

Fossil wood and Mid-Eastern Europe terrestrial palaeobiogeography during the Jurassic–Early Cretaceous interval

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Abstract

Palaeobiogeography plays an important role in the evolution of continental plants. This has been demonstrated mainly for modern biota and for past biota on a very large scale only. During the Jurassic–Early Cretaceous Mid-Eastern Europe was an archipelago, thus a particularly suitable area for a more detailed study. We investigated the area's plant palaeobiogeography, using fossil wood, with information from both a literature survey and investigation of new samples. There is a clear north–south differentiation of wood floras. The northern part of the archipelago, which was connected by a shallow sea, has a homogenous flora. A small terrane in the south, separated by true oceanic crust, seems to have had a peculiar flora, lacking widely distributed elements but displaying an endemic taxon with Gondwanan affinities. Compared to Western Europe, Mid-Eastern Europe has a Jurassic–Early Cretaceous wood flora with similar diversity, except for the Late Jurassic, when it was limited to a single taxon, the widespread *Agathoxylon* Hartig. The wood flora of northern Gondwana is less diverse across the time interval under consideration, except for the Late Jurassic again. Taphonomic bias cannot be ruled out, but this low diversity during the Late Jurassic suggests stressful climatic conditions for Mid-Eastern Europe.

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1. Introduction

Geographic isolation as well as later reunification are known to be major factors in recent plant evolution (Briggs and Walters, 1997; Emerson and Kolm, 2005). In the past, isolated floristic provinces have been cited as the

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origin of endemic taxa of high rank, such as the Gondwana for the Glossopteridales. At a more regional scale, however, there is very little evidence about the effect that palaeobiogeography may have had on past plant evolution. During the Mesozoic, Mid-Eastern Europe (*sensu lato*, see Fig. 1) evolved in the intricate context of tectonic micro-plates and isolated emerged lands (Dercourt et al., 2000; Csontos and Vörös, 2004). Such an archipelago, on the rim of a large continent, is of great interest to investigate the relationship between geographic context and the evolution of continental plant diversity during the Mesozoic.

Typical terrestrial organisms like Tracheophytes are valuable indicators of continental biota. Unfortunately, because of taphonomic process, the different plant parts are not usually found in connection, and palaeobotanists deal with morphogenera, a constraint that most of the time prevents them from accessing the history of natural taxa. Pollens and spores, fertile organs, leaves, twigs, wood, etc. all have their own taphonomy and taxonomy, and their biogeographic implications must be studied independently. Wood is rarely used for such studies, though it is not the worst avatar of plant natural taxa. Wood is, however, far less mobile than palynomorphs and more common than leaf imprints or compressions, especially in marine strata, a well dated geologic context.

Historically, Mesozoic fossil wood has not been the subject of much interest in Mid-Eastern Europe, except for Hungary (Felix, 1887; Tuzson, 1911; Andreanszky, 1949, 1951; Greguss *op. pl.*, e.g. 1949, 1952, 1956, 1974; Kedves, 1955; Philippe and Barbacka, 1997). Mid-Eastern Mesozoic wood is rarely found silicified, and until the 1980s palaeoxylogists usually dealt only with petrified material. New techniques have been developed to study fossil wood within a wide range of preservation (Philippe, 1995), which has helped renew Mesozoic plant palaeobiogeography (Philippe et al., 2004). We compiled a database within a unified taxonomic framework (Bamford and Philippe, 2001). About a third (39.07%) of these data were new, and we reviewed all previously published data. In this study the area covered is all “Eastern Europe s.l.”, i.e. in between 12° East and 50° East. Italy was not considered because its terrestrial phytocoenosis was typically Gondwanan at this time, with *Agathoxylon* and *Metapodocarpoxyton* (Philippe et al., 2003). The Arctic zone (e.g. Svalbard, King Charles Land, New-Zemlia) was not considered as its wood flora is still poorly known, both systematically and stratigraphically.

We focus on the Jurassic–Early Cretaceous period as it is a period with no major floristic turn-over that could obscure the biogeographic picture (Philippe et al., 1999b). Tectonically it is a more or less uniform period marked by

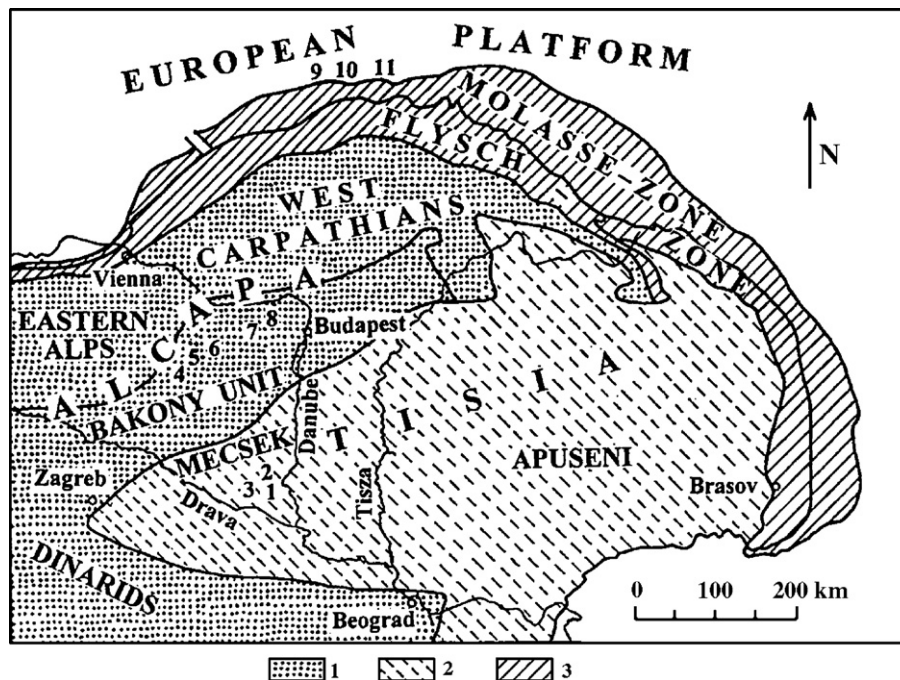


Fig. 1. Main tectonic elements of Carpathian–Pannonian Region (after Csontos and Vörös, 2002a simplified). Localities: 1 — Vasas, 2 — Komló, 3 — Pécsbánya, 4 — Sümeg, 5 — Úrkút, 6 — Eplény, 7 — Tata, 8 — Lábátlan, 9 — Jasna Góra, 10 — Łuków, 11 — Cracow. Zones: 1 (stippled) Alpaca zone; 2 (dashed) Tisza; 3 (hatched) flysch and molasse zone.

the opening of the Penninic Ocean and the partitioning of emerged lands on the Tethys northern rim.

The database of mid-Eastern Europe fossil wood is analysed in order to determine if this intricate geographic context played a role on the evolution of the continental plant diversity in Mid-Eastern Europe as compared to Western Europe and Maghreb, two areas previously reviewed (Philippe, 1995; Philippe et al., 2004).

2. Short geologic outline of Mid-Eastern Europe and its environs

For convenience Mid-Eastern Europe is defined as the area from circa 12°E eastward to the Ural, circa 55°E. To the East and South it is limited by the Caspian Sea, Caucasus, Black Sea and Mediterranean Sea. Most of this area belongs to the European platform, consisting of a variety of tectonic blocks consolidated during the Variscan orogeny (Carboniferous), and had a rather simple geologic history during the Jurassic and Early Cretaceous. The southwesternmost part of area considered belongs to the Alpine folded belt – a composite of minor tectonic blocks – which is still an active orogen today. The Eastern Alps–Carpathian–Pannonian Region consists of two palaeogeographic units (ALCAPA and Tisia [or Tisza] Megaunits [see in detail later]), of fundamentally different origin and character (Haas and Péró, 2004). The last major tectonic displacements occurred in the Neogene, and there are still active orogenic processes in several subregions. Our fossil wood localities are distributed in the three regions, the European platform, ALPACA and Tisia megaunits.

Our study – discussing land-based organisms – is a contribution towards the better understanding of temporal and spatial distribution of the Mesozoic terrestrial environment in Europe. During the Jurassic the study area displayed a fundamentally different palaeogeographic pattern than today. The European continent in the northwest and the African continent in the southwest enclosed a V-shaped Tethys ocean. The eastward opened ocean was dotted with a set of ribbon continents (Dewey, 1988). While the extent of emerged land in Europe and Africa is relatively well known (e.g. Ziegler, 1988; Dercourt et al., 2000), the size and shape of islands on top of the ribbon continents is practically unknown, best evidence being bauxite (e.g. Mindszenty et al., 1995), and dinosaur localities (e.g. Weishampel et al., 1991; Dalla Vecchia, 2001; Ösi, 2004). Three types of terrestrial environments are recognised in the region in respect of tectonic background:

(a) Continental platforms: alternation of land and sea environments as determined by eustatic sea-level

changes (Bloos, 1990). There is no major relief. Uniform sedimentary facies of significant lateral extent. Extensive alluvial plains. Clastic sediments are fine-grained, and may alternate with evaporites. The thickness of the stratigraphic column is ca. few hundred metres, depositing during tens of millions of years. Areas of erosion (source of sediments) consist of low hills. Examples: Lower Jurassic of Poland and the Ukraine. Continental platforms existed throughout the Jurassic and Early Cretaceous.

- (b) Rifted margins: distribution of land and sea environments is determined by extensional tectonics. Tilted blocks of rifted margins can form high-altitude topography (area of erosion), intersected by deep basins. Fluvial sediments: coarse to fine. Extensive alluvial plains on subsiding blocks; might alternate with shallow-marine strata. Rapid uplift and subsidence created rifted half-basins with terrestrial to shallow marine successions several km thick. Eroded areas (source of sediments) might be deeply dissected, producing coarse to fine sediments. Weathering is climate-influenced; deep to shallow soils occur. Subsiding areas attract sedimentation from sources external to the rift zone. Areas proximal to sediment sources receive predominantly clastic sediments (Mecsek Keuper and Gresten facies: Komló, Pécsbánya, Vasas, Villány-Bihar zone), while carbonate sedimentation predominates in distal areas (low-lying islands bearing coal measures within the Calcarei grigi carbonate platforms in the Dolomites). Volcanoes reaching above sea level, surrounded by atolls occur in the late stage of rifting (Mecsek). Rifting started in Late Triassic and persisted until Early Cretaceous along the north-western and south-western margins of the Tethys ocean; also occurred within the ribbon continents. Dinarids were a proximal part of the rifted margin of Adria microplate, and had a shallow carbonate platform during the Jurassic–Lower Cretaceous period (Haas et al., 1999).
- (c) Orogenic zones: distribution of land and sea environments is determined by compression tectonics. Pelagic deep-sea sedimentation prevailed during Late Liassic–Lower Cretaceous period (Transdanubian Range), redeposited sediments may have accumulated in the continental slope (Bükk, Aggtelek Mts.) (Haas et al., 1999). Low to high-altitude regions alternate with lands inundated by the sea. High elevation on land is possible. Lowlands and alluvial plains are restricted in extent. Short rivers bring substantial amounts

of coarse to fine sediment from the mountains. Provenance of sediments was mostly from the immediate vicinity of the sedimentation area. Weathering is low, mostly shallow soils in the mountains. Example: Vardar zone extending from the Eastern Alps to the Dinarides, e.g. Lábatlan in Hungary. The age is restricted to Late Jurassic–Early Cretaceous.

The present-day distribution of fossil localities is mostly determined by Neogene tectonic displacements (Csonotos and Vörös, 2004). European platform forms an embayment, today occupied by the Carpathian–Pannonian Region. There are two major tectonic units within the Carpathian region, which originated far apart, and were juxtaposed by Neogene tectonics. The ALCAPA Megaunit consists of the Eastern Alps, West Carpathians, and the Transdanubian Central Range (Bakony, Vértes, Gerecse) and Dinarids. Its origin was in the north-eastern margin of the Adriatic microplate (so-called southern origin). The Tisia Megaunit (Mecsek, Villány, Apuseni Mts. and inner part of the Eastern Carpathians) was rifted off the European continental margin in Jurassic–Early Cretaceous (so-called northern origin) (Kovács et al., 1997) (see Fig. 1). Tisia

contrasting origin is revealed by the mix of Adriatic and European marine faunas (Géczy, 1973; Vörös, 1993), while Neogene compression and strike-slip tectonics are responsible for juxtaposition in a reverse order (i.e. European Tisia Megaunit south of Adriatic ALCAPA Megaunit) (Csonotos, 1995). Fig. 2 shows a series of Jurassic–Early Cretaceous palaeogeographic sketches.

3. Palaeobotanic framework

Early Jurassic compression floras were recorded in Poland, Hungary, Serbia and Romania as well as in Georgia (Raciborski, 1890, 1894; Vakhrameev and Krassilov, 1961; Reymanówna, 1963a,b, 1973, 1992; Wesley, 1970; Svanidze, 1971; Vakhrameev, 1991; Wcisło-Lurancie, 1991a,b, 1992a,b; Barbacka, 1992, 1997, 2000, 2001, 2002; Ziaja, 1992; Popa, 1998, 2000a,b). These Early Jurassic floras are pure Mesophytic floras, with dominant gymnosperms, subordinate Pteridophytes and no Angiosperms. Pteridophytes are represented during the Early and Middle Jurassic mainly by filicalean families such as Matoniaceae, Dicksoniaceae and Dipteridaceae, while Sphenopsids are reduced in diversity but relatively common and Lycopsids are even

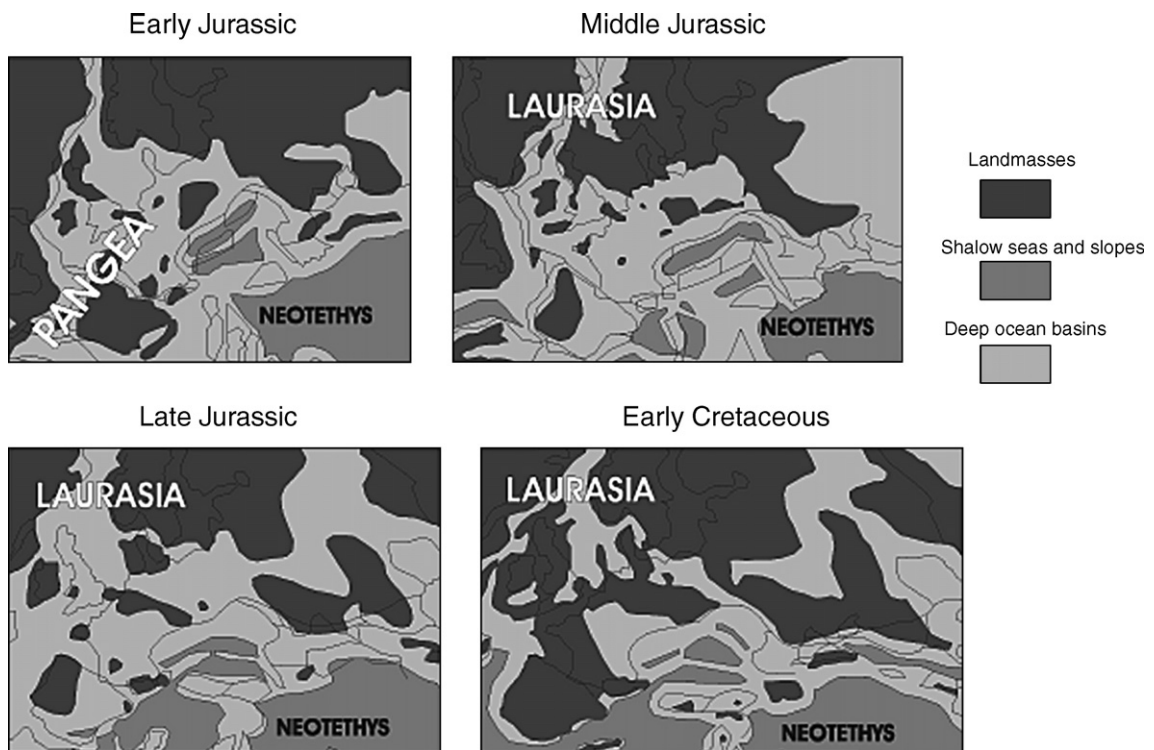


Fig. 2. Lower Jurassic, Middle Jurassic, Late Jurassic, and Early Cretaceous palaeogeography of southeastern Europe (after Csonotos and Vörös, 2002b simplified).

uncommon. Among Gymnosperms, Pteridosperms, including *Corystospermales* (*Pachypteris*) and Caytoniales (*Sagenopteris*, *Caytonia*), are diverse and ubiquitous. Cycadales (*Nilssonia*, *Ctenis*) and especially Bennettitales diversify explosively, as do the Ginkgoales (*Baiera*, *Spenobaiera*, *Ginkgo*) and Coniferales (Araucariaceae, Cheirolepidiaceae or Incertae sedis). Within this flora, only the Ginkgoales and Coniferales produced significant amounts of secondary xylem.

Middle Jurassic compression floras of Central and Eastern Europe are similar to the Early Jurassic assemblages, however their record is affected by the Middle Jurassic transgression, and this is why Middle Jurassic floras were predominantly described on drifted material collected from shallow marine deposits. It is the case of the South and East Carpathians or Dobroudja (Eastern Romania), in Romania (Dragastan and Bărbulescu,

1980; Givulescu and Bucur, 1985; Popa, 2000a,b), Bulgaria (Teshlenko, 1987), or Serbia. For Poland (Makarowiczówna, 1928; Raciborski, 1894; Reymanówna, 1963a,b, 1968, 1970, 1973, 1977, 1985, Wcisło-Luraniec, 1985, 1989; Wcisło-Luraniec and Barbacka, 2000) and the Caucasus (Doludenko and Svanidze, 1968; Barale et al., 1991), the drifted character is less dominant. The flora is still a genuine Mesophytic flora, with dominant gymnosperms.

Late Jurassic compression floras are rare for Central and Eastern Europe. There is a small flora in Poland (Liszkowski, 1972; Vakhrameev, 1991), and what appears as a more diversified flora in the Caucasus (Doludenko and Svanidze, 1969). Although it is poorly documented, the Late Jurassic flora for Eastern Europe can be considered as Mesophytic (Voronova and Yanovskaya, 1991).

For the Early Cretaceous, Neocomian floras with *Weichselia* and *Frenelopsis*, were recorded in Serbia,

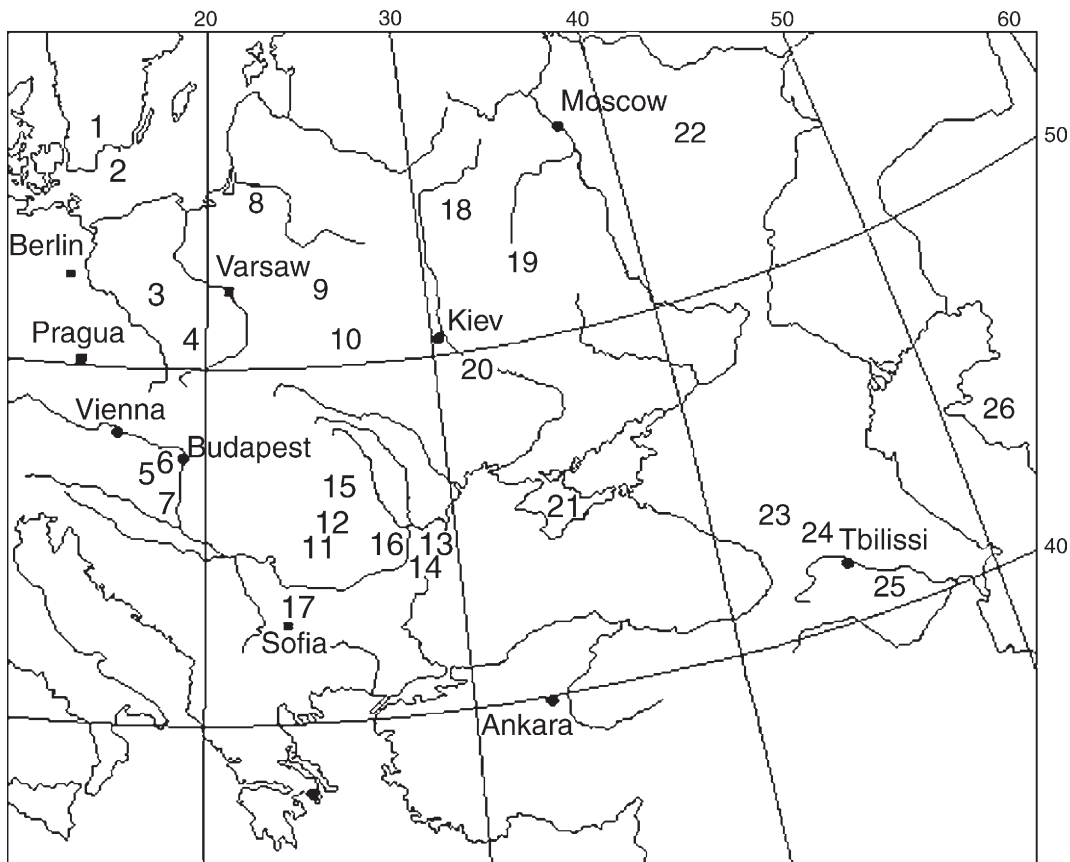


Fig. 3. Locality distribution through Mid-eastern Europe: 1 Skåne, Sweden; 2 Bornholm Island, Denmark; 3 Lubin, Poland; 4 Częstochowa, Poland; 5 Bakony Mts., Hungary; 6 Tata and Labatlan, Hungary; 7 Mecksek Mts., Hungary; 8 Sovetsk, Russia; 9 Łuków, Poland; 10 Stempiny, Poland; 11 Șuncuiuș, Romania; 12 Brasov area, Romania; 13 Dobrogea, Romania; 14 Oborichte and Dobromir, Bulgaria; 15 Hăghimaș, Romania; 16 Tichilești, Romania; 17 Zhablyano, Berende and Izvor, Bulgaria; 18 Kirov, Russia; 19 Kursk, Russia; 20 Kanev, Ukraine; 21 Chalimov, Crimea; 22 Voronejsk, Russia; 23 Tqvarchéli, Georgia; 24 Tkibuli, Georgia; 25 Armenia; 26 Mangichlak and Charoukar, Kazakhstan.

Table 1

Data rejected as insufficiently supported by their protologue (P) or, when we reviewed it, by their associated material (M)

Morphogenera	Infrageneric indications	Reference	Reject	Note
<i>Araucarioxylon</i>	sp.	Lilpop (1917)	P	
<i>Araucarioxylon</i>	sp. 8	Greguss (1967)	P and M	Holotype reviewed
<i>Araucarioxylon?</i>	“Fossilie Nr.3”	Greguss (1956)	P and M	= <i>Araucarioxylon</i> sp. 11 in Greguss (1967); holotype reviewed
<i>Pinites</i>	<i>jurassicus</i>	Göppert (1845)	P and M	
<i>Pinites</i>	<i>jurassicus</i>	Mercklin (1855)	P and M	
<i>Pinites</i>	<i>jurassicus</i>	Eichwald (1868)	P	
<i>Pinites</i>	<i>jurensis</i>	Felix (1882)	P	
<i>Podocarpoxylon</i>	“Fossilie Nr.1”	Greguss (1956)	P and M	= <i>Podocarpoxylon</i> sp. 1 in Greguss (1967)
<i>Podocarpoxylon</i>	“Fossilie Nr.5”	Greguss (1956)	P and M	= <i>Podocarpoxylon</i> sp. 2 in Greguss (1967)
<i>Podocarpoxylon</i>	“Fossilie Nr.2”	Greguss (1956)	P and M	= <i>Podocarpoxylon</i> sp. 3 in Greguss (1967)
<i>Podocarpoxylon</i>	sp. 4	Greguss (1967)	P and M	Holotype reviewed
<i>Podocarpoxylon</i>	sp. 5	Greguss (1967)	P and M	Holotype reviewed
<i>Podocarpoxylon?</i>	None	Greguss (1952)	P and M	= <i>Podocarpoxylon</i> sp. 7 in Greguss (1967); holotype reviewed
<i>Podocarpoxylon</i>	sp.	Gothan (1906)	P	= <i>Protopodocarpoxylon jurassicum</i> Eckhold
<i>Xenoxylon</i>	None	Serra (1966)	P	

Poland and Hungary (Barale et al., 2002). Aptian floras were recorded around Moscow, Voronez and Kaluga (Prynada, 1937; Vakhrameev, 1991), while important Albian leaf floras were described from Ukraine, from Simpheropol and Kanev area (Barale and Doludenko, 1985; Vakhrameev, 1991) as well as from Georgia. In Romania, scarce, isolated remains of conifers were recorded from Aptian and Albian molassic sequences in the South Carpathians and in South Dobroudja (Iamandei and Iamandei, 1999; Iamandei, 2004). Early Cretaceous floras are represented by less diverse Pteridophytes, mainly with ferns of the Matoniaceae (Weichselia), or Tempskyaceae (Tempskyia). Gymnosperms are dominated by conifers, with families such as Cheirolepidiaceae and Taxodiaceae. The Cycadales and Bennettitales progressively lose their diversity and the Ginkgoales become rare. Though purely Mesophytic and dominated by Gymnosperms at first, Early Cretaceous flora of Eastern Europe experienced the rise and boom of Angiosperms. These were present at least from the Aptian onward, making the transition towards Neophytic flora.

4. Materials and methods

We obtained fossil wood data for Jurassic–Early Cretaceous from Hungary, Poland, Romania, Bulgaria, former Eastern Germany, Southern Sweden (Scania), Denmark (Bornholm Island), and the European part of former USSR (CIS) including Georgia, Crimea and Transcaucasia (Fig. 3). These data are new or from a reappraisal of the bibliography. Unfortunately, no data have been obtained from the former Yugoslavia. Lignite fragments are reported from the Liassic of Vrška Čuka in Serbia (Petkovic et al., 1958; Semaka, 1967), but we did

not find any preserved structures among the samples kindly sent to us by Vladan Radulovic. The taxonomy and nomenclature of all bibliographic data have been reviewed in order to homogenise the data. If the protologue (text and figures) was not clear enough, or if the associated material found did not allow any generic attribution, data were rejected (Table 1). The nomenclature follows Philippe (1993, 1995), Philippe et al. (1999c) and Bamford and Philippe (2001). Main wood genera are illustrated in Fig. 3.

For the investigation of new samples we used several methods: geologic thin sections (a polished face of the sample is glued on glass and the sample is subsequently ground to desired thickness), razor blade thin sections (samples are boiled in a mixture of water and glycerol for 4 to 5 h and then hand cut with a disposable razor blade), pyroxylin casts (Parlodion® dissolved in isoamyl acetate applied to a radial fracture of the sample, allowed to dry for 24 h and then peeled back) and scanning electron microscopy (samples are mounted on aluminium stubs, coated with gold/palladium, and observed on a Jeol 35-CF under 10 kV acceleration voltage). This array of methods allows the examination of most fossil wood specimens with preserved anatomic structures.

5. The data set

A bibliographic review was done. Several data from literature were found to be dubious. Table 1 gives a list of the data that we did not include because they are insufficiently supported, either by their protologue (i.e. with poor description and/or illustration) or by their types (i.e. type material does not allow the observation of diagnostic features). Reappraisals of Jurassic and Early Cretaceous woods from Hungary have been already

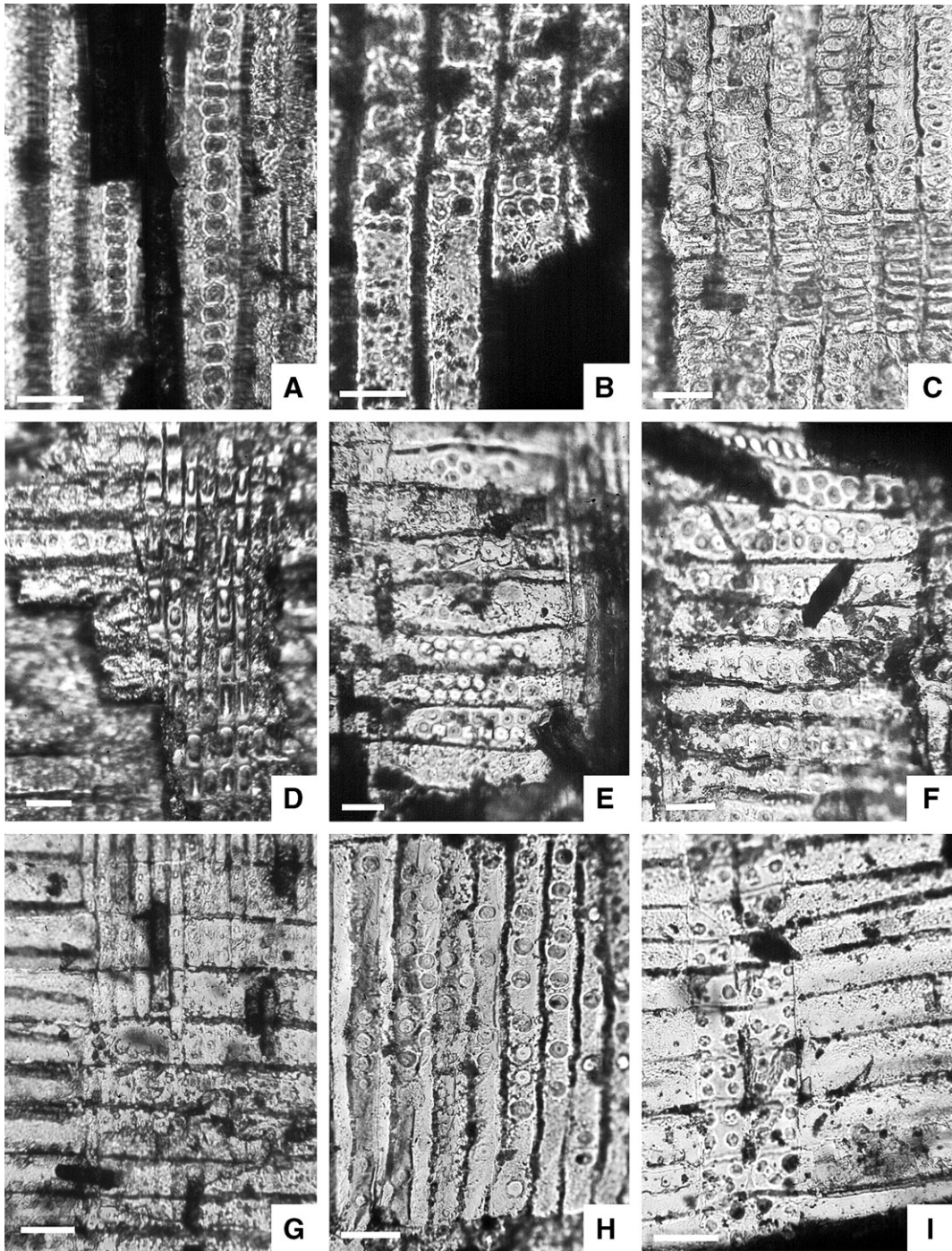


Fig. 4. Main wood genera, illustrated with specimens from the Bathonian of Poland. Scale bar 50 μm . A — *Agathoxylon*, sample MP1525, radial view, long uniseriate araucarioid radial pitting of the tracheids. B — *Agathoxylon*, sample MP1525, radial view, araucarioid cross-field pitting. C — *Xenoxylon*, sample MP1554 (sample assigned to *X. phyllocladoides*), radial view, ray and tracheid pitting. D — *Xenoxylon*, sample MP1554, radial view, typical cross-field pitting. E — *Protaxodioxylon*, sample MP1568, radial view, biseriate araucarioid radial pitting of the tracheids. F — *Protaxodioxylon*, sample MP1568, radial view, mixed type radial pitting of the tracheids. G — *Protaxodioxylon*, sample MP1568, radial view, taxodioid cross-field pitting. H — *Protopodocarpoxyton*, sample MP1523, radial view, mixed type radial pitting of the tracheids. I — *Protopodocarpoxyton*, sample MP1556, radial view, podocarpoid cross-field pitting.

published (Philippe and Barbacka, 1997; Barale et al., 2002). Some cases require more clarification:

- “*Podocarpoxyylon* (vel *Glyptostroboxyylon* ?) sp.”, Gothan, 1906, Teofilów near Częstochowa, Bathonian — this wood, which has been subject of taxonomic dispute, was first renamed *Protopodocarpoxyylon jurassicum* by Eckhold (1923), and then transferred to *Xenoxylon* by Kräusel (1949), before being chosen by Vogellehner as the generotype for his genus *Protopolyporoxyylon* (Vogellehner, 1968). Nevertheless the original slides have apparently never been reviewed (Philippe et al., 2002) and we have not been able to locate them in the main Polish palaeontological collections. To avoid more confusion we shall not use these data. It is noteworthy, however, that close to the type locality and in the same strata we collected abundant new material fitting Gothan’s description (see Fig. 4 — H and I). A study of this material is in progress, but we provisionally assign these topotypes to *Protopodocarpoxyylon*.
- *Pinites jurassicus* Göppert is another doubtful species. First described by Göppert (1845: 147) based on material from Poland, it has been subsequently quoted and illustrated by Mercklin (1855) with Russian material and by Eichwald (1868) with Lithuanian material. Eckhold (1923) transferred this taxon to his new genus *Protocupressinoxylon*, even though he did not study the holotype. In the Komarov Institute of St-Petersburg (Russia) some of the original material of Mercklin can be found as well as some slides sent by Göppert himself. Based on this material the corresponding data are considered as doubtful;
- *Pinites jurensis* Rouillier and Fahrenkohl was described in 1847 (Rouillier and Fahrenkohl, 1847) on the basis of material from the vicinity of Moscow and said to be Jurassic. As pointed out by Eichwald (1868: 54) who described *P. undulatus* from the same place, this “oolithic” formation actually belongs to the Early Cretaceous. This age is now confirmed (Akmetiev and Hermann personal communication). Later, Felix (1882) assigned a wood from the Dogger of Poland to *P. jurensis*, but this assignment is doubtful, however (Philippe, 1995);
- The occurrence of *Xenoxylon* in Hungary (according Serra, 1966 p. 20) is not supported by any data and is not considered here;
- Woods of Taxodiaceae and Cupressaceae are mentioned from Epleny by Greguss and Kedves (1961) without any generic attribution, and are thus not included in the database;
- Petrescu and Nuțu (1970) reported an araucarian wood from Romania, which they dated as Early Cretaceous, but it was subsequently demonstrated to be Late Cretaceous in age (Iamandei, 2004).

Following is the whole data set that we used.

Division: CYCADOPHYTA

Order: CYCADALES

Morphogenus *Cycadoxyylon* Renault

* *Cycadoxyylon* sp.

Romania, Hăghimaș, Dogger, Iamandei and Iamandei (2003).

Division : CONIFEROPHYTA

Order: CONIFERALES (incl. GINKGOALES)

Morphogenus *Agathoxyylon* Hartig

* *Agathoxyylon agathiforme* (Kedves) Philippe et Barbacka

Hungary, Úrkút, Upper Liassic; probably Toarcian (Philippe & Barbacka, 1997).

* *Agathoxyylon desnoversii* (Lemoigne) Philippe

Poland, Łuków, Middle Callovian; described as *Araucarioxyylon* sp. by Reymanówna (1956) (see Philippe, 1995).

* *Agathoxyylon pannonicum* (Greguss) Barale, Barbacka et Philippe

Hungary, Lábatlan, Aptian or Albian (Greguss, 1952; Barale et al., 2002).

* *Agathoxyylon parenchymatosum* (Greguss) Philippe, Zijlstra et Barbacka

Hungary, Úrkút, Upper Liassic, probably Toarcian (Philippe et al., 1999c).

* *Agathoxyylon* sp.

Armenia, Alaverdi, Late Jurassic; new data, sample N75 in Komarov Institute palaeobotanical collection;

Bulgaria, Zhablyano, Sofia District, Polaten Fm., Bajocian; new data, sample MP1091;

Bulgaria, Oborichte, Varna Dpt., Barremian; new data, sample MP1042;

Hungary, Vasas, probably Sinemurian or Hettangian; this sample was described as *Pteridospermaexylon theresiae* (Greguss, 1952), and then as *Araucarioxyylon* sp. 7 (Greguss, 1967), as demonstrated by Philippe et al. (1999c), is an *Agathoxyylon* (Philippe & Barbacka, 1997);

Hungary, Komló, Sinemurian or Hettangian (Philippe & Barbacka, 1997);

Hungary, Pécsbányatelep, Sinemurian or Hettangian (Philippe & Barbacka, 1997);

Hungary, Tata, Late Aptian; at this locality and in the same strata fossil wood is associated with *Chelonicerax* sp., which indicates a Late Aptian age (S. Reboullet personal communication); Greguss described *Araucarioxyylon* sp. 11 from this locality (Greguss, 1967), but reviewing his

holotype we found that cross-field pits are not preserved; our data are thus new, samples MP926 and 960;

Poland, Rhaeto–Liassic of Kraków-Częstochowa Upland (Brzyski and Helfik, 1994);

Poland, Jasna Góra cerca Częstochowa, “Clay under the Lower Oolithe, Bathonian”; this wood was described by Gothan (1906) as *Dadoxylon* sp.;

Poland, vicinity of Częstochowa, Uppermost Bajocian to Upper Bathonian, Parkinsonii, Zigzag, Tenuiplicatus, Morrissi, Bremeri and Retrocostatum zones; new data, samples MP1525–27, 1529, 1534, 1536–7, 1540, 1551, 1555, 1557, 1559, 1570, 1575, 1580, 1582–4;

Poland, Ogrodzieniec, Callovian; new data, sample MP 1587;

Poland, Stempiny, Barremian (Reymanówna, 1956);

Romania, Tichilești, Bathonian; this sample, VM0285 in Bucharest palaeobotanical collection, has been kindly lent by O. Dragastan for study in Lyon; it had been previously determined as *Sahnioxylon* sp. (Dragastan & Bărbulescu, 1980) and subsequently revised (Philippe et al., 1999a).

Morphogenus *Baieroxylon* Greguss

* *Baieroxylon lindicianum* Khan

Hungary, Eplény, Liassic (Philippe & Barbacka, 1997).

Morphogenus *Brachyoxylon* Hollick et Jeffrey

* *Brachyoxylon avramii* Iamandei

Romania, Medgidia (South Dobroudja), Gherghina Fm., Aptian (Iamandei, 2004).

* *Brachyoxylon* sp.

Bulgaria, Berende Izvor, Sofia district, Western Bulgaria, Ozirovo Fn., Dolni Loukovit Mb., Domerian, Stokesii zone; new data, sample MP1046;

Hungary, Komlo, Hettangian; new data, sample MP647;

Hungary, Sümeg, Valanginian, described as *Araucarioxylon* sp. no. 9 in Greguss (1967); we located the holotype (Bx11 in the Hungarian Geological Survey collections at Ráckózi-telep) and reviewed it, hence the new generic attribution;

Romania, Holbav and Cristian, close to Brasov, Central Romania, Hettangian–Sinemurian; (Popa, 2000a); and new data, samples MP936, 937, 938, 939, 940, 941, 1100;

Ukraine, Kanev, Albian; wood observed within *Frenelopsis* leafy twigs by Shilkina and Doludenko (1985) is provisionally assigned to this genus.

Morphogenus *Chamaecyparixylon* Khudayberdyev

* *Chamaecyparixylon privegillii* Iamandei et Iamandei

Romania, South Dobroudja, Țibrinu, Gherghina Fm., Aptian; Iamandei & Iamandei (1999).

Morphogenus *Circoporoxylon* Kräusel

* *Circoporoxylon grandiporosum* Müller-Stoll et Schultze-Motel

Bulgaria, Dobromir, Balaban, Varna, Pliensbachian, new data, samples MP1266 and MP1267.

Morphogenus *Cupressinoxylon* Göppert (*nomen conservandum* see Bamford et al., 2002; Skog, 2003)

* *Cupressinoxylon kiprianovii* Mercklin

Russia, Kursk, Early Cretaceous, holotype revised in Komarov Institute palaeobotanical collection, no. 318.

* *Cupressinoxylon kiroviense* Shilkina

Russia, Kirov, Valanginian; Shilkina (1989).

* *Cupressinoxylon* sp.

Denmark, Bornholm, Early Cretaceous; in the Stockholm Naturhistoriska Riksmuseet collections, as determined from SEM study of specimen S1356; this specimen had been studied by Gothan, his hand-writing states “*Die Preparete gestatten nicht zur Bestimmung der Gattung. Cf. Cedroxylon*”.

“Morphogenus” [*Dicotyledoxylon*]

* [*Dicotyledoxylon*] sp.

Hungary, Lábatlan, Aptian or Albian (Barale et al., 2002); this name is much used for dicotyledonous woods of dubious affinities, albeit it is nomenclaturally invalid.

Morphogenus *Keteleerioxylon* Shilkina

* *Keteleerioxylon fokinii* Shilkina

Russia, Kirov, Valanginian; Shilkina (1986).

Morphogenus *Phyllocladoxylon* Gothan

* *Phyllocladoxylon dorofeevii* Shilkina

Russia, Kirov, Valanginian; Shilkina (1989).

Morphogenus *Podocarpoxyylon* Gothan

* *Podocarpoxyylon svanidzei* Barale et al.

Georgia, Tkibouli, Bathonian (Barale et al., 1991);

Georgia, Tkvarcheli, Bathonian; new data, sample collected by Delle, in Komarov Institute palaeobotanical collection, unnumbered.

* *Podocarpoxyylon* sp.

Hungary, Lábatlan, Aptian or Albian (Barale et al., 2002); Greguss (1967) described several *Podocarpoxyylon* sp. from the Early Cretaceous of Tata (*P.* sp. 1, 2 and 3); three sets of slides are preserved as holotypes for these *P.* sp.; however none of them is well enough preserved for generic attribution.

Morphogenus *Protaxodioxyylon* Bamford et Philippe

* *Protaxodioxyylon* sp.

Hungary, Pécsbányatelep, Sinemurian or Hettangian, sample determined as *Taxodioxyylon* sp. by Greguss and

Kedves (Philippe and Barbacka, 1997) and new material from Vasas (sample MP674) and Pecs (samples MP896, 897, 898); this wood is similar to a wood described from the Dogger of Iran in an unpublished thesis by Nadjafi (1982) as [*Protosciadopityoxylon boureaui*] (not a validly published name); the name *Protosciadopityoxylon* was validly published by Zhang et al. (1999) with a type which displays strongly xenoxylid radial pitting and cross-field pitting similar to that of the sample from König's Karl Land assigned by Gothan to *Xenoxylon phyllocladoides* (Gothan, 1910); although the Hungarian material has clear affinities with modern *Sciadopitys*, e.g. largely open taxodioid crossfield pits in the earlywood, we cannot assign it to *Sciadopityoxylon* Schmalhausen as the latter genus is probably a synonym of *Xenoxylon* (Philippe and Thévenard, 1996). We shall refer to this Hungarian material as *Protaxodioxylon* sp., waiting for a reappraisal of the complex of Laurasian Mesozoic softwoods with some *Sciadopitys* features;

Poland, Gnaszyn, Bathonian, Morrissi zone. New data (sample MP1568), with an anatomy intermediate between previous wood and *Taxodioxylon lemoignei* Philippe.

Morphogenus *Protelicoxylon* Philippe

* *Protelicoxylon parenchymatosum* (Greguss) Philippe
Hungary, Úrkút, Upper Liassic, probably Toarcian (Philippe & Barbacka, 1997).

* *Protelicoxylon* sp.

Hungary, Pécsbányatelep, Sinemurian or Hettangian (Philippe & Barbacka, 1997).

Romania, Holbav, Hettangian ?–Sinemurian; new data, sample MP1102.

Morphogenus *Protocedroxylon* Gothan

* *Protocedroxylon magnoradiatum* Shilkina
Russia, Kirov, Valanginian; Shilkina (1989); this species is reported here under the name used by Shilkina, even though this binomial was already used by Eckhold (1923) who reassigned *Anomaloxylon magnoradiatum* Gothan to the genus *Protocedroxylon*. We reinvestigated Gothan's original material, in Stockholm and agree with Eckhold's position, and make the hypothesis that Shilkina's material from Kirov is most probably related to *Protocedroxylon araucarioides* Gothan.

* *Protocedroxylon kryshstofovichii* Shilkina

Russia, Kirov, Valanginian; Shilkina (1986).

Morphogenus *Protocircoporoxylon* Vogellehner

* *Protocircoporoxylon* sp.

Romania, Holbav, Hettangian–Sinemurian; new data, sample MP1101.

Morphogenus *Protocupressinoxylon* Eckhold

* *Protocupressinoxylon dragastanii* Iamandei et Iamandei.

Romania, South Dobroudja, Cernavoda, Gherghina Fm., Aptian (Iamandei & Iamandei, 1999).

* *Protocupressinoxylon* sp.

Romania, South Dobroudja, Cuza Voda, Gherghina Fm., Aptian (Iamandei, 2004);

CIS, Voronejsk, Jurassic–Early Cretaceous; new data, sample 29/5763 in Komarov Institute palaeobotanical collection.

Morphogenus *Protopodocarpoxylo* Eckhold (*nomen conservandum*, see Philippe et al., 2002; Skog, 2003)

* *Protopodocarpoxylo dobrogiacus* Iamandei

Romania, South Dobroudja, Medgidia, Gherghina Fm., Aptian (Iamandei, 2004)

* *Protopodocarpoxylo* sp.

Poland, Częstochowa area, Bajocian and Bathonian, in Parkinsoni, Zigzag (Convergens and Macrescens subzones), Morrissi, Bremeri and Retrocostatum zones; new data, samples MP1523, 1524, 1528, 1530–1533, 1535, 1538, 1552, 1556, 1560–1563, 1565–1567, 1573, 1579, 1585, 18586, 1590–1592;

Romania, Holbav, Hettangian ?–Sinemurian; new data, samples MP1106, 1142–1148, 1150, 1151;

Romania, Tichilești, Bathonian; sample T214 in the Bucarest palaeobotanical collection has been kindly lent by X. Dragastan for study in Lyon; new data.

Romania, Cernavoda, Dobroudja, Aptian; sample MP1195 sent by Petrescu to Lemoigne years ago, probably from Gherghina Fm.; new data.

Morphogenus *Simplicioxylon* Andreánsky

* *Simplicioxylon hungaricum* Andreánsky

CIS, Charoukar, Caspian Sea, Liassic (Philippe, 1995);
Denmark, Bornholm, Early Liassic, as *Brachyoxylo* *rotnaensis* by Mathiesen in 1957 (see Philippe, 1995);

Hungary, Úrkút, Upper Liassic, probably Toarcian (Philippe and Barbacka, 1997; Polgari et al., 2005) and new samples, MP1160 and MP1175 sent by Marta Polgari;

Hungary, Eplény, Liassic (Philippe & Barbacka, 1997; Philippe, Zijlstra & Barbacka, 1999);

Romania, Șuncuiuș (NW Romania), Early Liassic (new data, sample MP1196, formerly given to Lemoigne by Petrescu);

Sweden, Scania, Skromberga, Rhaeto–Liassic, samples S1098 and S1073 in the palaeobotanical collection of the Swedish Museum of Natural History, new data.

Morphogenus *Taxaceoxylon* Kräusel et Jain

* *Taxaceoxylon jarmolenkoi* Shilkina

Russia, Kirov, Valanginian; Shilkina (1989).

Morphogenus *Taxodioxyton* Hartig

* *Taxodioxyton* sp.

Ukraine, Kanev, Albian; wood observed in *Cryptomeria* leafy twigs by Shilkina and Doludenko (1985) is provisionally assigned here to this genus.

Morphogenus *Xenoxylon* Gothan

* *Xenoxylon latiporosum* (Cramer) Gothan

Crimea, Chalimov, Middle Jurassic (Shilkina and Khudayberdyev, 1971; Philippe, 1995; Philippe & Thévenard, 1996); sample 688 in Komarov Institute palaeobotanical collection;

Georgia, Tkvarcheli, Early Bathonian (Delle, 1960);

Poland, Karnocice by Lubin, Middle Aalenian (Philippe, 1995; Philippe & Thévenard, 1996);

Poland, Częstochowa, Bathonian, Zigzag and Morisi zones; new data (samples MP1550, 1553, 1558);

Kazakhstan, Mangichlak, Liassic (Philippe & Thévenard, 1996).

* *Xenoxylon phyllocladoides* Gothan

Poland, Iron mine Łojki by Częstochowa, dump of the main iron layer (Gothan, 1906; Reh binder, 1914); the Łojki wood-bearing level, given as Bathonian by Gothan (1906) belongs to the uppermost Bajocian Parkinsoni zone;

Poland, vicinity of Częstochowa, uppermost Bajocian, Parkinsoni zone; new data, sample MP1539;

Poland, vicinity of Częstochowa, Mid-Bathonian, Bremeri zone; new data, samples MP 1569 and 1571;

Poland, vicinity of Częstochowa, Upper Bathonian, Retrocostatum Zone; new data, samples MP1572 and 1588;

Russia, Sovetsk (formerly Tilsit) near Kaliningrad, Late Callovian, Gothan in Kräuse (Gothan, 1939).

Table 2 summarises these data at generic level. In this table, time is subdivided into four periods (Liassic, Dogger, Malm and Early Cretaceous) framed by the five floristic turnovers described previously in Western Europe (Philippe et al., 1999b; Philippe, 2000). In this table, one datum is understood as the determination of a genus at a locality in the stratigraphic interval under consideration. Perhaps the most striking fact in Table 2 is the almost complete lack of data from the Malm for Mid-

Table 2

Wood data at generic level from Mid-Eastern Europe for the Jurassic and Early Cretaceous. Time is subdivided in four periods: (1) Liassic, from Hettangian Planorbis Zone, to the end of Mid-Aalenian Murchisonae Zone; (2) Dogger, from Late Aalenian Concavum Zone to the end of the Mid-Callovian Coronatum Zone; (3) Malm, from the Late Callovian Athleta Zone to the end of the Jurassic; and (4) Early Cretaceous. Numbers given (ex. $n=a/b$) are respectively the total number of data (a) and the number of new data (b). Underlined names are based, at least partly, on new data.

Countries: stages	Poland, Denmark, Sweden and western Russia	Northern Hungary	Southern Hungary	Romania	Bulgaria	Armenia, Caspian sea, Crimea, Georgia, Eastern Russia and Ukraine
Liassic:	<i>Agathoxylon</i>	<i>Agathoxylon</i>	<i>Agathoxylon</i>	<i>Brachyoxyton</i>	<i>Brachyoxyton</i>	<i>Simplicioxyton</i>
Planorbis to Murchisonae zones	<u><i>Simplicioxyton</i></u> <u><i>Xenoxylon</i></u>	<i>Baieroxyton</i> <i>Protelicoxyton</i> <i>Simplicioxyton</i>	<u><i>Brachyoxyton</i></u> <u><i>Protaxodioxyton</i></u> <u><i>Protelicoxyton</i></u>	<u><i>Protelicoxyton</i></u> <u><i>Protocircoporoxylon</i></u> <u><i>Protopodocarpoxyton</i></u> <u><i>Simplicioxyton</i></u>	<u><i>Circoporoxylon</i></u>	<i>Xenoxylon</i>
	$n=4/1$	$n=7/1$	$n=7/3$	$n=6/5$	$n=2/2$	$n=2/0$
Dogger:	<i>Agathoxylon</i>	No data	No data	<i>Agathoxylon</i>	<i>Agathoxylon</i>	<i>Podocarpoxyton</i>
Concavum to Coronatum zones	<u><i>Protopodocarpoxyton</i></u> <u><i>Protaxodioxyton</i></u> <u><i>Xenoxylon</i></u>			<u><i>Cycadoxylon</i></u> <u><i>Protopodocarpoxyton</i></u>		<i>Xenoxylon</i>
	$n=9/6$			$n=3/2$	$n=1/1$	$n=4/2$
Malm:	<u><i>Agathoxylon</i></u> <u><i>Xenoxylon</i></u>	No data	No data	No data	No data	<u><i>Agathoxylon</i></u>
Athleta to Giganteus zones	$n=3/1$					$n=1/1$
Early Cretaceous	<i>Agathoxylon</i> <u><i>Cupressinoxyton</i></u>	<i>Agathoxylon</i> <u><i>Brachyoxyton</i></u> <u>[<i>Dicotyledoxyton</i>]</u> <u><i>Podocarpoxyton</i></u>	No data	<i>Brachyoxyton</i> <i>Chamaecyparixylon</i> <i>Protocupressinoxyton</i> <i>Protopodocarpoxyton</i>	<i>Agathoxylon</i>	<i>Brachyoxyton</i> <i>Cupressinoxyton</i> <i>Keteleerioxylon</i> <i>Phyllocladoxylon</i> <i>Protocedroxylon</i> <i>Taxaceoxylon</i> <i>Taxodioxyton</i>
	$n=2/1$	$n=6/2$		$n=6/1$	$n=1/1$	$n=8/0$

Eastern Europa. Lack of fossil wood in Upper Jurassic sediments might be due to several interacting causes:

- (a) minor amounts of marine sediments suitable for preservation;
- (b) high eustatic sea level on the European platform (Ziegler, 1988), associated with major subsidence in the Alpine orogen (Winterer and Bosellini, 1981);
- (c) misidentification of the age of the Vardar orogen: its peak should be Early Cretaceous rather than Late Jurassic; therefore land masses emerged above sea level after Jurassic times only. There are carbonate platforms of Tithonian age in the region, although they are known mostly from redeposited sediments (Tollmann, 1981). Islands – even if associated with them – were of minor extent.

It must be emphasized, however, that the Upper Jurassic, especially after the Middle Oxfordian, is considered to be a period of globally dry climate all over Europe (Dromart et al., 2003), and thus not very favourable to tree growth. It is thus significant that three out of the four data that we have for the Upper Jurassic are from the northern part of the studied range.

Local wood-rich deposits with relatively high diversity, as in the Bathonian of Poland, demonstrate that the limited data for the Dogger is probably due to a geologic bias, possibly the general lack of taphonomically suitable conditions for the preservation of fossil wood.

The other strong limitation of our results is that the generic diversity, i.e. the number of genera occurring in a given area for a given time interval, is strongly linearly correlated to the number of data for this area and interval (correlation coefficient=0.78), despite the fact that we almost doubled the number of data as compared to the literature. This makes it difficult to interpret the absence of a genus.

6. Discussion

During the Liassic the wood floras in Mid-Eastern Europe are rather uniform, with the noticeable absence of *Simplicioxylon* in Southern Hungary (despite numerous samples having been studied from the Mecsek Mountains area by us as well as by other authors). This genus is definitely the most common one in the Liassic of Europe, being widespread and common from southern France to Sweden and to the Caspian Sea. Surprisingly, *Agathoxylon* is absent in our record from the easternmost part of the studied range, albeit very common in the western part of Mid-Eastern Europe. *Xenoxylon*, an indicator of relatively wetter/cooler

climates (Philippe and Thévenard, 1996), is almost absent in the studied area, whereas it is common in the Liassic of UK, France and Germany as well as in Middle Asia and Iran on. The only occurrence of *Xenoxylon* for the Liassic of Mid-Eastern Europe is at the very end of that time period (upper Middle Aalenian) and from a glacial boulder found in northern Poland, but probably originating from Russia.

For the Dogger, data are more scarce. The wood flora looks quite uniform. Unfortunately there are no data for Southern Hungary after the Liassic. *Xenoxylon* is well represented in the northernmost part of the area, mainly during the Bathonian. *Cycadoxylon*, rather rare, is reported (Iamandei and Iamandei, 2003) from an area in Eastern Carpathians that was an island during the Jurassic and the Cretaceous.

After the long silence of the Malm, the record starts again in the Early Cretaceous, mainly during its later stages (Aptian and Albian). The wood flora is somewhat renewed. *Xenoxylon* is absent (known at this time only around the Arctic). For most of Mid-Eastern Europe, except Russia and Ukrainia, there is no representative of genera with Pinaceae features (like *Protocedroxylon* or *Piceoxylon*) whereas these are common at this time in Western Europe. The dicotyledons enter the record with only one poorly differentiated wood (Crawley, 2001).

To sum up, keeping in mind the limitations given above, we consider the most reliable results for the Jurassic and the Early Cretaceous wood flora of Mid-Eastern Europe to be:

- 1) the wide distribution of *Simplicioxylon* in the Liassic, with the exception of Southern Hungary;
- 2) the restriction of *Xenoxylon* to the Dogger (apart from one marginal exception);
- 3) the restriction of *Protocedroxylon*-like woods to the north-easternmost part of the range.

6.1. Distribution of wood genera within Mid-Eastern Europe

The Southern Hungary record covers only the Liassic, but is clearly different from that of the rest of the geographical study zone. First, as pointed out above, the Southern Hungary record does not have the common genus *Simplicioxylon*. Moreover, it is the only area with *Protaxodioxylon* sp. This wood morphogenus is also known in the Liassic of France (Philippe, 1995), but the samples observed in Eastern Mecsek are most similar to a wood described from the Early-Middle Jurassic of Iran (Nadjafi, unpublished). The coeval wood flora of Iran, however,

Table 3

Comparing wood generic diversity through the Jurassic–Early Cretaceous period, in western Europe (west of 12°E; data from Philippe, 2000), Eastern Europe (East of 12°E; this study) and Northern Gondwana (from Morocco to Lebanon; data from Philippe, 2000)

	Europe, West of 12°E	Europe, E of 12°E	Northern Gondwana
Liassic	<i>Agathoxylon</i> <i>Baieroxylon</i> <i>Brachyoxylon</i> <i>Circoporoxylon</i> <i>Protaxodioxyton</i> <i>Protelicoxylon</i> <i>Protocupressinoxylon</i> <i>Protophyllocladoxylon</i> <i>Simplicioxylon</i> <i>Xenoxylon</i>	<i>Agathoxylon</i> <i>Baieroxylon</i> <i>Brachyoxylon</i> <i>Circoporoxylon</i> <i>Protaxodioxyton</i> <i>Protelicoxylon</i> <i>Protocircoporoxylon</i> <i>Protopodocarpoxyton</i> <i>Simplicioxylon</i> <i>Xenoxylon</i>	<i>Agathoxylon</i> <i>Brachyoxylon</i>
Dogger	<i>Agathoxylon</i> <i>Brachyoxylon</i> <i>Circoporoxylon</i> <i>Cupressinoxylon</i> <i>Protaxodioxyton</i> <i>Protocupressinoxylon</i> <i>Protopodocarpoxyton</i> <i>Xenoxylon</i>	<i>Agathoxylon</i> <i>Cycadoxylon</i> <i>Podocarpoxyton</i> <i>Protaxodioxyton</i> <i>Protopodocarpoxyton</i> <i>Xenoxylon</i>	<i>Agathoxylon</i> <i>Brachyoxylon</i> <i>Metapodocarpoxyton</i>
Malm	<i>Agathoxylon</i> <i>Brachyoxylon</i> <i>Circoporoxylon</i> <i>Cupressinoxylon</i> <i>Phyllocladoxylon</i> <i>Podocarpoxyton</i> <i>Protocupressinoxylon</i> <i>Protopinuxylon</i> <i>Taxodioxyton</i> <i>Xenoxylon</i>	<i>Agathoxylon</i> <i>Xenoxylon</i>	<i>Agathoxylon</i> <i>Metapodocarpoxyton</i> <i>Protopodocarpoxyton</i>
Early Cretaceous	<i>Agathoxylon</i> <i>Brachyoxylon</i> <i>Cupressinoxylon</i> [<i>Dicotyledoxyton</i>] <i>Phyllocladoxylon</i> <i>Piceoxylon</i> <i>Pinuxylon</i> <i>Podocarpoxyton</i> <i>Protophyllocladoxylon</i> <i>Protopiceoxylon</i> <i>Protopinuxylon</i> <i>Protopodocarpoxyton</i> <i>Taxodioxyton</i> <i>Widdringtonioxylon</i>	<i>Agathoxylon</i> <i>Brachyoxylon</i> <i>Chamaecyparixylon</i> <i>Cupressinoxylon</i> [<i>Dicotyledoxyton</i>] <i>Keteleerioxylon</i> <i>Phyllocladoxylon</i> <i>Podocarpoxyton</i> <i>Protocedroxylon</i> <i>Protocupressinoxylon</i> <i>Protopodocarpoxyton</i> <i>Taxaceoxylon</i> <i>Taxodioxyton</i>	<i>Agathoxylon</i> <i>Brachyoxylon</i> <i>Metapodocarpoxyton</i> <i>Protocircoporoxylon</i> <i>Protopodocarpoxyton</i>

includes *Xenoxylon*, a typical Laurasian element that is missing from our south-Hungarian record, and *Protelicoxylon*, a genus also known in the Liassic of Romania (this study) and France (Philippe, 1995). The tectonic units scattered between Southern Hungary and Iran are almost unknown from a xylologic point of view; the only data we are aware of is the occurrence of *Agathoxylon* in the Jurassic of Turkey (samples kindly given to us by Erdei

Boglarka, our identification). This lack of data precludes us from proposing a hypothesis about Southern Hungarian palaeobiogeographic relationships.

Aside from Southern Hungary, the rest of Mid-Eastern Europe has a relatively uniform flora, throughout the Jurassic–Early Cretaceous. The absence in some areas of otherwise common genera like *Brachyoxylon* in the Liassic, *Protopodocarpoxyton* in the Dogger, or

Cupressinoxylon in the Early Cretaceous, is probably due to a lack of data, and should not be interpreted in terms of palaeobiogeography.

The distribution of *Xenoxylon* is remarkable. It is restricted to the northernmost part of this region. This fits with the hypothesis that this genus, with a circumpolar distribution, is linked to cold and/or humid climates (Philippe and Thévenard, 1996).

6.2. Comparisons with western Europe and Northern Gondwana

As a whole the evolution of wood generic diversity in Mid-Eastern Europe is parallel to what is known in Western Europe (Table 3). Keeping in mind the limitation due to the relatively small dataset, the wood generic diversity of Mid-Eastern Europe is equal to that of Western Europe during the Liassic, is slightly lower during the Dogger, almost non-existent during the Malm, and lower during the Early Cretaceous.

In Mid-Eastern Europe as well as in Western Europe, several Liassic taxa are restricted to this time interval, for example *Simplicioxylon* and *Protelicoxylon*. The floristic turn-over found for Western Europe at the end of the Mid-Aalenian also occurred in Mid-Eastern Europe at the same time. It is unfortunate that the lack of data in the Dogger of Southern Hungary makes it impossible to know if this floristic turn-over extended to this area.

Dogger wood flora are rather impoverished, with little regionalism, in both Mid-Eastern and Western Europe. All the genera represented are common throughout the Jurassic and the Cretaceous in Laurasia. For the Malm, the contrast is striking between the relatively rich wood flora of Western Europe and the single and common genus *Agathoxylon* found in Mid-Eastern Europe. This contrast indicates that the lack of data in Mid-Eastern Europe is due to local conditions (e.g. palaeoecology, taphonomy) rather than to a global cause.

Eventually a new rise in wood diversity clearly occurred in the Early Cretaceous, in both western and Mid-Eastern Europe. Wood genera represented in the Early Cretaceous of Mid-Eastern Europe are common and widespread, almost all of them being already documented in the Jurassic of that area. In contrast, in Western Europe a floristic turn-over is obvious, with the noticeable occurrence of several genera more or less related to the Pinaceae. These are absent from Mid-Eastern Europe, with the exception of Russia, where abundant material is reported (Shilkina, 1986, 1989), assigned to genera like *Keteleerioxylon* and *Protodroxylon*. Apparently, the new wood genera that appeared during the Early Cretaceous in Europe were

mostly migrants from arctic biota, and reached Mid-Eastern Europe only marginally.

Comparisons indicate that the Northern Gondwana wood flora was much less diverse, probably because the area had a much more constraining palaeoecology, with a long dry season (Philippe et al., 2004). Perhaps the most striking fact in Northern Gondwana record is the appearance of the successful genus *Metapodocarpoxylon* by the Dogger (Philippe et al., 2003). As it is the rim of a large and stable plate with terrestrial continuity (Bosellini, 2002), Northern Gondwana displays no partition of its continental flora. It does not seem to be affected by the floristic turn-overs that occur in Laurasia during the Aalenian and at the Jurassic/Cretaceous boundary. In contrast, the archipelago palaeogeography of Europe (in both its Western and Eastern parts), as well as its connection with Arctic biota, seems to have enhanced floristic turn-overs.

Southern Hungary is difficult to discuss as data are scarce, but its palaeobiogeographic peculiarities have already been discussed several times. Most authors emphasize a close palaeobiogeographic relationship with north-western Europe (for a review see Vörös, 2001), while the significance of odd, Gondwanan faunal elements is stressed by Kozur and Mock (1997). It is remarkable that a typical northern Gondwana element, the pollengenus *Afropollis*, has been found there within Lower Cretaceous sediments (H. Meon, personal communication). On the other hand, the leaf flora from Mecsek Liassic deposits has clear Laurasian affinities. According to Csontos and Vörös (2004), the southern part of Hungary was separated by oceanic crust from the European mainland and did not join it before the Aptian. The peculiarities of the wood and pollen floras can thus be considered as significant, remembering that within phytocoenosis different elements may have different palaeobiogeographic affinities (Philippe et al., 2003).

7. Conclusions

Despite its incompleteness, our wood record clearly demonstrates a partition of Mid-Eastern European continental floras. This was not an unexpected result, as at this time the area was an archipelago with changing palaeogeography. Although there were sea sounds dividing it, the northern part of the studied zone has a rather uniform flora, at least during most of the Jurassic.

The sea sounds between the different parts were probably rather narrow (less than 100 km) but of various depths. The shallow ones between the several emerged lands of the European platform induced little floristic differentiation. On the contrary, the deep sea sounds that

separated the ribbon continents of the truly oceanic zones resulted in much more endemism. The parallel is striking with the present day Indonesian Archipelago which is divided into two palaeobiogeographic areas. The northern islands (Sumatra, Java, Sarawak) belong to the Malayan platform and have palaeotropical and even palaeoarctic relationships, while the rest of the Archipelago (Bali, Sulawesi, Flores, Timor, Irian Jaya, etc.) has clear australasian affinities. More research, focussed on Southern Hungary and south-eastward to Greece, could help in identifying this “palaeo Wallace’s line”.

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