoxylon* Gothan, 1905

Type species: Piceoxylon pseudotsugae Gothan, 1906; Tertiary; Sierra Nevada, California, USA.

Piceoxylon piceae Roessler, 1937

Fig. 3A–F.

1913 *Picea* sp.; Kraeusel 1913: 29.

1920 *Piceoxylon* sp.; Kraeusel 1920: 437, pl. 28: 4–6; pl. 36: 1–4.

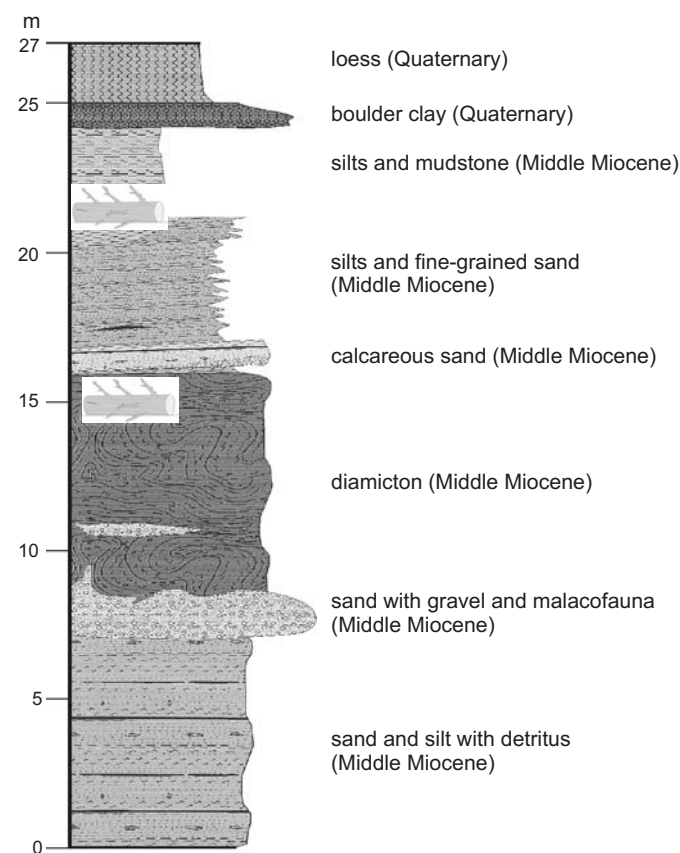


Fig. 2. Lithological log of Hebdów exposure.

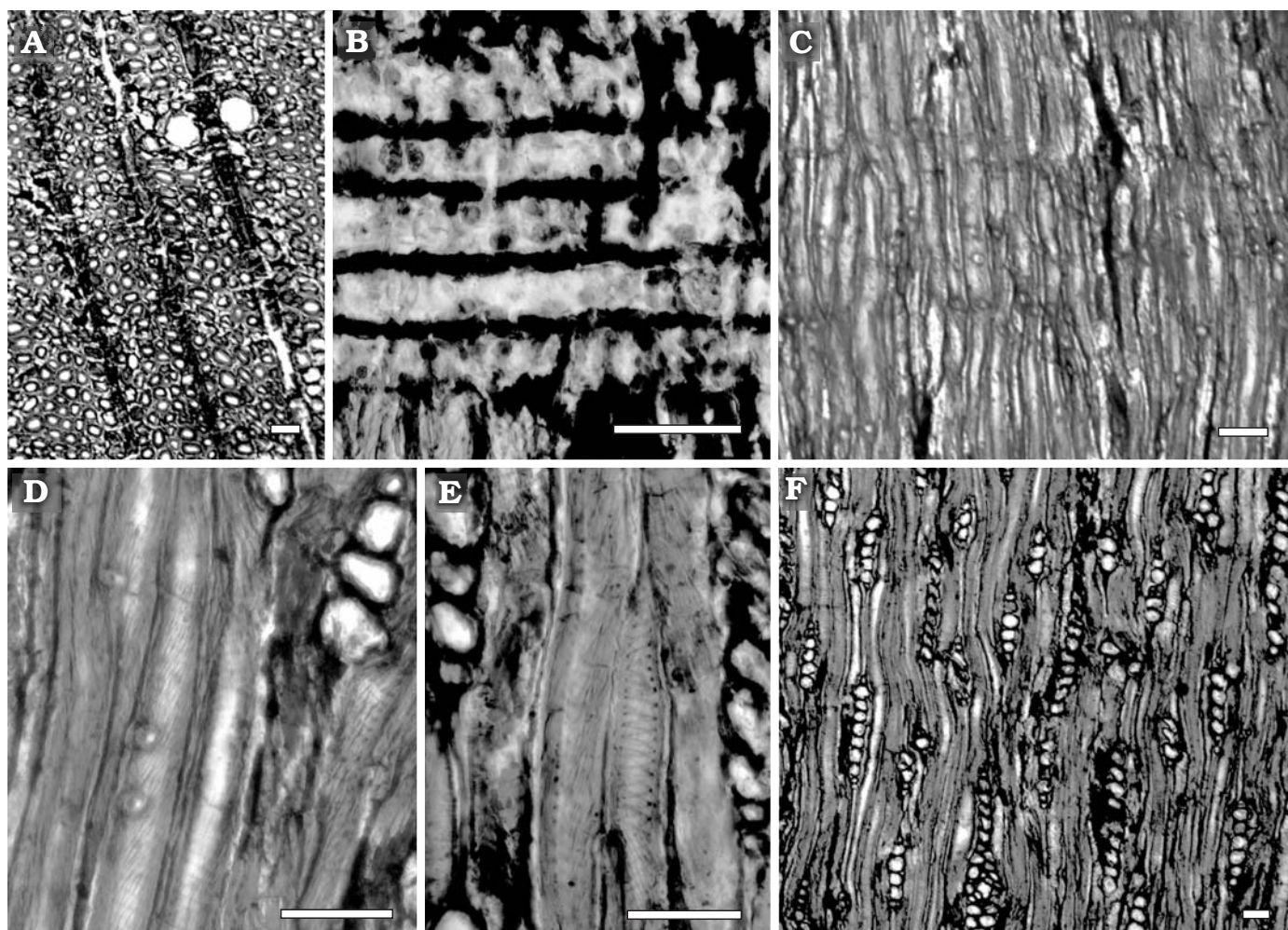


Fig. 3. Microphotographs of fossil wood *Piceoxylon piceae* Roessler, 1937 from Tarnów-Gumniska, Middle Miocene; specimen MZ LXVa. **A.** Vertical resin canals within reaction wood (TS). **B.** Crossfield pitting (RLS). **C.** Pitting on radial walls of tracheids (RLS). **D.** Bordered pits on tangential walls of tracheids (TLS). **E.** Latewood tracheids with spiral thickening (TLS). **F.** Uniseriate rays and rays with resin canals (TLS). Scale bars 50 µm.

1932 *Picea* sp.; Slijper 1932: 21.

1937 *Piceoxylon piceae* Roessler, 1937; Roessler 1937: 82, pl. 3: 10; pl. 4: 11–12.

Material.—Six specimens from Tarnów-Gumniska, marked as MZ LXVa–d, MZ LVIII, MZ LXXI. Wood is silicified, white or black, 15–25 cm long. Description is based on specimen MZ LXVa (Fig. 3A–F).

Description.—The wood corresponds to fragments of trunks of at least 15 cm in diameter. Growth rings are distinct, the transition from early- to latewood is gradual. The vertical resin canals have thick-walled epithelial cells. The resin ducts are commonly paired (Fig. 3A). The axial parenchyma is absent.

The pitting on radial walls of tracheids is uniseriate and pits are loosely spaced (Fig. 3C). Bordered pits are circular and they measure 13–17 µm in diameter. Pit apertures are circular or elliptical and obliquely oriented. Tangential walls of tracheids have circular bordered pits (6.5–8.5 µm in diameter). These pits are arranged in a single irregular, scattered row (Fig. 3D). Pit apertures have slit-like or elliptical shape

and they are obliquely oriented. Distinct spiral thickenings are confined to latewood tracheids (Fig. 3E).

Rays are uniseriate or partially biseriate, they have 3–20 cells in height. Some rays have resin canals (Fig. 3F). Horizontal resin ducts are usually located in the central part of the ray. Transverse and tangential walls of rays are thick and well pitted. Ray parenchyma cells show 2–6 piceoid pits (7–9 µm diameter) in each cross-field. These pits are circular and possess slit-like or elliptic apertures. Cross-field pits are usually grouped in two rows (Fig. 3B). Marginal ray tracheids have no spiral thickenings.

One of the specimens from the Tarnów-Gumniska locality (MZ LXVd) has the characteristic features of reaction wood. Reaction wood in conifers reveals thick-walled, rounded tracheids, an increased angle of microfibrils and of spiral thickenings, distorted tips and short length of cells (Scurfield 1973; Schweingruber 1996). All these anatomical features were observed in the analysed specimen.

Remarks.—The wood is characterised by the presence of axial and radial resin canals with thick-walled epithelial cells, the

existence of well marked pits on the transverse wall of ray cells and the appearance of loosely spaced pitting on radial and tangential walls of tracheids. Moreover wood possesses spiral thickenings of longitudinal tracheids and ray tracheids without thickenings. All these features indicate that the analysed woods belong to the genus *Piceoxylon* Gothan, 1905 (Philippe and Bamford 2008). This taxon consists of the contemporary wood of *Larix* Miller, 1754, *Picea* D. Don ex Loudon, 1838 and *Pseudotsuga* Carriere, 1867 (Greguss 1967).

Because of the presence of spiral thickenings confined to latewood cells, classification to the genus *Pseudotsuga* can be ruled out. However, identification of the analysed specimens as larch or spruce is quite a difficult task. The most reliable anatomical feature which allows these genera to be distinguished is the relative proportion of pit types in the ray tracheids. Ray tracheids of spruce usually have thick pit borders with angular extensions into the cell lumen and small pit apertures, while smooth pit borders and large pit apertures of ray tracheids are the characteristic of larch (Bartholin 1979; Anagnost et al. 1994). The state of preservation of the analysed wood, however, did not allow the types of pit in the ray tracheids to be established. Therefore, to determine the taxonomic affiliation of the specimens, other observed anatomical features were used: gradual transition between the earlywood and latewood zone, uniseriate pits on radial walls of tracheids, and transverse resin ducts usually located in the central part of the rays. These are typical features of spruce wood (Jagels et al. 2001; Blokhina and Afonin 2009). Comparison with the fossil wood taxa allows the analysed specimens to be classified as the species *Piceoxylon piceae* Roessler, 1937. The diagnosis of *Piceoxylon piceae* species was formed on the basis of Pliocene wood from Gleichenberg, Austria (Roessler 1937). Its nearest living relative is Norway spruce (*Picea abies* [Linnaeus, 1753] Karsten, 1881) (Roessler 1937).

Stratigraphic and geographic range.— Tertiary; Europe.

Family Cupressaceae Richard ex Bartling, 1830

Morphogenus *Juniperoxylon* (Houlbert, 1910)

Kraeusel, 1919

Type species: *Juniperoxylon turonense* Houlbert, 1910; Tertiary, Miocene; Les Faluns de Touraine, France.

Juniperoxylon pachyderma (Goeppert, 1850) Kraeusel, 1949

Fig. 4A–F.

1850 *Cupressinoxylon pachyderma* Goeppert, 1850; Goeppert 1850: 199, pl. 25: 1, 2.

1872 *Cupressoxylon pachyderma* (Goeppert, 1850) Kraus, 1872; Kraus 1872: 374.

1890 *Cupressinoxylon (Glyptostrobus) neosibiricum* Schmalhausen, 1890; Schmalhausen 1890: 21, pl. 2: 44–49.

1850 *Cupressinoxylon fissum* Goeppert, 1850; Goeppert 1850: 200, pl. 25: 3–5.

1872 *Cupressoxylon fissum* (Goeppert, 1850) Kraus, 1872; Kraus 1872: 375.

1913 *Cupressinoxylon juniperoides* Kraeusel, 1913; Kraeusel 1913: 35.

1913 *Juniperus silesiaca* Prill, 1913; Prill 1913: 30.

1919 *Juniperoxylon silesiacum* (Prill, 1913) Kraeusel, 1919; Prill and Kraeusel 1919: 297, pl. 22: 10.

1913 *Juniperus pauciporosa* Prill, 1913; Prill 1913: 35.

1919 *Juniperoxylon pauciporosum* (Prill, 1913) Kraeusel, 1919; Prill and Kraeusel 1919: 302, pl. 22: 5–6.

1920 *Juniperoxylon* sp.; Kraeusel 1920: 420, pl. 29: 4; pl. 36: 8.

1931 *Juniperoxylon* sp.; Jurasky 1931: 161.

1937 *Juniperoxylon* sp.; Roessler 1937: 77.

1944 *Juniperoxylon neosibiricum* (Schmalhausen, 1890) Selling, 1944; Selling 1944: 14.

1949 *Juniperoxylon pachyderma* (Goeppert, 1850) Kraeusel, 1949; Kraeusel 1949: 177.

Material.—Eight small specimens (2–10 cm long) of coalified and to a small extent silicified wood (MZ LXXa–h) from Zgłobie site. Description is based on specimen MZ LXXc (Fig. 4A–F).

Description.—The wood constitutes fragments of trunks or large branches. Growth rings are narrow. Transition between earlywood and latewood zones is gradual. Axial parenchyma is abundant and arranged in tangential rows (Fig. 4A). Transverse walls of parenchyma cells have beadlike thickenings (Fig. 4F).

Tracheids are thick-walled and rounded. On radial and tangential walls of tracheids occur uniseriate bordered pits (Fig. 4C). Pits on radial walls of tracheids possess circular borders (9–11 µm in diameter) and oval apertures. On tangential walls of tracheids pits are scattered and circular in outline (diameter 6–7 µm). These pits have oval or slit-like, obliquely oriented apertures (Fig. 4D).

Rays are uniseriate, 1–15 cells tall, usually between 4 and 9 cells high (Fig. 4E). They consist of very thick and usually smooth transverse walls. Tangential walls contain beadlike or dentate thickenings. Indentures are absent. Crossfield regions possess 1–2 pits, arranged in one row (Fig. 4B). Pits have circular or oval outlines (7–8 µm in diameter) and oblique apertures. Rays often include resinous filling.

Remarks.—The lack of resin ducts, abundant axial parenchyma, type of tracheids pitting, cupressoid pits in the cross field, lack of ray tracheids and presence of thickenings in tangential walls of ray cells makes it possible to establish that the analysed wood belongs to the species *Juniperoxylon pachyderma* (Goeppert, 1850) Kraeusel, 1949. The basionym of this taxon is *Cupressinoxylon pachyderma* species which was created by Goeppert in 1850 on the basis of Miocene wood from Łazany. *Juniperoxylon pachyderma* was established by Kraeusel (1949), who transferred to this new species numerous previously described woods (see list of synonyms). However he has not determined its holotype. *Juniperoxylon pachyderma* does not have also an unambiguous nearest living relative. Most probably, it is closely related to the present-day *Juniperus virginiana* Linnaeus, 1753 wood (Müller-Stoll 1951). However, it is quite anatomically diversified and encompasses trees belonging to different contemporary genera (Prill and Kraeusel 1919). The specimens analysed have features

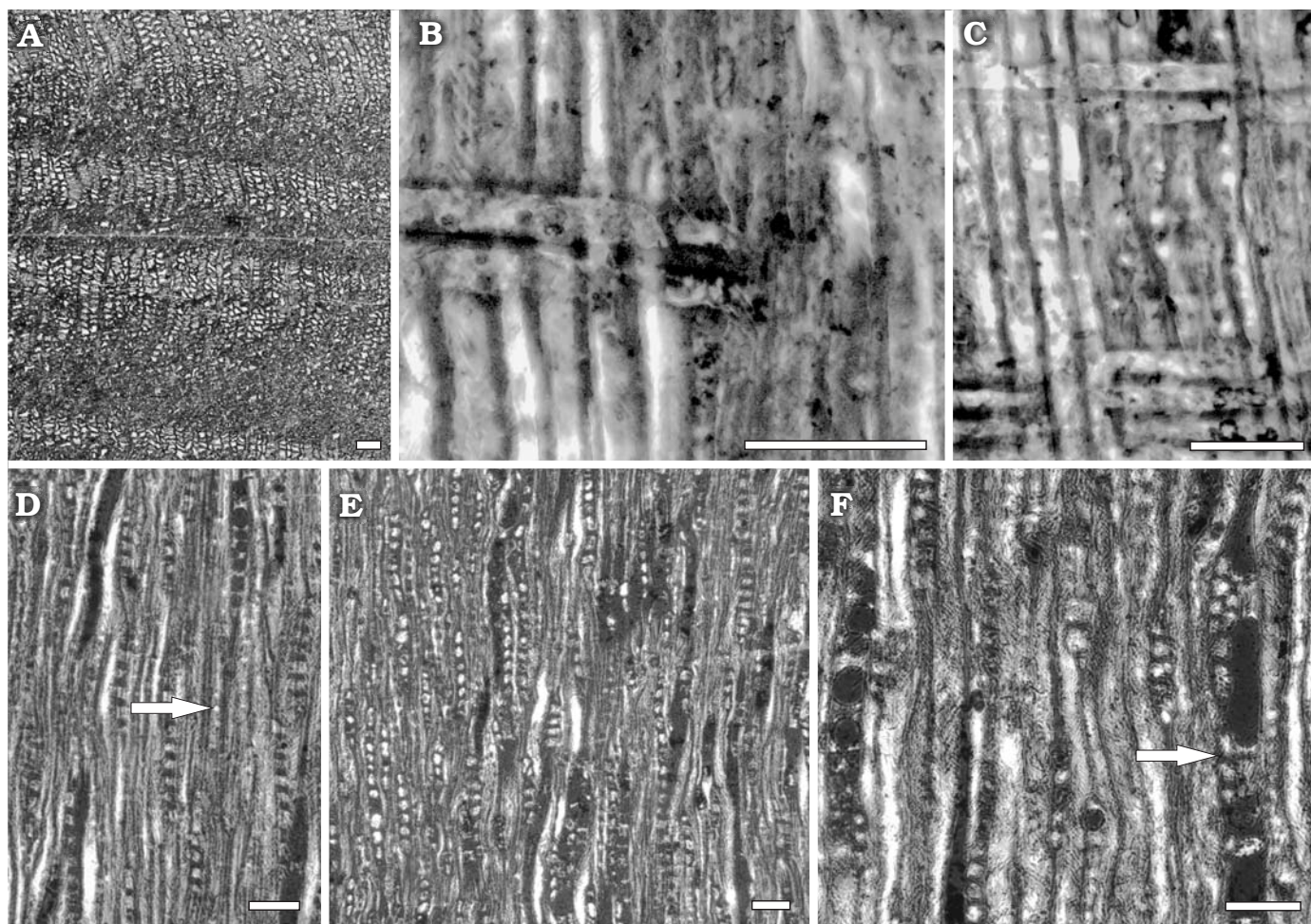


Fig. 4. Microphotographs of fossil wood *Juniperoxylon pachyderma* (Goeppert, 1850) Kraeusel, 1949 from Zgłobice, Middle Miocene; specimen MZ LXXc. **A.** Growth rings with abundant axial parenchyma (TS). **B.** Crossfield pitting (RLS). **C.** Uniseriate pits on tracheid walls (RLS). **D.** Bordered pits (arrow) on tangential walls of tracheids (TLS). **E.** Uniseriate rays (TLS). **F.** Beadlike thickenings (arrow) on axial parenchyma horizontal walls (TLS). Scale bars 50 µm.

characteristic of the group embracing *Cupressus* Linnaeus, 1753, *Diselma* Hooker, 1857, *Fitzroya* Hooker ex Lindley, 1851, *Juniperus* Linnaeus, 1753, and *Libocedrus* Endlicher, 1847 wood. In consideration of the significant similarity that exists within this group, the slight differences in their wood anatomy are used to identify the particular genera.

The species belonging to *Diselma* and *Fitzroya* are distinguished from the analysed specimen because of the smaller amount of axial parenchyma, pitted transverse walls of ray cells, more pits in the cross field and the presence of indentures. Additionally, *Diselma* is characterised by the presence of ray tracheids, while *Fitzroya* often possesses vestured pits. *Cupressus* and *Libocedrus*, in turn, are usually devoid of thickenings in tangential walls of ray cells; they often have pitted transverse walls of ray cells and possess indentures (Greguss 1955). The structure that shows greatest similarity to the analysed specimen is that of species of the genus *Juniperus*. Juniper is characterised by the presence of pronounced bead-like thickenings in the tangential walls of ray cells and it also possesses intercellular spaces visible in the cross-section of wood (Phillips 1941). Large intercellular spaces and rounded

tracheids can also signify the presence of compression wood (Schweingruber 1996). The analysed specimens have intercellular spaces, but do not otherwise show features typical of reaction wood. Thus this detail of anatomical structure supports its classification to *Juniperus*.

Stratigraphic and geographic range.— Tertiary; Europe and East Asia.

Morphogenus *Cupressinoxylon* Goeppert, 1850 (nom. cons.)

Type species: *Cupressinoxylon gothanii* Kraeusel, 1920; Tertiary, Miocene; Węgliniec, Silesia, Poland (typ. cons.).

Cupressinoxylon canadense (Schroeter, 1880) Kraeusel, 1949

Fig. 5A–F.

1880 *Sequoia canadensis* Schroeter, 1880; Schroeter 1880: 17, pl. 2: 11–21; pl. 3: 22–26.

1913 *Sequoia wellingtonioides* Prill, 1913; Prill 1913: 48.

1919 *Cupressinoxylon wellingtonioides* (Prill, 1913) Kraeusel, 1919; Prill and Kraeusel 1919: 293, pl. 22: 7, 8.

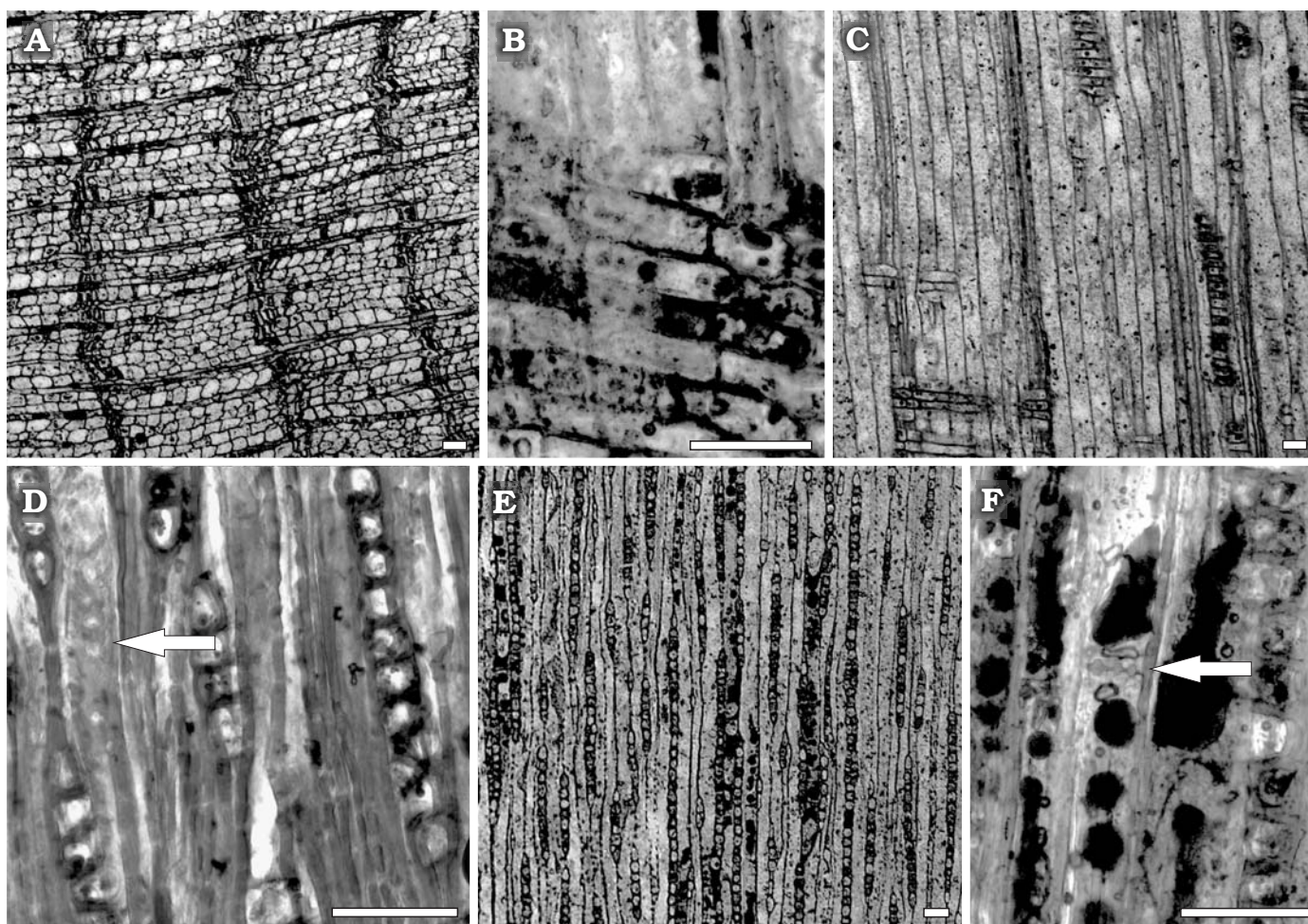


Fig. 5. Microphotographs of fossil wood *Cupressinoxylon canadense* (Schroeter, 1880) Kraeusel, 1949 from Hebdów, Middle Miocene; specimen MZ LXXII. **A.** Narrow growth rings (TS). **B.** Crossfield pitting (RLS). **C.** Bordered pits on radial walls of tracheids (RLS). **D.** Tangential walls of tracheids with bordered pits (arrow) (TLS). **E.** Tall, uniseriate rays (TLS). **F.** Horizontal walls of parenchyma cells with dentate thickenings (arrow) (TLS). Scale bars 50 µm.

1949 *Cupressinoxylon canadense* (Schroeter, 1880) Kraeusel, 1949; Kraeusel 1949: 175.

Material.—One coalified fragment of wood, about 10 cm long, sourced from Hebdów locality and marked as MZ LXXII (Fig. 5A–F).

Description.—The specimen comprises the part of the branch. Growth rings are narrow, with thin latewood layer (Fig. 5A). Axial parenchyma appears sparse. Transverse walls of parenchyma cells are smooth or sometimes with dentate thickenings (Fig. 5F).

Tracheids have angular shape and thin walls. On radial walls of tracheids occur uniseriate or biseriate bordered pits, 8.5–13 µm in diameter, arranged in opposite, continuous rows. Pits are circular or sometimes slightly compressed along the sides of contact. Pit apertures are also circular in earlywood or slit-like, obliquely oriented in latewood (Fig. 5C). Bars of Sanio occur frequently. Tangential walls of tracheids have bordered pits arranged in a single irregular, scattered row (Fig. 5D). Pits possess circular shape (8.5–10.5 µm in diameter) and slit-like, oblique apertures.

Rays are uniseriate or sometimes partially biseriate, 2–45 cells high (Fig. 5E). They are composed of oval or rectangular cells. Rays have thin and smooth, sporadically pitted transverse walls and smooth tangential walls with no indentures. Cross-field pits, 8–9 µm in diameter, in median cells form a single row, then 1–3 pits appear per field. In marginal cells, occur usually 2–6 pits organised in two rows (Fig. 5B). Pits have circular or oval outlines. Pit apertures are obliquely oriented in earlywood and latewood. Ray parenchyma often includes resinous contents. Ray tracheids occur rarely.

Remarks.—The described features of wood anatomical structure, especially the absence of resin canals, character of cross-field pitting and bordered pits on the walls of tracheids, indicate the affiliation of the examined specimen to *Cupressinoxylon canadense* (Schroeter, 1880) Kraeusel, 1949. *Cupressinoxylon canadense* was established by Kraeusel (1949) on the basis of previously defined taxa. This name referred to *Sequoia canadensis* originating from Miocene of North Canada (Schroeter 1880). Kraeusel (1949) interpreted as *Cupressinoxylon canadense* also Miocene wood from

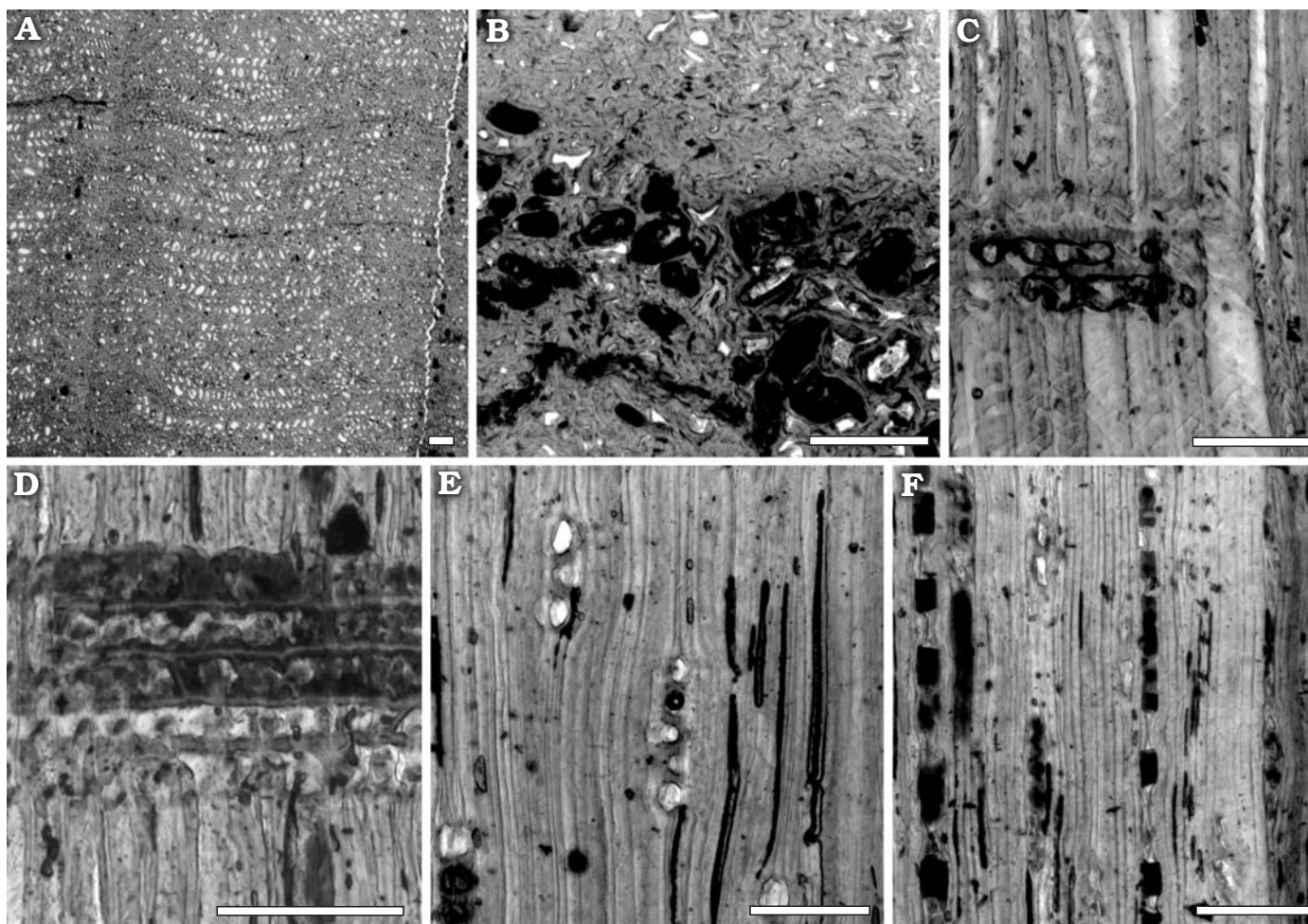


Fig. 6. Microphotographs of fossil wood *Cupressinoxylon polonicum* (Kostyniuk, 1938) Kraeusel, 1949 from Hebdów, Middle Miocene; specimen MZ LIX. **A.** Slightly disturbed growth rings (TS). **B.** Frost ring with deformed tracheids and rays (TS). **C.** Pitting on radial walls of tracheids masked by spiral checking of tracheid walls (RLS). **D.** Crossfield pitting (RLS). **E.** Short, uniseriate rays (TLS). **F.** Axial parenchyma (TLS). Scale bars 50 µm.

Opole (Poland). The taxonomical position of this wood was revised many times. It had been initially attributed to *Sequoia wellingtonioides* Prill, 1913 later re-classified to *Cupressinoxylon wellingtonioides* (Prill, 1913) Kraeusel, 1919 (Prill and Kraeusel 1919) and finally determined as *Cupressinoxylon canadense* (Kraeusel 1949). Taking into consideration living trees, analysed wood is most similar to the wood known from *Glyptostrobus* Endlicher, 1847, *Metasequoia* Hu and Cheng, 1948, *Taxodium* Richard, 1810, and *Sequoia* Endlicher, 1847. Among the mentioned genera, *Glyptostrobus* wood differs from the examined specimen in the presence of glyptostroboïd cross-field pitting, nodular transverse walls of wood parenchyma cells and the absence of ray tracheids. The rays are homogeneous also in *Metasequoia* and *Taxodium* wood. The wood of *Metasequoia*, *Taxodium*, and *Sequoia*, in distinction from the analysed specimen, possess taxodioid pits in the cross field. Moreover, the genus *Taxodium* is marked by the presence of conspicuous thickenings of transverse walls of axial parenchyma cells and occasionally up to triseriate bordered pits on radial walls of tracheids (Henry and McIntyre 1926; Visscher and Jagels 2003). The anatom-

ical structure of the analysed specimen is, in turn, consistent with giant sequoia wood (*Sequoiadendron giganteum* [Lindley, 1853] Buchholz, 1939). This species is characterised by the presence of cupressoid pits in the cross field. In fossil wood taxonomy, giant sequoia corresponds to *Cupressinoxylon canadense* species (Prill and Kraeusel 1919; Kraeusel 1949). This fact confirms above established classification.

Stratigraphic and geographic range.— Tertiary; Europe, North America.

Cupressinoxylon polonicum (Kostyniuk, 1938) Kraeusel, 1949

Fig. 6A–F.

1938 *Cupressinoxylon* sp.; Kostyniuk 1938: 44, pl. 3: 3, 4.

1949 *Cupressinoxylon polonicum* (Kostyniuk, 1938) Kraeusel, 1949; Kraeusel 1949: 175.

Material.—One fragment of coalified wood from the Hebdów locality, 10 cm long and marked as MZ LIX (Fig. 6A–F).

Description.—The wood is derived from branch and contains the pith. Growth rings have narrow latewood zone (Fig. 6A). Resin canals are absent. Axial parenchyma appears

abundantly (Fig. 6F) and forms tangential rows. Transverse walls of parenchyma cells usually are smooth or sometimes with beadlike thickenings.

Tracheids have thick walls. On the radial walls of tracheids appears uniseriate pitting, loosely spaced in latewood (Fig. 6C). Pits are bordered, circular or oval, 11–13.5 µm in diameter. Pit apertures have circular shape in earlywood and slit-like, oblique outline in latewood. Tangential walls of tracheids possess uniseriate, sparse pits. Pits are circular, 6.5–7.5 µm in diameter. They demonstrate narrow, obliquely oriented apertures.

Uniseriate rays, typically 2–9 cells high (Fig. 6E), are characterised by smooth transverse and tangential walls without indentures. Cross fields contain cupressoid pits, oval or circular in outline, 6.5–8.5 µm in diameter. Pits usually are arranged in one row, 1–2 pits occur in cross field (Fig. 6D).

Two separate damages, most likely frost rings, appear within this specimen (Fig. 6B). Frost rings in coniferous species are composed of underlignified, deformed tracheids, collapsed cells, bent rays and traumatic parenchyma cells (Glerum and Farrar 1966; LaMarche and Hirschboeck 1984). These disturbances have been observed in the analysed wood (Fig. 6B).

Remarks.—The type of tracheary and cross-field pitting, the character of ray cells and the absence of resin canals refer to the *Cupressinoxylon* genus. Among fossil taxa, the most similar species is *Cupressinoxylon polonicum* (Kostyniuk, 1938) Kraeusel, 1949. It is characterised by the occurrence of low, uniseriate rays and by the absence of ray tracheids. *Cupressinoxylon polonicum* was described for the first time from Bielany near Grójec (Kostyniuk 1938). This wood, collected from Pliocene formations, had been initially named as *Cupressinoxylon* sp., later, however, it was classified as a separate species (Kraeusel 1949). *Cupressinoxylon polonicum* does not have a defined counterpart among contemporary trees. This species is most similar to the group which encompasses *Platycladus* Spach, 1841, *Fokienia* Henry and Thomas, 1911, *Thuja* Linnaeus, 1753, *Thujopsis* Siebold and Zuccarini ex Endlicher, 1842, *Chamaecyparis* Spach, 1841, and *Microbiota* Komarov, 1923 woods. The first four genera differ from the analysed specimen because of the higher number of pits in the cross field and the presence of indentures. In the cases of *Platycladus*, *Thuja*, and *Thujopsis* disagreement results also from the existence of pitted transverse walls of ray cells. Moreover, *Platycladus*, *Fokienia*, and *Thuja* wood possesses uniseriate or biseriate bordered pits on radial walls of tracheids, while *Fokienia* and *Thuja* sometimes have biseriate or triseriate pits on tracheid tangential walls. Meanwhile, *Microbiota* wood is marked by the presence of smooth transverse walls of axial parenchyma cells as well as the occurrence of pitted transverse walls of ray cells (Schweingruber 1990; García Esteban et al. 2004). All these features allow those genera to be eliminated. The analysed specimen displays the highest similarity to *Chamaecyparis* wood. This fact is established on the basis of cupressoid type of cross-field pitting, the presence of uniseriate pits on radial and

tangential walls of tracheids and the occurrence of uniseriate rays up to 9 cells high.

Stratigraphic and geographic range.— Tertiary; Europe.

Discussion

The fossil wood species described in this paper have not been known in the area of Polish Carpathian Foredeep so far. However, their occurrence is registered in the close neighbourhood of an analysed region (see SOM: Supplementary Online Material available at http://app.pan.pl/SOM/app59-Klusek_SOM.pdf). The first described species, *Piceoxylon piceae* Roessler, 1937, is documented from the Miocene of Lower Silesia, from Węgliniec and Jaworów localities (Kraeusel 1913, 1920, 1949). The wood from Węgliniec had been initially classified as *Piceoxylon* sp. (Kraeusel 1920), and later defined accurately, by the same author as *Piceoxylon piceae* (Kraeusel 1949). A similar situation occurred in the case of the wood from the Jaworów site. First it was described as *Picea* sp. (Kraeusel 1913), and then specified as *Piceoxylon piceae* (Kraeusel 1949).

Apart from this taxon, there are plenty of other Tertiary *Piceoxylon* woods described from neighbouring areas. One of them is *Piceoxylon arcticum* (Schmalhausen, 1890) Kraeusel, 1949 that is the equivalent to the undetermined species of living larch (Kraeusel 1919). *Piceoxylon arcticum* is noted from the Miocene of Gliwice and Żarów. The woods coming from these sites had been initially ascribed to *Larix silesiaca* Kraeusel, 1913 (Kraeusel 1913). Then the specimen from Gliwice was reassigned to *Piceoxylon laricinum* Kraeusel, 1919 and the specimen from Żarów to *Piceoxylon* sp. (*laricinum*?) Kraeusel, 1919 (Prill and Kraeusel 1919). Finally, both of them were identified as *Piceoxylon arcticum* (Kraeusel 1949). Similarly, the Miocene wood *Piceoxylon laricinum* originating from Posądz near Kraków (Rubczyńska and Zabłocki 1924) was also reclassified as *Piceoxylon arcticum* (Kraeusel 1949).

The next *Piceoxylon* species described from other areas of Poland are *Piceoxylon pseudotsugae* Gothan, 1906 from the Miocene of Konin (Grabowska 1956) and *Piceoxylon macrocarpum* (Prill, 1913) Kraeusel, 1919 from the Miocene of Gliwice (Reyman 1956). *Piceoxylon macrocarpum* is also detailed from Miocene locality in Opole (Prill and Kraeusel 1919), but in this case, it had been initially assigned as *Pseudotsuga macrocarpa* var. *miocenica* Prill, 1913 (Prill 1913). Both of these mentioned *Piceoxylon* species differ significantly from the spruce wood and both of them are closely related to the extant *Pseudotsuga* Carriere, 1867. According to Kraeusel 1919, the first is most similar to *Pseudotsuga douglasii* Carriere, 1867 and the second corresponds to *Pseudotsuga macrocarpa* Mayr, 1900.

From the close neighbourhood of the Carpathian Foredeep are also known *Piceoxylon* woods with unspecified affinity. This group includes the woods of *Picea* sp. and

Piceoxylon sp. from the Pliocene of Krośnice (Kostyniuk 1950), as well as the wood of *Piceoxylon* sp. from the Miocene of Otwock (Kostyniuk 1938). Kraeusel (1919) defined as *Piceoxylon* also some Tertiary specimens from Ostrołęka and Łazany, assigned previously to *Taxites ayckii* Goeppert, 1850, as well as Tertiary woods originating from Lubliniec and earlier described as *Pinites silesiacus* Goeppert, 1850 (Goeppert 1850). Taxonomic classification of all these woods remains questionable and both larch and spruce may be their nearest living relatives (Kraeusel 1919).

Miocene woods belonging to *Juniperoxylon pachyderma* (Goeppert, 1850) Kraeusel, 1949 are especially numerous from the Silesia region. Among them occur specimens originating from Gliwice, Radomierzyce, Zielona Góra, Nowa Wieś Królewska, and Zgorzelec. The specimens from Zielona Góra had been initially described as *Juniperus silesiaca* Prill, 1913 and *Juniperus pauciporosa* Prill, 1913 (Prill 1913), and later reclassified as *Juniperoxylon silesiacum* (Prill, 1913) Kraeusel, 1919 and *Juniperoxylon pauciporosum* (Prill, 1913) Kraeusel, 1919 respectively (Prill and Kraeusel 1919). Similarly, the woods from Gliwice and Radomierzyce at the beginning were assigned to *Juniperoxylon pauciporosum* (Prill and Kraeusel 1919) and the woods from Zgorzelec had been ascribed to *Juniperoxylon silesiacum* (Kraeusel 1920). In turn, the wood from Nowa Wieś Królewska, had been identified as *Juniperoxylon* sp. (Kraeusel 1920). Finally, all these specimens were reassigned to *Juniperoxylon pachyderma* (Kraeusel 1949).

As for *Juniperoxylon pachyderma*, numerous Miocene woods from Turów open pit lignite mine were also assigned to this taxon (Zalewska 1953; Kostyniuk 1967). Moreover, among the specimens from Turów new species belonging to the *Juniperoxylon* were defined. The first of these is *Juniperoxylon lusaticum* Kostyniuk, 1967 having the anatomical structure similar to the present-day *Juniperus* Linnaeus, 1753, but differing from it by taxodioid pits in cross-fields (Kostyniuk 1967). The next described species from Turów is *Juniperoxylon glyptostroboides* Kostyniuk, 1967, similar to living *Juniperus* and *Heyderia* Koch, 1873. Its specific characteristics are simple pits in cross-fields (Kostyniuk 1967). Another species classified from Turów as *Juniperoxylon turoviense* Kostyniuk, 1967, possesses the features of extant *Juniperus* and *Athrotaxis* D. Don, 1838 genera but has also taxodioid pits on cross-fields (Kostyniuk 1967). Later, however, two of these new species were transferred to *Taxodioxylon* Hartig, 1848. These were *Taxodioxylon lusaticum* (Kostyniuk, 1967) Suess and Rathner, 1998 and *Taxodioxylon turoviense* (Kostyniuk, 1967) Suess and Rathner, 1998 (Suess and Rathner 1998).

The following site, where wood of *Juniperoxylon* type was recorded, is Dobrzyń on the Vistula River. The Miocene woods from this site were classified as *Juniperoxylon silesiacum* and *Juniperoxylon* sp. (Kownas 1951). Furthermore, part of the specimens from Dobrzyń became the basis for the creation of a new species, *Taxodioxylon juniperoides* Kownas, 1951. This wood is closely related in its anatomic structure to *Juniperoxy-*

lon, but, similarly to the species of Turów, it has taxodioid pits in its cross-fields (Kownas 1951). Some Miocene woods from Konin open pit lignite mine were also assigned to this new species (Grabowska 1956). The name *Taxodioxyton juniperoides*, however, was deemed to be invalid and the woods were reclassified as *Juniperoxyton juniperoides* (Kownas, 1951) Huard, 1966 (Huard 1966; Suess and Velitzelos 1997).

Miocene wood ascribed to *Cupressinoxylon canadense* (Schroeter, 1880) Kraeusel, 1949 have been found, in the vicinity of Opole and Węgliniec. The wood from Opole had been initially described as *Sequoia wellingtonioides* Prill, 1913 (Prill 1913), later reclassified to *Cupressinoxylon wellingtonioides* (Prill, 1913) Kraeusel, 1919 (Prill and Kraeusel 1919) and finally to *Cupressinoxylon canadense* (Kraeusel 1949). Also the specimen from Węgliniec had been originally assigned to *Cupressinoxylon wellingtonioides* (Kraeusel 1920). Furthermore, *Cupressinoxylon canadense* is known from the Miocene of Dobrzyń on the Vistula River (Kownas 1951) (as *Cupressinoxylon wellingtonioides*) and from the area of the Turów open pit lignite mine (Zalewska 1953). In turn, *Cupressinoxylon polonicum* (Kostyniuk, 1938) Kraeusel, 1949 was described from Pliocene of Bielany near Grójec as *Cupressinoxylon* sp. (Kostyniuk 1938). *Cupressinoxylon polonicum* was also recorded from Miocene deposits of Turów (Zalewska 1953) and Konin lignite mines (Grabowska 1956).

The woods of *Cupressinoxylon* type are exceptionally numerous in the fossil record (Bamford et al. 2002). Therefore, there are also many other *Cupressinoxylon* species originated from close vicinity of the Carpathian Foredeep anatomically similar to the wood described in this paper. Miocene woods that belong to this morphotype are *Cupressinoxylon gothani* Kraeusel, 1919 from Węgliniec, *Cupressinoxylon cupressoides* Kraeusel, 1919 from Zaręba (Kraeusel 1920) and *Cupressinoxylon hausricanum* Hofmann, 1927 from Turów lignite mine (Zalewska 1953). The first of these is equivalent to the present-day genera of *Callitris* Ventenat, 1808 and *Widdringtonia* Endlicher, 1842, the second one corresponds to *Cupressus* Linnaeus, 1753 and *Chamaecyparis* Spach, 1841, and the third one—to *Cryptomeria japonica* D. Don, 1839 wood (Kraeusel 1919, 1949). The next species of *Cupressinoxylon* is *Cupressinoxylon luckense* (Kostyniuk, 1938) Kraeusel, 1949 that was noted from Oligocene or Miocene sediments in Niebożka near Łuck (Kostyniuk 1938). The wood from Niebożka had initially been named as *Cupressinoxylon* sp. Then, on this basis, the diagnosis of a new species was established (Kraeusel 1949). *Cupressinoxylon luckense* wood was afterwards recognised also among Miocene lignites of Konin (Grabowska 1956).

On the other hand, the significant amount of Tertiary woods of the Foredeep vicinity, assigned initially to various species of *Cupressinoxylon*, was later re-classified to other taxa. Kraeusel (1919, 1949) assigned Miocene woods *Cupressinoxylon aequale* Goeppert, 1850 from Łazany and Żarów (Goeppert 1850) and *Cupressinoxylon aequale* (Goeppert, 1850) Conwentz, 1881 from Nowogrodziec in Silesia (Conwentz 1881) to *Taxodioxydon gypsaceum* (Goep-

pert, 1842) Kraeusel, 1949 or, conditionally, *Taxodioxyton taxodii* Gothan, 1906. Similar transformation involved also the following Miocene woods: *Cupressinoxylon leptotichum* Goeppert, 1850 from Łaźany and Zielona Góra, as well as *Cupressinoxylon multiradiatum* Goeppert, 1850 and *Cupressinoxylon opacum* Goeppert, 1850 from Łaźany (Goeppert 1850). More unambiguous classification, as *Taxodioxyton gypsaceum*, was possible for *Cupressinoxylon fissum* (Goeppert, 1850) Conwentz, 1882 from Miocene of Skorogoszcz (Conwentz 1882), and for *Cupressinoxylon nodosum* Goeppert, 1850 and *Cupressinoxylon subaequale* Goeppert, 1850 from Miocene of Łaźany (Goeppert 1850). The other Miocene species, namely: *Cupressinoxylon fissum* Goeppert, 1850 from Zielona Góra, *Cupressinoxylon pachyderma* Goeppert, 1850 from Łaźany (Goeppert 1850) and *Cupressinoxylon juniperoides* Kraeusel, 1913 from Gliwice and Radomierzyce in Silesia (Kraeusel 1913), were assigned by Kraeusel (1919, 1949) as *Juniperoxylon pachyderma*.

The main problem with *Cupressinoxylon* classification is the huge number of species that are frequently very similar in anatomic features (Kraeusel 1949). It seems that a renewed, critical review of these taxa is necessary. In addition, the diagnosis of *Cupressinoxylon* genus itself requires specification and updating (Bamford et al. 2002; Dolezych and Schneider 2006). Because of the existing terminology problems, many woods of *Cupressinoxylon* remain without precise species diagnosis. For example, Miocene woods originating from Skorogoszcz (Prill 1913; Prill and Kraeusel 1919), Dobrzyń on the Vistula River (Lilpop 1917; Kownas 1951), Turów (Zalewska 1953; Kostyniuk 1967), and Konin lignite mines (Grabowska 1956) were named only as *Cupressinoxylon* sp. The case of one of them, namely *Cupressinoxylon* sp. from the Turów open pit mine (Kostyniuk 1967), shows that the outdated, inaccurate classification might be updated. The wood from Turów was believed to be identical to the specimens from the Welzow mine in Germany. On this basis, a diagnosis of a new species *Cupressinoxylon kostyniukii* Dolezych, 2006 (Dolezych and Schneider 2006) was defined.

Concluding remarks

The Miocene fossils studied in this paper were identified as *Piceoxylon piceae*, *Cupressinoxylon canadense*, *Juniperoxylon pachyderma*, and *Cupressinoxylon polonicum*. The nearest living relatives of these species are, in sequence: the Norway spruce, the giant sequoia and undefined species of juniper and cypress. Apart from the giant sequoia, these taxa have wide present-day geographical and habitat ranges (Schweingruber 1993). Only the giant sequoia occurs in the region limited to the western slopes of the Sierra Nevada Mountains (Harvey et al. 1980). This is, however, a relict distribution of this tree, which does not permit an authoritative opinion about the requirements of Miocene trees. The other factor which limits the possibility of drawing conclusions concerning the palae-

oecological conditions from taxonomical results obtained is the rather small number of wood species determined.

In spite of this, some observed features of the analysed wood may be helpful in reconstructing the Miocene environment. The first is the presence of growth rings in all analysed samples from the Carpathian Foredeep. This fact points to seasonal climate fluctuations (Creber and Chaloner 1984). However, the development of growth rings is not determined by weather effect alone. Some tree species form rings even in areas characterised by uniform external conditions. In these cases, the presence of growth interruptions depends on genetic legacy and is not influenced by external factors (Creber 1977; Brison et al. 2001). This kind of ring usually shows great variability in width and has a small portion of latewood. These increments distinguish themselves also by a symmetrical distribution of cell sizes on both sides of ring boundaries and by a lack of continuity around the circumference of the stem (Ash and Creber 1992; Falcon-Lang 2003). Nevertheless, such features do not correspond to the way the growth rings developed in the analysed wood. Moreover, only the absence of true growth rings in the prevailing number of trees from the examined territory indicate that they grew under non-seasonal conditions. Therefore, the occurrence of regular growth rings, distinctly marked throughout the whole circumference of the stem, in all analysed woods from the Carpathian Foredeep, as well as in the other Miocene woods from neighbouring localities, proves the seasonal changeability of the palaeoenvironment.

Seasonality of temperature and rainfall in the Miocene Epoch is also evidenced by the results of other palaeontological research (Boucot and Gray 2001; Mosbrugger et al. 2005). This research demonstrates that a warm temperate and humid climate prevailed in the area of the Central Paratethys (Böhme 2003; Böhme et al. 2007; Syabryaj et al. 2007). On the other hand, the results of ectothermic vertebrate research proved also the occurrence of frost periods (Böhme 2003). The existence of presumable frost rings within *Cupressinoxylon polonicum* wood may support this assumption. Such rings are formed when, during cambium activity, the air temperature drops below freezing point (LaMarche and Hirschboeck 1984; Raitio 1992). Similar disturbance zones within growth rings could develop as a result of insect activity, bacterial infection, local damages caused by fire and mechanical injury or as an effect of diagenetical changes of wood (Glerum and Farrar 1966; Schweingruber 1996). However, the frost origin of the aforementioned damage is highly probable if one assumes that the wood had been transported from the Carpathian area. This region was characterised by a lower temperature of the cold months and more seasonal changeability in comparison with the lower-lying neighbourhood stands (Bruch et al. 2007; Utescher et al. 2007). Moreover, analysed rings occur within the fragment of branch or young stem. These parts of tree are covered with thin layer of bark and are predisposed to frost rings development (Chapman 1994). This additionally supports presented presumption.

Acknowledgements

I would like to thank to the late Stanisław Brud (Jagiellonian University, Kraków, Poland) for donating the specimens of fossil woods and for describing their occurrence in the area of the Carpathian Foredeep. I thank the reviewers, Marc Philippe (Université Claude Bernard Lyon 1, Villeurbanne, France), Mihai E. Popa (University of Bucharest, Romania) and an anonymous reviewer, for the detailed review and constructive comments.

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