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Fossil wood from the Roztocze region (Miocene, SE Poland) — a tool for palaeoenvironmental reconstruction

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This article presents the results of anatomical and growth ring analyses of Badenian fossil wood from the Roztocze region. All the wood specimens examined are classified as *Taxodioxylon taxodii* Goth. The growth rings of these woods are very narrow, and they vary considerably in width. Tracheids have large diameters and thin cell walls.The latewood zone is wide; the transition between early and latewood is gradual. Both false and wedge rings and also reaction wood zones are often found. These characteristics of the fossil wood make it a suitable aid to reconstructing the environmental conditions prevailing while the trees were alive. The environmental requirements of these ancient Roztocze trees are interpreted by comparison with those of their nearest living relatives, with the conclusion that they lived in waterlogged or temporarily flooded stands under seasonally changing environmental conditions and with a long growing season. The climate was warm and humid and characterized by significant variability, mainly as regards the amount of precipitation.

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INTRODUCTION

Like other types of animal or plant fossil, wood remains carry information about the environmental conditions that existed while the trees were alive. The character of palaeoclimatic factors is usually reconstructed on the basis of the taxonomic identification of fossil remains, so that the climatic requirements of ancient species can be compared with those of their nearest living relatives (Mosbrugger and Utescher, 1997). However, analysis of the growth rings of fossil wood can shed further light on palaeoclimatic factors.

Besides the genetically determined characteristics of individual species, the manner of growth ring development depends mainly on temperature, water supply and the duration of the growing season (Creber and Chaloner, 1984). The influence of these environmental factors on trees is often expressed within their wood by variation in the number and size of the cells as well as by the thickness of cell walls. As a result, wood is characterized by nonuniform growth ring width and a variable ratio of early and latewood zones (Chaloner and Creber, 1973; Creber and Chaloner, 1985). Detailed analyses of fossil wood and the interpretation of palaeoenvironmental conditions based on such analyses are the subject of palaeodendrological studies (Creber and Francis, 1999).

Examples of palaeodendrological analyses are especially numerous for sites lying in polar regions (Jefferson, 1982; Francis, 1986, 1991; Parrish and Spicer, 1988; Spicer and Parrish, 1990; Kumagai *et al*., 1995; Francis and Poole, 2002) and also those in Britain and the United States (Francis, 1983, 1984; Morgans, 1999; Morgans *et al*., 1999; Falcon-Lang, 1999*a*, *b*, 2003; Wheeler and Lehman, 2005). In Poland there have to date been no studies devoted to palaeodendrological analysis, although the presence of fossil wood in some regions provides a convenient opportunity for such research.

The Roztocze area is one such place. Accumulations of mineralised tree trunks and smaller pieces of wood have long been known to occur here. The first reports on "petrified trees in Roztocze" appeared as early as in the 15th century, when Jan Długosz described them in his Chronicle as one of "...two peculiarities of the Polish country..." (*cf*. Buraczyński, 2002). The present paper presents a study of fossil wood originating from the Roztocze area on the basis of anatomical and growth ring analyses, with the aim of reconstructing the environmental conditions in this area during the Badenian stage.

MATERIAL

Petrified wood was obtained from the Roztocze Rawskie region, mainly from the village of Siedliska (Fig. 1). Some material was also taken from the region of Lubycza Królewska and Hrebenne. In addition, some specimens belonging to private collections of Roztocze fossil wood were also used for the analyses. A proportion of the examined specimens is now stored in the collection of the Herbarium and Palaeobotanical Museum at the Institute of Botany of the Jagiellonian University.

Fragments of fossil wood were taken from a layer of modern soil. Dating these remains is enabled by earlier finds of Roztocze woods which have been described in the literature. Fossil wood derived from primary deposits is known from the areas of Goraj, Chrzanów and Lipowiec, as well as from the Roztocze Lwowskie region, where they have been described from the areas of Chlebowice, Glińsko, Łozina, Stracz and Gliniska near Żołkiew (Brzezińska, 1961; Areń, 1962, 1992; Buraczyński, 2002; Radwański and Wysocka, 2001; Maruszczak, 2001). On the basis of the age of the deposit in which these woods were found *in situ*, it is clear that the fossil age should be linked with the Early to Mid Badenian stage.

The fact that petrified woods from the Roztocze region most often occur in secondary deposits is the result of erosion and weathering which led to the partial removal of Neogene deposits from this area. It is also an effect of later redeposition associated with the activity of continental glaciers during the Pleistocene (Rzechowski, 1997; Brzyski, 1998).

All of the wood analysed came from secondary deposits. The size of the specimens studied ranged from several to tens of centimetres. The material was preserved in the form of fragments of trunks and large branches. Samples of small twigs or roots were very seldom analysed. Specimen surfaces were smooth and rounded and frequently covered with “desert varnish” (Fig. 2A), the latter forming after the wood had mineralised, in the desert climate present in the Roztocze area at the end of the Miocene (Areń, 1992; Maruszczak, 2001). The surface of the analysed wood also bore numerous dwarf shoot traces (Fig. 2B). Moreover, borings left by wood-eating insects were visible in some specimens (Fig. 2C). There was no other biological damage in the wood, and the presence of deformed or crushed parts of specimens was burial-related. Wood structure preservation depended also on the degree of mineral crystallisation (Fig. 2D).

Mineralogical studies showed the structure of the petrified wood to be best preserved in parts of specimens originally mineralised with chalcedony. The wood anatomy is less distinct or completely invisible in places where chalcedony has recrystallised into quartz and in specimens impregnated with cryptocrystalline silica (Heflik, 1996). Mineralogical studies showed also that besides these main silica compounds, the fossil wood include admixtures of pyrite, allophanes and organic mater (Heflik, 1996).

Fig. 1. Simplified geologic map of the South Roztocze area (without Quaternary cover), showing the location of sampling sites (white circles); modified after Cieśliński *et al.*, (1994)

METHODS

Due to the abundance of the study material, a preliminary selection of specimens was made. For anatomical studies, the most morphologically differentiated material was selected, to provide greater taxonomic variety. For growth ring analysis only wood from the external layers of trunks was used, since the manner of growth ring development depends on the age of a tree and also on the function of its organs (Schweingruber, 1990; Chapman, 1994). Assessment of whether a specimen belongs to a trunk, branch or twig was based on observing ring curvature and the divergence of rays. It was also decided that wood selected for growth ring measurement should have at least 24 rings, since shorter sequences do not provide reliable results during their mutual correlation. Using these criteria, 106 fragments of mineralised wood were used for anatomical analysis and only 25 specimens qualified for tree ring research.

For anatomical analysis, standard petrographic thin sections were used. Sections were prepared for each specimen along three perpendicular planes: transverse (TS), radial longitudinal (RLS) and tangential longitudinal (TLS). Measurements of individual cellular elements of wood were taken using a microscope eyepiece equipped with a micrometer scale. Photographic documentation was carried out using an *Olympus BX51* transmission light microscope coupled with a *DP12* camera.

In order to determine the details of anatomical structure, which are hard to discern under an optical microscope, scanning microphotographs were made of 41 specimens. Fragments of wood several millimetres long were taken for scanning electron microscopy. To obtain a more distinct surface the wood was briefly immersed in a 10% solution of hydrofluoric acid (for approx. one minute). Etching time and acid concentration were selected individually for each specimen. For the scanning examination a *Philips XL 30* microscope was used.

Growth ring analysis was performed on wood cut along its transverse plane. Measurements were often taken along several

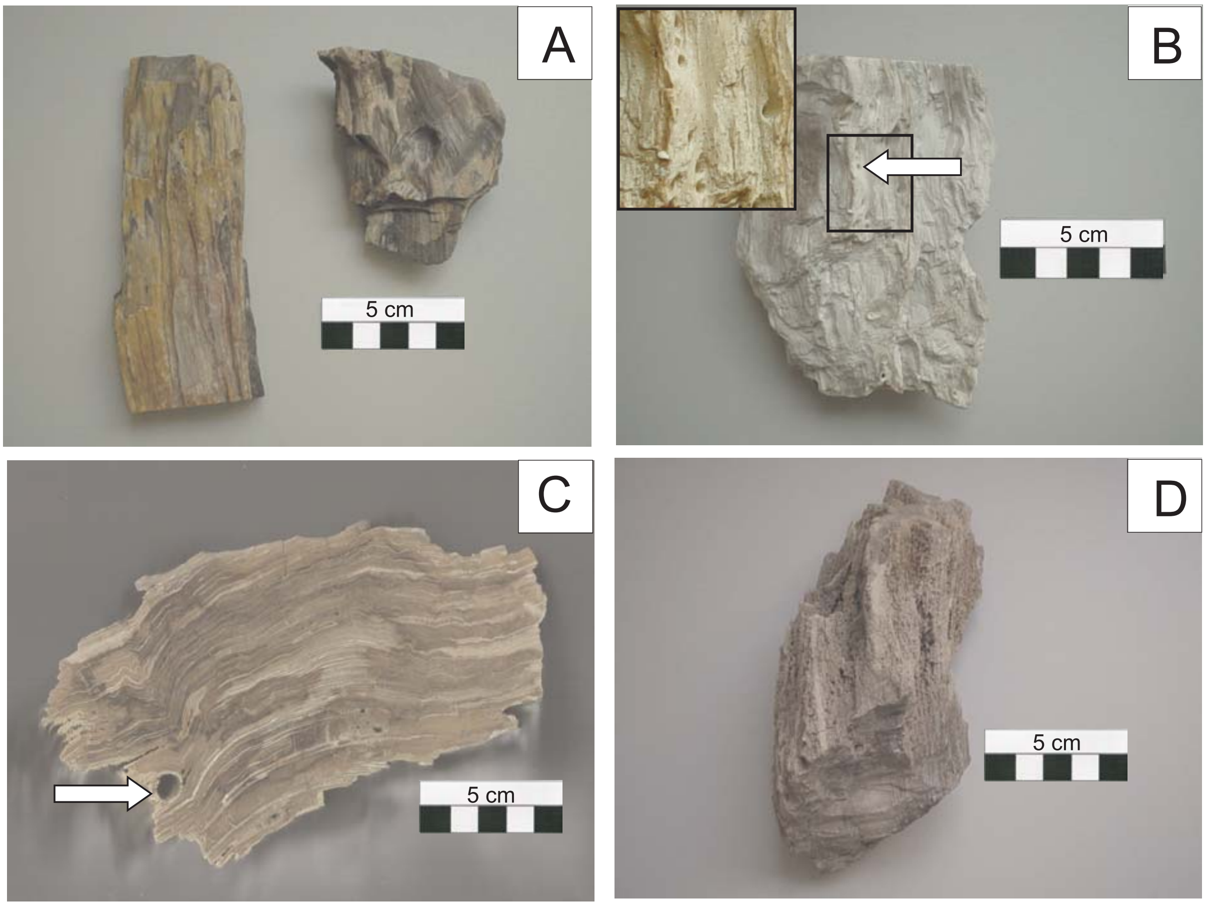


Fig. 2. Wood from the Roztocze area

A — wood surface covered by layers of desert varnish (specimens XXIII and XLV), **B** — dwarf shoot traces (specimen II), **C** — distinct growth rings and borings formed due to the activity of wood-eating insects (specimen ROZ 25), **D** — coarse crystalline silica mineralization (specimen VI)

radii, in order to eliminate crushed or mineralised zones that disturbed the structure of growth rings. DENDROLAB measuring equipment was used, making it possible to determine tree ring width with a precision of up to 0.01 mm (Zielski and Krąpiec, 2004).

Sequences of rings obtained as a result of the measurements taken were compared with each other using standard correlation procedures used in dendrochronological analyses (Cook and Kairiukstis, 1990). This was undertaken in order to establish whether there were specimens from trees of the same age or possibly belonging to the same trunk among the material analysed. To define the similarity of measurement sequences, linear correlation coefficients and "*t*" values were calculated for individual pairs of the sequences, using *TRRAD* software (Zielski and Krąpiec, 2004). The ring sequences were also compared visually. A graphic analysis was carried out with *QUERCUS* software (Walanus, 2005).

The next stage of growth ring examination was to establish the coefficients of annual sensitivity (*AS*) and mean sensitivity (*MS*) for the analysed wood. These coefficients were obtained using the following formulae (Douglass, 1936):

$$AS = \left| \frac{2(x_{t+1} - x_t)}{x_{t+1} + x_t} \right| \qquad [1]$$

where: x — ring width, t — year number of each ring.

$$MS = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(x_{t+1} - x)_t}{x_{t+1} + x_t} \right| \qquad [2]$$

where: x and t are as above, n — number of rings.

Annual sensitivity expresses the difference in width for two consecutive rings, while mean sensitivity expresses ring width variability within a longer measurement sequence. Values of *AS* and *MS* can, in theory, range from 0 for rings with no width changes, to 2 for increments with the greatest variation in width. In practice, it is assumed that rings for which the *MS* coefficients are below 0.3 were formed in favourable climatic conditions. These rings are called "complacent" as opposed to "sensitive" rings for which *MS* values are above 0.3. Such high *MS* values indicate the influence of changing, growth-limiting external conditions on a tree (Fritts, 1976).

During growth ring analysis the ratio of early to latewood was also established. Measurements of tracheid radial diameter were made for 50 selected rings with well-preserved wood tissue. Examinations were carried out in transverse thin sections of woods, using micrometer scales mounted in the microscope eyepiece. Analyses were made along a single row of cells forming a ring. From the measurements taken, a sequence of cumulative algebraic sums of deviations from the mean of the radial cell diameters was obtained. A graph representing these together with measurement values of cell radial diameter was used to determine the boundary between early and latewood zones (*cf*. Creber and Chaloner, 1984).

RESULTS OF ANATOMICAL ANALYSIS

The results of anatomical analysis showed all the specimens of fossil wood from the Roztocze region to represent the same type of anatomical structure. On this basis the woods were classified as follows:

Taxodioxylon (Hartig) Gothan, 1905
Taxodioxylon taxodii Gothan, 1906
(Gothan, 1906, 176, fig. 1–4)

Diagnostic criteria based on wood anatomy. Coniferous wood with distinct growth rings (Fig. 3A, B, C). Transition from early- to latewood mostly gradual. Width of growth rings and number of tracheids in early- and latewood very variable (see next paragraph).

Outline of tracheids rectangular or polygonal, slightly rounded; in latewood cells radially flattened (Fig. 3A, B, C). Radial diameters of tracheids 50–60 μm in earlywood and 10–20 μm in latewood zones. Tangential diameter of tracheids 20–50 μm. Thickness of tracheid walls 3–4 μm in earlywood and 5–6 μm in latewood. Bordered pits on radial walls of tracheids (Fig. 3D) mostly uniseriate or biseriate, occasionally up to triseriate. In multiseriate rows pits aligned opposite. Pits contiguous and sometimes slightly compressed along the sides of contact in earlywood and more spaced out in latewood. Bars of Sanio frequently present. Pits circular or slightly flattened (diameter 14.5–17.5 μm) possessing circular apertures in earlywood and short-elliptic, obliquely oriented apertures in latewood. Bordered pits on tangential walls confined to latewood. Pits circular (9.0–12.5 μm in diameter), arranged in a single irregular, scattered row. Pit apertures elliptical or slit-like, obliquely oriented.

Axial parenchyma (Fig. 3F) partially filled with remains of resinous contents, diffusely distributed throughout growth ring or aligned in tangential bands. Diameter of parenchyma cells 30–70 μm. In longitudinal sections cells rectangular or barrel-shaped, 60–120 μm in height. Horizontal walls of parenchyma elements thick and nodular (Fig. 3F).

Adjacent rays separated by 2–12 rows of tracheids (Fig. 3A, B, C). Rays entirely parenchymatous, uni- or sometimes partially biseriate, 1–35 cells high (Fig. 3F). Horizontal walls of ray cells 3–4 μm thick and occasionally with simple pits. Tangential walls thin and smooth, 2–3 μm thick, vertical or oblique. Identures absent. Rays composed of cells 60–160 μm in length, 16–28 μm in height, and 16–32 μm in width. Crossfield pits (Fig. 3E) in median cells in a single horizontal row, 1–3 pits per field. In marginal cells usually 2–6 pits arranged in two rows. Pits circular or short-elliptical (7.5–10.0 μm in diameter), with apertures large and horizontal in earlywood and slit-like, obliquely oriented in latewood.

The features of anatomical structure presented above, especially the type of tracheary pits, the taxodioid earlywood crossfield pitting, the entirely parenchymatous rays with generally smooth and thin walls, and the absence of resin ducts, placed these woods in the genus *Taxodioxylon*. The analysed fossils were precisely assigned to the species *Taxodioxylon taxodii* Goth. on the basis of nodular thickenings on the horizontal walls of axial parenchyma cells. From the point of view of wood anatomy, a modern counterpart of this taxon is the bald cypress (*Taxodium distichum* (L.) Rich.; Kräusel, 1919; Zalewska, 1955).

RESULTS OF GROWTH RING ANALYSIS

Analysis of fossil wood from the Roztocze region showed it to have distinct and narrow growth rings, which are variable in width and have a wide latewood zone. The presence of reaction wood and false or wedging rings is also characteristic of this wood.

The examined reaction wood zones showed an increase in ring width, a higher proportion of latewood and a more gradual transition between early and latewood than normal. Tracheid walls in the reaction wood were also found to be rounded and thicker (Fig. 3C). Wedging rings which occurred in some specimens were visible as places in which width decrease led to the disappearance of rings (Fig. 3B). False rings are often present, both within early and latewood zones. False rings are marked by a gradual decrease in cell diameter and increase in wall thickness, after which there is a smooth transition to larger lumens and thinner tracheid cellular walls (Fig. 3A). Due to the anomalies described and the frequent waviness of rings only fragments of specimens with undisturbed wood structure were selected for growth ring measurements.

The number of rings within sequences obtained from these measurements ranged from 24 to 125 for individual specimens. Ring width varied from 0.07 to 4.04 mm, the mean being 0.87 mm. In the majority of specimens (73%) the mean width of the rings was below 1 mm. Maximum ring width was over 2 mm in 35% of measured sequences. Detailed results of the analyses are presented in Table 1 and Figure 4.

The measured sequences of rings were compared with each other by calculating correlation coefficients and by analysing graphs. However, no ring sequences exhibiting sufficient mutual similarities were found for them to have belonged to trees of the same age. The reason for this may be that the wood analysed most probably represents a broad timespan.

The results of growth ring measurements were also used to determine annual sensitivity (*AS*) and mean sensitivity (*MS*) coefficients. Calculated *AS* values showed the existence of a similar proportion of ring pairs for which *AS* values were below and above 0.3 (Table 1). Despite this, the *MS* coefficient expressing general variability in the ring width was frequently over 0.3 (in 73% of specimens) and was 0.36 on average. The reason for these high *MS* values was the irregular occurrence of very high *AS* coefficients within the ring sequences of the wood analysed (Fig. 5).

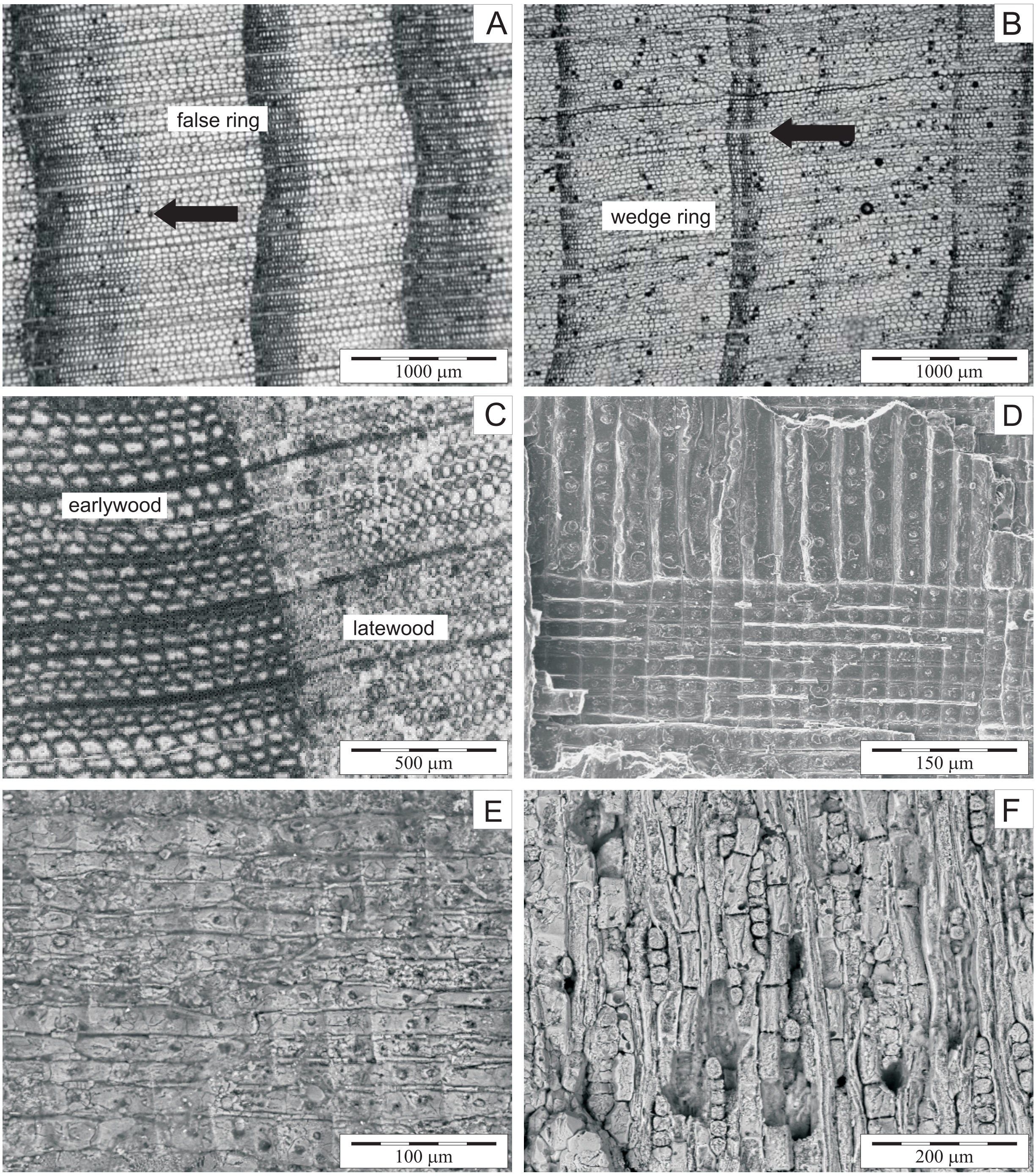


Fig. 3. ***Taxodioxylon taxodii*** **Goth. from the Roztocze region**

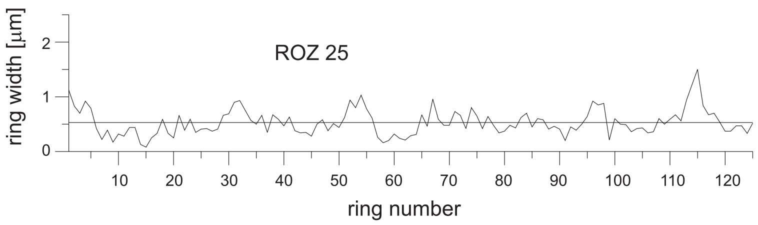
A — false ring (specimen 200/30), TS; **B** — wedging ring (specimen VIII), TS; **C** — growth ring boundary within reaction wood (specimen XI), TS; **D** — cross-field pits and intertracheary pitting (specimen III), RLS; **E** — cross-field with taxodioid pits (specimen XXXVIII), RLS; **F** — uniseriate rays and axial parenchyma cells with nodular thickening of horizontal walls (specimen L), TLS; A, B, C — pictures taken through an optical microscope; D, E, F — scanning microphotographs

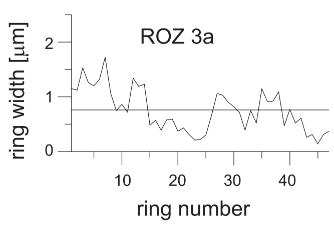
Detailed analysis of individual growth rings allowed also the ratio of early to latewood to be determined; this was based on measurements of tracheid radial diameter. The rings analysed were found to start with earlywood for which average cell diameter ranged from 50 to 60 μm. The size of the last rows of tracheids was usually 10–20 μm. The variability in cell diameter within an individual ring was frequently associated with the existence of false rings (Fig. 6). These analyses showed also that the specimens studied were characterized by a gradual transition from early to latewood and by a wide latewood zone. The latewood band was usually 20–30% of the whole ring width (Fig. 7).

Table 1

Results of growth ring analysis

Specimen number	Number of rings	Mean ring width [mm]	Minimum ring width [mm]	Maximum ring width [mm]	Mean sensitivity	Percent of ring pairs with *AS*≥0.3	Number of false rings	Number of wedge rings
ROZ1	27	1.15	0.65	1.67	0.26	46.2		
autoROZ 2	30	0.61	0.27	1.12	0.21	31.0		
ROZ 3a	47	0.76	0.14	1.72	0.33	50.0	1	
ROZ 3b	79	0.45	0.11	1.05	0.40	57.7		
ROZ 4	36	0.96	0.40	1.95	0.28	34.3	3	
ROZ 5	46	0.44	0.12	1.33	0.63	73.3		
ROZ 6	43	0.57	0.26	1.15	0.36	54.8		1
ROZ 7	28	1.20	0.42	2.85	0.49	77.8		
ROZ 8	43	1.31	0.22	4.04	0.40	50.0		
ROZ 9	51	0.87	0.32	1.85	0.23	30.0	1	
ROZ 10	29	1.64	0.21	3.34	0.34	39.3		
ROZ 11	33	0.95	0.31	1.96	0.31	40.6	1	
ROZ 12	43	1.00	0.25	1.69	0.34	50.0		
ROZ 13	46	0.74	0.17	2.59	0.40	57.8		
ROZ 14	30	0.67	0.16	2.10	0.43	51.7		
ROZ 15	24	2.00	0.36	3.38	0.44	60.9	5	
ROZ 16	48	0.73	0.07	1.78	0.41	62.5		
ROZ 17	68	0.50	0.13	1.59	0.35	52.2	2	
ROZ 18	45	0.82	0.16	2.13	0.36	40.9		≈3
ROZ 19	63	0.79	0.24	2.12	0.50	66.1		
ROZ 20	45	0.79	0.30	1.29	0.25	31.8		
ROZ 21	38	0.68	0.26	1.45	0.34	51.4		
ROZ 22	51	1.05	0.30	2.15	0.27	38.0		
ROZ 23	24	0.79	0.29	1.36	0.33	39.1		
ROZ 24	32	0.69	0.35	1.27	0.27	41.9		
ROZ 25	125	0.53	0.08	1.50	0.33	42.4		





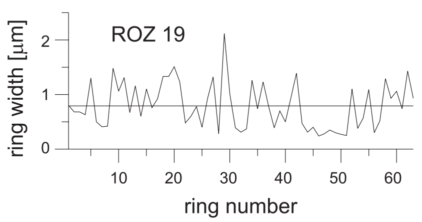


Fig. 4. Dendrographs showing variability of ring width occurring within selected specimen

Horizontal lines show mean ring widths for each specimen

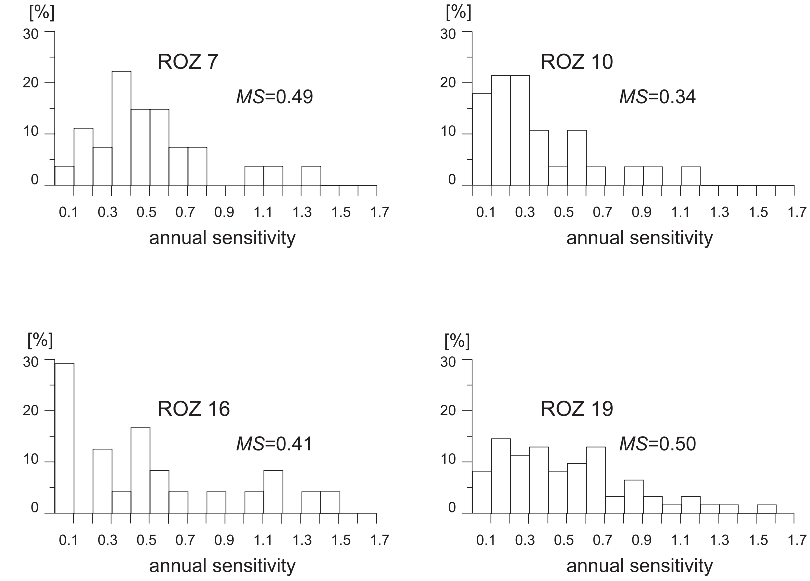


Fig. 5. Percentage values *AS* coefficient for selected specimens

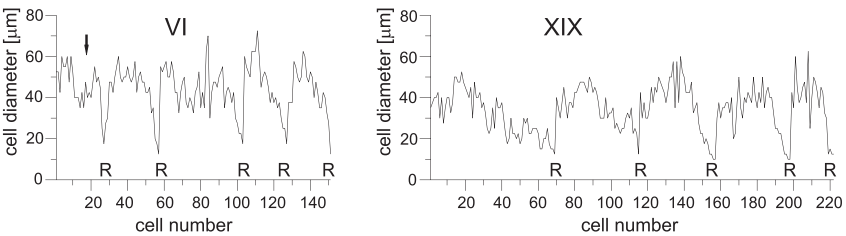


Fig. 6. Variability of cell radial diameters in rings of selected specimens

In each sample measurements were made for five consecutive rings (R); arrows point to visible tracheid diameter changes within the zone of false rings

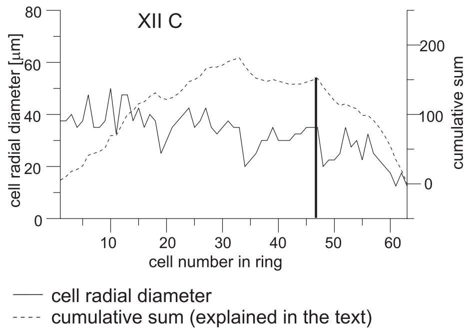


Fig. 7. Early and latewood zones in selected specimens

Vertical line shows the boundary between zones

DISCUSSION

The results of anatomical analysis allowed all the examined woods to be classified as being of the species *Taxodioxylon taxodii* Goth. The large number of specimens analysed, as well as their preliminary selection from abundant wood collections, suggest that this is probably the only type of fossil wood to occur in the Roztocze area studied. This demonstrates also that *T. taxodii* was a very numerous or even dominant tree species there during the Badenian stage.

Taxonomic determination of the fossil wood made it possible to reconstruct to some extent the environmental conditions in which the ancient trees grew. This interpretation is based on comparing the environmental requirements of the fossil plants with those of contemporary species to which they are closely related. The nearest living relative of *Taxodium taxodii* is the bald cypress (*Taxodium distichum* (L.) Rich.). This tree grows in periodically flooded habitats such as swamps, river floodplains or tidal estuaries. The native range of the bald cypress is restricted to warm and humid climate regions (Wilhite and Toliver, 1990; Schweingruber, 1993). This suggests that similar environmental conditions occurred in Roztocze when the fossil trees were living.

Sites suitable for the trees were certainly present in low-lying coastal areas. Such areas existed here before the marine transgression which gradually embraced different parts of the Roztocze area during the Badenian stage (Musiał, 1987; Peryt *et al.*, 1998; Wysocka, 2002).

This conclusion as regards palaeoclimate conditions is consistent with results of palaeontological research and also with results of carbon and oxygen isotope ratio investigations. These studies showed that during the Badenian period the area of Southern Poland remained in the humid moderately warm climate zone (Brzezińska, 1961; Stuchlik, 1980; Pisera, 1985; Planderova *et al.*, 1993; Gonera, 1997; Durakiewicz *et al.*, 1997; Bicchi *et al.*, 2003).

Like living bald cypresses, the trees of Roztocze most probably grew in deltas and swamp environments, subject to flooding. This fact may explain the lack of taxonomic variety in the wood analysed. Such unfavourable habitat conditions, to which only a small number of species adapt, are the reason why modern bald cypress forests frequently form pure stands (Devall, 1998). A similar situation most probably existed in the case of the Roztocze trees.

The occurrence of the Roztocze trees in delta or waterlogged areas was also conducive to their preservation, because in such an environment fallen trunks could be rapidly buried by layers of sediment. Moreover, processes of biological tissue decomposition were slowed in the anaerobic conditions of such an environment. These factors contributed to the presence of a large amount of mineralised wood in the Roztocze region.

Furthermore, the original mineralization of woods with silica and pyrite minerals suggests that their petrification may have taken place in river and delta areas. This suggestion is based on facts that wood silification is a process that usually takes place within terrestial sediments (Sigleo, 1979; Jefferson, 1987), while syngenetic pyrite mineralization of wood usually takes place in a flowing water environment rich in organic substances from plant matter decay (Buurman, 1972; Fowler *et al.*, 1973).

In order to interpret the environmental conditions during the Badenian in the Roztocze region, the results obtained from analysis of growth rings of fossil wood were also used. The development of growth rings is most frequently the result of a seasonal climate. Occasionally, however, some species form rings even in areas characterized by uniform external conditions. In these cases, the presence of growth interruptions is genetically determined rather than being influenced by climatic factors (Creber, 1977). This kind of ring usually shows great variability in width and has a small portion of latewood. The increments are also characterized 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). However, such features do not correspond to the way the growth rings developed in wood from the Roztocze region. The rings of the fossil wood fragments here have distinct borders, clearly marked throughout the whole circumference of the stem, and a broad latewood zone. This ring structure suggests seasonal variability of the environment in which the ancient trees grew.

The mean ring width of the wood analysed is 0.87 mm. Ring width is a species-specific feature but narrow rings, especially those less than 1 mm wide, suggest the unfavourable influence of external factors on a tree (Schweingruber, 1996). For the Roztocze trees the formation of such narrow rings was probably the result of growth limitation caused by a flooded environment. A similar situation is observed in modern bald cypresses, which grow more slowly in stands associated with high water level than at sites characterized by moderate water inflow (Yamamoto, 1992; Prezeshki, 2001). An additional factor which can also contribute to reduction in ring width in living bald cypresses is the increased salinity that exists in areas affected by seawater influx (Allen *et al*., 1996). External conditions of this kind might also be the reason for the small width of growth rings in fossil trees from the Roztocze region.

The growth of the ancient trees on waterlogged and unstable ground is also suggested by the frequent presence of reaction wood and wedging rings within the wood specimens analysed. The reasons for the occurrence of wedging rings may, beside other things, be marked eccentricity of the stem or the influence of growth-limiting factors on a tree (Larson, 1956). Their colonization of flood-prone, soft, and unstable ground most probably limited the trees' growth and presumably caused trunks to lean away from the vertical. In both cases this would ultimately lead to the formation of wedging rings. Moreover, changes in the direction of tree tilt led to the development of reaction wood within the circumference of the stem (Spurr and Hyvärinen, 1954; Low, 1964).

The analyses performed show also a large variability in fossil wood ring width. The main reason for this is the influence of variable external conditions on a tree, especially the most growth-limiting environmental factor. The observed differentiation in fossil ring width is expressed by high values of *AS* and *MS* coefficients. High values of *AS* indicate significant changes in external conditions during consecutive seasons. The irregularity with which such high values of *AS* occur in measurement sequences reflects the variability in intensity of growth-limiting factors through time. The ring width of living bald cypresses shows a high correlation with the amount of rainfall during consecutive years (Stahle *et al*., 1985; Stahle and Cleaveland, 1992, 1994; Reams and van Deusen, 1998). On this basis it must be assumed that similar variation in precipitation may be a reason for the described changeability in ring widths formed by the ancient trees.

Changeable conditions of the palaeoenvironment in which these trees grew are also reflected by the existence of false rings observed within the wood specimens analysed. False ring formation in living bald cypresses is the effect of temporary growth cessation or retardation during periods of decreased water level. Their existence is often also the result of growth stimulation associated with inflow of nutrient-rich water at the end of a growing season (Bowers *et al*., 1990; Wilhite and Toliver, 1990). Therefore a variable amount of precipitation probably also caused the frequent presence of false rings in fossil wood from the Roztocze region.

The character of palaeoenvironmental conditions could be also inferred from the analysis of cells forming individual rings. The measurements of tracheid radial diameter showed that the rings of the wood examined have a gradual transition between early and latewood zones and a wide band of latewood. This ring structure is probably an effect of trees growing in an environment characterized by a long growing season and unlimited water supply (Creber and Chaloner, 1984). The existence of adequate water resources at sites where trees grew is confirmed also by presence of thin cell walls and large tracheid diameters within the wood analysed (*cf*. von Wilpert, 1991). In the case of the ancient trees from the Roztocze region, high humidity was undoubtedly connected with the waterlogged character of their stands.

The percentage of latewood within the rings could be also determined by the time of needle retention by trees. A broad zone of latewood and distinctly marked ring boundaries suggest the deciduous character of a tree (Falcon-Lang, 2000*a*, *b*; Falcon-Lang and Cantrill, 2000). However, in the wood analysed needle traces crossing the structure of the rings indicate long needle retention by the Roztocze trees (*cf*. Jalkanen and Kurkela, 1992). Thus the influence of environmental conditions on the plants is a more convincing explanation of the described structure of rings found in the wood specimens examined.

SUMMARY

1. Anatomical and growth ring analyses of fossil wood allowed the interpretation of palaeoenvironmental conditions present in the Roztocze area during the Badenian stage. The results obtained were interpreted on the basis of comparing the habitat and climate requirements of ancient trees with those of their nearest living relatives.

2. The anatomical analyses show that all the fossil wood specimens analysed belong to the species *Taxodioxylon taxodii* Goth. With respect to the anatomical structure of its wood this taxon corresponds to the living bald cypress tree (*Taxodium distichum* (L.) Rich.).

3. Since modern bald cypresses grow in waterlogged or temporarily flooded stands in warm and humid climatic regions, the conditions of habitat in the Roztocze area were presumably similar when the ancient trees were alive.

4. Frequently appearing wedging rings, reaction wood and generally narrow rings observed within the wood specimens analysed also support the idea that these trees grew in flooded stands.

5. Rings present in the wood analysed demonstrate seasonal variability of the climate in which the trees grew.

6. The changeable character of external factors is also suggested by variable growth ring width and the frequent presence of false rings in the wood analysed.

7. Comparisons with the environmental requirements of contemporary bald cypresses show that the variability of the palaeoenvironment must have been largely associated with variable volumes of precipitation over a single growing season and during consecutive years.

8. The influence of environmental conditions on trees is also reflected in the structure of individual rings. The large diameters of tracheids and their thin cell walls, the significant percentage of latewood and the gradual transition between early and latewood zones suggest a long growing season and adequate water supply.

9. Adequate water resources in the case of the Roztocze trees were doubtless connected with the waterlogged nature of their stands.

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REFERENCES

ALLEN J. A., PEZESHKI S. R. and CHAMBERS J. L. (1996) — Interaction of flooding and salinity stress on bald cypress (*Taxodium distichum*). Tree Physiol., **16**: 307–313.

AREŃ B. (1962) — The Miocene of the Lublin Roztocze range between the Sanna and Tanew rivers (in Polish with English summary). Pr. Inst. Geol., **30** (3): 5–77.

AREŃ B. (1992) — *Taxodioxylon sequoianum* Goth. Prz. Geol., **40** (12).

ASH S. and CREBER G. (1992) — Palaeoclimatic interpretation of the wood structures of the trees in the Chinle Formation (Upper Triassic) in the area of Petrified Forest National Park, Arizona, U.S.A. Palaeogeogr. Palaeoclimat. Palaeoecol., **96**: 299–317.

BICCHI E., FERRERO E. and GONERA M. (2003) — Palaeoclimatic interpretation based on Middle Miocene planktonic Foraminifera: the Silesia Basin (Paratethys) and Monferrato (Tethys) records. Palaeogeogr. Palaeoclimatol. Palaeoecol., **196**: 265–303.

BOWERS L. J., GOSSELINK J. G., PATRICK W. H. and CHOONG E. T. (1990) — Investigation of six anatomical and four statistical features of bald-cypress (*Taxodium distichum*) tree rings. For. Ecol. Manage., **33/34**: 503–508.

BRZEZIŃSKA M. (1961) — The Miocene of the boundary zone between the Western Roztocze (Roztocze Zachodnie) and Sandomierz Depression (Kotlina Sandomierska) (in Polish with English summary). Biul. Inst. Geol., **158**: 5–112.

BRZYSKI B. (1998) — On the protection of petrified trees in Roztocze (in Polish with English summary). Chrońmy Przyr. Ojcz., **54**: 7–13.

BURACZYŃSKI J. (2002) — Roztocze — środowisko przyrodnicze. Wyd. Lubelskie. Lublin.

BUURMAN P. (1972) — Mineralization of fossil wood. Scripta Geol., **12**: 1–43.

CHALONER W. G. and CREBER G. T. (1973) — Growth rings in fossil woods as evidence of past climates. In: Implications of Continental Drift to the Earth Sciences (eds. D. H. Tarling and S. K. Runcorn): 425–437. Acad. Press. London and New York.

CHAPMAN J. L. (1994) — Distinguishing internal developmental characteristics from external palaeoenvironmental effects in fossil woods. Rev. Palaeobot. Palynol., **81**: 19–32.

CIEŚLIŃSKI S., KUBICA B. and RZECHOWSKI J. (1994) — Mapa Geologiczna Polski w skali 1:200 000 (bez utworów czwartorzędowych), arkusz Tomaszów Lubelski, Dołhobyczów. Państw. Inst. Geol.

COOK E. R. and KAIRIUKSTIS L. A. (1990) — Methods of Dendrochronology. Applicat. Envir. Sc. Kluwer Acad. Publ. Dordrecht, Boston, London.

CREBER G. T. (1977) — Tree rings: a natural data-storage system. Biol. Rev., **52**: 349–383.

CREBER G. T. and CHALONER W. G. (1984) — Influence of environmental factors on the wood structure of living and fossil trees. Bot. Rev., **50** (4): 357–448.

CREBER G. T. and CHALONER W. G. (1985) — Tree growth in the Mesozoic and Early Tertiary and the reconstruction of palaeoclimates. Palaeogeogr. Palaeoclimat. Palaeoecol., **52**: 35–60.

CREBER G. T. and FRANCIS J. E. (1999) — Fossil tree-ring analysis: palaeodendrology. In: Fossil Plants and Spores: modern techniques (eds. T. P. Jones and N. P. Rowe): 245–250. Geol. Soc. London.

DEVALL M. (1998) — An interim old-growth definition for cypress-tupelo communities in the southeast. General Technical Report SRS-19. United States Department of Agriculture, Forest Service, Southern Research Station. Stoneville: 1–13.

DOUGLASS A. E. (1936) — Climatic Cycles and Tree-Growth. Vol. III. Carnegie Institution of Washington Publication 289.

DURAKIEWICZ T., GONERA M. and PERYT T. (1997) — Oxygen and carbon isotopic changes in the Middle Miocene (Badenian) Foraminifera of Gliwice area (SW Poland). Bull. Pol. Acad. Sc. Earth Sc., **45** (2–4): 145–156.

FALCON-LANG H. J. (1999*a*) — The Early Carboniferous (Courceyan-Arundian) monsoonal climate of the British Isles: evidence from growth rings in fossil woods. Geol. Mag., **136**: 177–187.

FALCON-LANG H. J. (1999*b*) — The Early Carboniferous (Asbian-Brigantian) seasonal tropical climate of Northern Britain. Palaios, **14** (5): 116–126.

FALCON-LANG H. J. (2000*a*) — A method to distinguish between woods produced by evergreen and deciduous coniferopsids on the basis of ring anatomy: a new palaeoecological tool. Palaeontology, **43**: 785–793.

FALCON-LANG H. J. (2000*b*) — The relationship between leaf longevity and growth ring markedness in modern conifer woods and its implications for palaeoclimatic studies. Palaeogeogr. Palaeoclimat. Palaeoecol., **160**: 317–328.

FALCON-LANG H. J. (2003) — Growth interruptions in silicified conifer woods from the Upper Cretaceous Two Medicine Formation, Montana, USA: implications for palaeoclimate and dinosaur palaeoecology. Palaeogeogr. Palaeoclimat. Palaeoecol., **199**: 299–314.

FALCON-LANG H. J. and CANTRILL D. J. (2000) — Cretaceous (late Albian) coniferales of Alexander Island, Antarctica. 1. Wood taxonomy: a quantitative approach. Rev. Palaeobot. Palynol., **111**: 1–17.

FOWLER K., EDWARDS N. and BRETT D. W. (1973) — In situ coniferous (*Taxodiaceous*) tree remains in the Upper Eocene of Southern England. Palaeontology, **16**: 205–217.

FRANCIS J. E. (1983) — The dominant conifer of the Jurassic Purbeck (Upper Jurassic) fossil forest. Palaeontology, **26**: 277–294.

FRANCIS J. E. (1984) — The seasonal environment of the Purbeck (Upper Jurassic) fossil forest. Palaeogeogr. Palaeoclimat. Palaeoecol., **48**: 285–307.

FRANCIS J. E. (1986) — Growth rings in Cretaceous and Tertiary wood from Antarctica and their palaeoclimatic implications. Palaeontology, **29**: 665–684.

FRANCIS J. E. (1991) — The dynamics of polar fossil forest: Tertiary fossil forest of Axel Heiberg Island. Canadian Arctic Archipelago. In: Tertiary Fossil Forest of the Geodetic Hills, Axel Heiberg Island, Arctic Archipelago (eds. R. L. Christie and N. J. Mc Millan). Geol. Surv. Can. Bull., **403**: 29–38.

FRANCIS J. and POOLE I. (2002) — Cretaceous and Early Tertiary climates from Antarctica: evidence from fossil wood. Palaeogeogr. Palaeoclimat. Palaeoecol., **182**: 47–64.

FRITTS H. C. (1976) — Tree Rings and Climate. Academic Press. London.

GONERA M. (1997) — Miocene Foraminiferal assemblages in the Gliwice area (Upper Silesia, Poland). Bull. Pol. Acad. Sc. Earth Sc., **45** (2–4): 97–105.

GOTHAN W. (1905) — Zur Anatomie lebenden und fossiler Gymnospermen-Hölzer. Abh. Kgl. Preuss. Geol. Landesanst., N. F., **44**.

GOTHAN W. (1906) — Die fossilen Koniferenhölzer von Senftenberg. Abh. Kgl. Preuss. Geol. Landesanst., N. F., **46**: 155–191.

HARTIG T. (1848) — Beiträge zur Geschichte der Pflanzen und zur Kenntnis der norddeutschen Braunkohlenflora. Bot. Z., **6**: 166–172.

HEFLIK W. (1996) — Investigation of fossilized trunks from the Roztocze region (in Polish with English summary). Pr. Muz. Ziemi, **44**: 127–130.

JALKANEN R. and KURKELA T. (1992) — VB-method for the determination of pine defoliation in the past. Proc. Tree Rings and Environment, Ystad, Sweden, September 3–9, 1990, Abstracts. Lundqua Rep., **34**: 153–157.

JEFFERSON T. H. (1982) — Fossil forest from the Lower Cretaceous of Alexander Island, Antarctica. Palaeontology, **25**: 681–708.

JEFFERSON T. H. (1987) — The preservation of conifer wood: examples from the Lower Cretaceous of Antarctica. Palaeontology, **30**: 233–249.

KRÄUSEL R. (1919) — Die Pflanzen des Schlesischen Tertiärs. Jb. Preuss. Geol. L.-A., **38** (2): 191–338.

KUMAGAI H., SWEDA T., HAYASHI K., KOJIMA S., BASINGER J. F., SHIBUYA M. and FUKAOA Y. (1995) — Growth-ring analysis of Early Tertiary conifer woods from the Canadian High Arctic and its paleoclimatic interpretation. Palaeogeogr. Palaeoclimat. Palaeoecol., **116**: 247–262.

LARSON P. R. (1956) — Discontinuous growth rings in suppressed slash pine. Trop. Woods, **104**: 80–99.

LOW A. J. (1964) — A study of compression wood in Scots Pine (*Pinus silvestris* L.). Forestry, **137**: 179–201.

MARUSZCZAK H. (2001) — Petrified wood from the Miocene forest in the Roztocze Ridge (SE Poland and NW Ukraine) (in Polish with English summary). Prz. Geol., **49** (6): 532–537.

MORGANS H. S. (1999) — Lower and Middle Jurassic woods of the Cleveland Basin (North Yorkshire), England. Palaeontology, **42**: 303–328.

MORGANS H. S., HESSELBO S. P. and SPICER R. A. (1999) — The seasonal climate of the Early-Middle Jurassic, Cleveland Basin, England. Palaios, **14**: 261–272.

MOSBRUGGER V. and UTESCHER T. (1997) — The coexistence approach — a method for quantitative reconstructions of Tertiary terrestrial palaeoclimate data using plant fossils. Palaeogeogr. Palaeoclimat. Palaeoecol., **134**: 61–86.

MUSIAŁ T. (1987) — Miocen Roztocza (Polska południowo-wschodnia). Biul. Geol. Uniw. Warszaw., **31**: 5–149.

PARRISH J. T. and SPICER R. A. (1988) — Middle Cretaceous wood from Nanunshuk Group, Central North Slope, Alaska. Palaeontology, **31**: 19–34.

PERYT T., JASIONOWSKI M., RONIEWICZ P. and WYSOCKA A. (1998) — Miocen Roztocza. In: Budowa Geologiczna Roztocza. LXIX Zjazd Naukowy Polskiego Towarzystwa Geologicznego, Krasnobród, Wrzesień 23–26, 1998. Wyd. UMCS. Lublin: 65–78.

PISERA A. (1985) — Paleoecology and lithogenesis of the Middle Miocene (Badenian) algal-vermetid reefs from the Roztocze Hills, south-eastern Poland. Acta Geol. Pol., **35** (1–2): 89–155.

PLANDEROVA E., ZIEMBIŃSKA-TWORZYDŁO M., GRABOWSKA I., KOHLMAN-ADAMSKA A., SADOWSKA A., SŁODKOWSKA B., STUCHLIK L. and WAŻYŃSKA A. (1993) — Wahania klimatyczne w neogenie Europy środkowej na podstawie zmiennego udziału w palinoflorze składników paleotropikalnych i arktycznotrzeciorzędowych. Prz. Geol., **41** (12): 829–835.

PREZESHKI S. R. (2001) — Wetland plant responses to soil flooding. Environ. Exp. Bot., **46**: 299–312.

RADWAŃSKI A. and WYSOCKA A. (2001) — Mass aggregation of Middle Miocene spine-coated echinoids *Echinocardium* and their integrated eco-taphonomy. Acta Geol. Polon., **51**: 295–316.

REAMS G. A. and VAN DEUSEN P. C. (1998) — Detecting and predicting climatic variation from old-growth bald cypress. In: The Productivity and Sustainability of Southern Forest Ecosystems in a Changing Environment (eds. R. Mickler and S. Fox): 701–716. Springer-Verlag. New York.

RZECHOWSKI J. (1997) — Trzeciorzęd i czwartorzęd wschodniej części Wyżyny Lubelskiej i Roztocza na Mapie Geologicznej Polski 1:200 000. Prz. Geol., **45** (11): 1202–1208.

SCHWEINGRUBER F. H. (1990) — Microscopic Wood Anatomy. Structural Variability of Stems and Twigs in Recent and Subfossil Woods from Central Europe. Swiss Feder. Inst. Forest. Berne.

SCHWEINGRUBER F. H. (1993) — Trees and Wood in Dendrochronology. Springer-Verlag. Berlin.

SCHWEINGRUBER F. H. (1996) — Tree Rings and Environment Dendroecology. Swiss Feder. Inst. Forest. Berne.

SIGLEO A. C. (1979) — Geochemistry of silicified wood and associated sediments, Petrified Forest National Park, Arizona. Chem. Geol., **26**: 151–163.

SPICER R. A. and PARRISH J. T. (1990) — Latest Cretaceous woods of the Central North Slope, Alaska. Palaeontology, **33**: 225–242.

SPURR S. H. and HYVÄRINEN M. J. (1954) — Compression wood in conifers as a morphogenetic phenomenon. Bot. Rev., **20**: 551–560.

STAHLE D. W., CLEAVELAND M. K. and HEHR J. G. (1985) — A 450-year drought reconstruction for Arkansas, United States. Nature, **316**: 530–532.

STAHLE D. W. and CLEAVELAND M. K. (1992) — Reconstruction and analysis of spring rainfall over the south-eastern U.S. for the past 1000 years. Bull. Amer. Meteor. Soc., **73** (12): 1947–1961.

STAHLE D. W. and CLEAVELAND M. K. (1994) — Tree-ring reconstructed rainfall over the southeastern U.S.A. during the Medieval Warm period and Little Ice Age. Clim. Change, **26** (2–3): 199–212.

STUCHLIK L. (1980) — Chronostratigraphy of the Neogene in southern Poland (northern part of the Central Paratethys) on the basis of palaeobotanical studies (in Polish with English summary). Prz. Geol., **28** (8): 443–448.

Von WILPERT K. (1991) — Intra-annual variation of radial tracheid diameters as monitor of site specific water stress. Dendrochronologia, **9**: 95–113.

WALANUS A. (2005) — Program QUERCUS. Users Manual. Kraków: 1–10.

WHEELER E. A. and LEHMAN T. M. (2005) — Upper Cretaceous–Palaeocene conifer woods from Big Bend National Park, Texas. Palaeogeogr. Palaeoclimatol. Palaeoecol., **226**: 233–258.

WILHITE L. P. and TOLIVER J. R. (1990) — *Taxodium distichum* (L.) Rich. Bald cypress. In: Silvis of North America, volume 1. Conifers (eds. R. M. Burns and B. H. Honkala): 563–572. Agricultural Handbook. Washington.

WYSOCKA A. (2002) — Clastic Badenian deposits and sedimentary environments of the Roztocze Hills across the Polish-Ukrainian border. Acta Geol. Pol., **52** (4): 535–561.

YAMAMOTO F. (1992) — Effects of depth of flooding on growth and anatomy of stems and knee roots of *Taxodium distichum*. IAWA Bull. n. s., **13** (1): 93–104.

ZALEWSKA Z. (1955) — Trzeciorzędowe szczątki drewna z Turowa nad Nysą Łużycką. Część II. Acta Geol. Pol., **5** (2): 277–304.

ZIELSKI A. and KRĄPIEC M. (2004) — Dendrochronologia (in Polish). Wydawnictwo Naukowe PWN. Warszawa.