European Jurassic floras:
statistics and palaeoenvironmental proxies

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ABSTRACT. The Jurassic floras of Europe show considerable diversity. To examine the extent of this diversity and its possible causes we used multivariate statistical methods (cluster analysis, PCA, NMDS) to compare all significant Jurassic floras in Europe. Data were based on 770 taxa from 46 fossiliferous occurrences (25 units) from France, Germany, Greenland, Hungary, Italy, Norway, Poland, Romania, Scotland, Serbia, Sweden, Switzerland, and the United Kingdom. Statistical analyses were applied at species level and genus level, and also performed for the major plant groups. The genus cladograms show affinities between different localities based on environmental factors, while the cladograms based on species affinities indicate only taxonomical correlations. The study shows that locality age does not seem to be of paramount importance for floral composition.

KEYWORDS: flora composition, autochthonous and allochthonous floras, cluster analysis, PCA, NMDS, Jurassic, Europe

INTRODUCTION

In the last decades, as taxonomic studies of numerous Mesozoic localities have been completed, palaeoenvironmental reconstruction of different floras/localities has become a focus of interest. Different methods have been applied to study plants' adaptation to environmental conditions and the mechanisms of plant distribution and migration. Methods include analyses of macromorphology and cuticular structure

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(Barbacka et al. 2006, Pott & McLaughlin 2009, Steinthorsdottir et al. 2011), traditional quantitative methods (Knobloch & Mai 1986, Kostina & Herman 2013), comparisons between macro- and microfloras (Kustatscher et al. 2010), analyses of the affinities between palynomorphs and their "mother" plants or sporomorph ecogroups (Abbink et al. 2004), and considerations of plants' environmental requirements based on statistical analyses (Spicer & Hill 1979, Rees et al. 2000, McElwain et al. 2007, Jasper et al. 2010, Barbacka 2011). Statistical analyses have also been used to compare floras on the global scale (Spicer & Hill 1979, Herman & Spicer 1997). These methods provide extensive information helpful in understanding the relationships between localities and taxa, and they can indicate possible migration pathways and distribution mechanisms, as is done for phytoprovinces (Vakhrameev 1991). Significant palaeogeographic and palaeoclimatic hypotheses have been proposed.

The aim of the present study was to compare fossil floras on a regional scale in Europe (except Russia) and to determine the most important factors influencing the similarities and dissimilarities between particular regions (i.e. palaeogeographical, temporal, environmental, and climatic factors), and in particular the degree to which the palaeoenvironment influenced the plant composition at the sites.

The study is based on literature data and on our unpublished data. Fortunately, in recent times some classic localities (France, Germany, Italy, Sweden, United Kingdom, some localities in Poland) have been taxonomically revised and re-examined according to the methodological standards of modern palaeobotany and supplemented by local environmental data. A number of new localities have been described (Serbia, some small Polish sites, Switzerland, Norway), and work on some localities is in progress (Hungary, Romania). For all localities, more or less comprehensive information on their palaeoenvironmental settings is available.

To date there has been no detailed study correlating different European floras of the Jurassic period except for a recent comparison of Middle Jurassic floras of Europe and northern palaeo-Africa that demonstrated dissimilarity in the floras of this period (Scanu et al. 2014). Such work is needed if we are to understand how uniform/diverse the floras of Europe were during the Jurassic, or to understand the compositional differences between the various floras and/or time slices in relation to their environmental or latitudinal settings. Since the number of species and genera described from the different floras over the years is very high, only multivariate statistical methods can be used. This is the first study comparing the various macrofloras and relating them to their palaeoecological settings.

MATERIAL AND METHODS

The database comprises 770 taxa from 46 Early, Middle and Late Jurassic localities in Europe (Table 1). For statistical reasons, floras with less than five well-defined species were not considered. The data are based mostly on classic and modern peer-reviewed works published up to 2013. For floras that were revised the latest list of taxa was used. Records from classic works which were not re-examined or only partly re-examined were used in their original form, supplemented by the new data. Because a large number of references are cited, they are given in tables (taxonomic references Table 2, environmental references Table 3) and are not repeatedly mentioned in the text. Records from France, Italy, Poland, Romania, and Greenland contain, besides published data, also unpublished data on taxa from revisions, most of them done by us. Taxa with uncertain determinations ("cf.") were recorded in the database as definite. Indeterminable taxa (sp.) were included only when they were the only representatives of a given genus. In other cases undetermined species (e.g. "sp.", "sp. A") were omitted.

Outcrops of the same age and depositional setting in a given area were treated as single units and labelled as such; examples are Yorkshire (United Kingdom), Franken (Germany), Scania (Sweden), Hungary, some Late Jurassic localities in France, the Holy Cross Mts. (Poland), the Veneto area (Italy), and Serbia (see Table 3).

The database was prepared using MS Excel software in a 1/0 (presence-absence) matrix for species and genera. The full database from the studied localities is attached as a supplement (http://botany.pl/ibwyd/acta_paleo/base1/act-p54_2_Barbacka.html).

The statistical and mathematical analyses employed the R program (R Development Core Team 2011). Sampling was affected by different factors at each locality (e.g. sample accessibility, size of outcrop, subjective selection of material, preservation); this should be borne in mind when interpreting the results. Rarefaction was not possible in this case as only binary data were available, without abundance data.

Statistical analyses:

1) Diversity indices. Alpha diversity (Bush & Bambach 2004) was calculated for all taxonomical groups in each locality. Both the total number of taxa and the alpha diversity of the localities and epochs were calculated. Alpha diversity provides important information about the locality but is strongly affected by differences in the manner of collecting fossils (open mines, dumps,

Table 1. Localities and locality units, with their depositional environments during the Jurassic of Europe

Country	Locality/environment								
	Lower Jurassic (L)			Middle Jurassic (M)			Upper Jurassic (U)		
	unit name	localities	depositional setting	unit name	localities	depositional setting	unit name	localities	depositional setting
Poland	Holy Cross-L	Studzianna Huta Odrowąż Gromadzice Chmielów Podszkodzie	fluvial	Grojec-M	Grojec	fluvial	Wólka-U	Wólka	lagoon
France	Vendée-L	Causses basin Deux-Sèvres Vendée Hettange	lagoon – marine	Causses-M / Mamers-M	Causses / Mamers	lagoon / lagoon	Jura-U	Armaille Creys Orbagnoux Jura	allochthonous lagoon – delta – paralic basin
Romania	Reşiţa-L	Anina Sirinia Cristian Holbav	fluvial						
Hungary	Mecsek-L	Mecsek Mts.	delta						
Germany	Franken-L	Bayreuth Nürnberg Bamberg	fluvial				Solnhofen-U	Solnhofen Nusplingen Brunn	lagoon, marine
Italy	Veneto-L	Rovére di Velo Rotzo Veneto	allochthonous	Sardegna-M	Sardegna	coastal fluvial			
Norway				Andoya-M	Andoya	fluvial			
Greenland	Scoresby-L	Scoresby Sound	delta						
UK				Yorkshire-M / Stonesfield-M	Yorkshire / Stonesfield	delta / coastal upland			
Scotland				Bearreraig-M / Brent-M	Bearreraig / Brent	allochthonous / allochthonous	Sutherland-U	Sutherland	river, delta, allochthonous
Serbia	Stara Planina-L	Stara Planina Mt. Dobra Ruj Mt. Vrška Čuka	fluvial/ delta						
Sweden	Scania-L	Scania	fluvial						
Switzerland							Basel-U	Basel	lagoonal

Table 2. References for taxonomic data of all studied localities

State	Locality	Age	References
France	general	Early Jurassic	Brongniart 1828–1837, 1849, Schimper 1869, Thévenard et al. 1995
	Vendée	Early Jurassic	Saporta 1873–1891, Carpentier 1950, Corsin 1950, Barale 1987
	Causses	Middle Jurassic	Philippe et al. 1998
	Mamers	Middle Jurassic	Lemoigne 1968, Philippe et al. 1998
	Armaille Creys Orbagnoux Jura	Late Jurassic	Barale 1981
Germany	Bayreuth	Early Jurassic	Schenk 1867, Weber 1968, Kirchner 1992, Gregor and Hauptmann 1998
	Nürnberg	Early Jurassic	Schenk 1867, Gothan 1914, Gregor and Hauptmann 1998
	Bamberg	Early Jurassic	Schenk 1867, Kräusel 1958, Kirchner 1992, Gregor and Hauptmann 1998
	Solnhofen	Late Jurassic	Kuhn 1961, Barthel et al. 1990, Jung 1974, Kräusel 1943, Wellnhofer 2008
	Nusplingen	Late Jurassic	Dietls G. and Schweigert G. 2011
	Brunn	Late Jurassic	Röper and Rothgaenger 1997
Greenland	Scoresby Sound	Early Jurassic	Harris 1926, 1931, 1932a, b, 1935, 1937, 1946
Hungary	Mecsek Mts.	Early Jurassic	Nagy 1961, Barbacka 1992, 1994a, b, 1997, 2000, 2001, 2002, 2009, 2011, Thévenard and Barbacka 2000, Wcisło-Luraniec and Barbacka 2000, Barbacka and Bodor 2008
Italy	Rotzo/Veneto/ Rovere di Velo	Early Jurassic	De Zigno 1856–1868, 1873–1885, Grandori 1913a, b, Wesley 1956, 1958, 1966, 1974, Bartiromo and Barone Lumaga 2009
	Sardinia	Middle Jurassic	Tornquist 1904, Krasser 1912, 1913, 1920, Edwards 1929, Comaschi Caria 1959, Dieni et al. 1983, Salard-Cheboldaeff and Vozenin-Serra 1984, Scanu et al. 2012
Norway	Andoya		Manum et al. 1991, Bruun Christensen 1995
Poland	Grojec	Middle Jurassic	Raciborski 1889, 1894, Reymanówna 1963, 1973, 1985, Wcisło-Luraniec, 1985, 1989, Jarzynka 2012
	Gromadzice	Early Jurassic	Raciborski 1882, 1891a, b, 1892a, b, Makarewiczówna 1928, Harris 1931, Karaszewski 1965, Grabowska et al. 1970, Pacyna and Zdebska 2011
	Huta	Early Jurassic	Barbacka et al. 2014
	Odrowąż	Early Jurassic	Wcisło-Luraniec 1991, 1992, 2001, Reymanówna 1992, Reymanówna et al. 1987, Barbacka et al. 2007, 2010,
	Podszkodzie	Early Jurassic	Makarewiczówna 1928, Samsonowicz 1929, Grabowska et al. 1970, Pacyna 2013
	Studzianna	Early Jurassic	Barbacka et al. 2014
Romania	Reşiţa Basin	Early Jurasssic (Hettangian-Sinemurian)	Krasser 1915, Semaka 1962a, b, 1965, 1970, Givulescu 1992, 1997, 1998, Popa 1997a, 1998, 2000a, b, 2009, Popa and Van Konijnenburg-van Cittert 2006
Scotland	Bearreraig	Middle Jurassic	Morton 1965
	Brent	Middle Jurassic	Bruun Christensen 1995
	Sutherland	Late Jurassic	Van der Burgh and Van Konijnenburg-van Cittert 1984, Van Konijnenburg-van Cittert and Van der Burgh 1989, Van Konijnenburg-van Cittert 2008
Serbia	Stara Planina Mt. Dobra Ruj Mt. Vrška Čuka	Early Jurassic	Djordjević-Milutinović 2010
Sweden	Scania	Early Jurassic	Nathorst 1876, 1878a, b, c, Halle 1908, Lundblad 1950, Pott and McLaughlin 2009
Switzerland	Basel	Late Jurassic	Van Konijnenburg-van Cittert and Meyer 1996
United Kingdom	Stonesfield	Middle Jurassic	Cleal and Rees 2003, Van Konijnenburg-van Cittert 2008
	Yorkshire	Middle Jurassic	Seward 1900, Harris 1961, 1964, 1969, 1979, Harris and Millington 1974, Harris and Miller 1974, Hill 1985, Van Konijnenburg-van Cittert & Morgans 1999, Van Konijnenburg-van Cittert 2008

boreholes) and unequal numbers of taxa found in each flora. To make the data comparable, normed values for each locality were calculated: (1) is the value assigned to the plant group showing the highest diversity at a given locality, and (0) is the value assigned for an absent plant group. Then the diversity of a particular plant group is assigned a numerical value between 0 and 1 (see Table 4).

2) Multivariate methods. Sample-centred (Q mode) community analytical methods were performed.

Table 3. References for depositional environments of particular floras

Country	Abbreviation	References for environment
France	Vendée-L	Barale 1981
	Causses-M	Bernier et al. 2014
	Mamers-M	Bernier et al. 2014
	Jura-U	Barale 1981
Germany	Franken-L	Weber 1968, Gregor and Hauptmann 1998
	Solnhofen-U	Barthel et al. 1990
	Nussplingen	Dietls and Schweigert 2011
	Brunn	Röper and Rothgaenger 1997
Greenland	Scoresby-L	Seward 1911
Hungary	Mecsek-L	Nagy 1961, Püspöki et al. 2012
Italy	Veneto-L	Bartiromo and Barone Lumaga 2009, Scanu et al. 2012
	Sardegna-M	Costamagna et al. 2007, Scanu et al. 2012, 2014
Norway	Brent-M	Bruun Christensen 1995
	Andoya-M	Manum et al. 1991
Poland	Holy Cross-L	Pieńkowski 2004
	Grojec-M	Jarzynka 2012
	Wólka-U	Liszkowski 1972
Romania	Reşiţa-L	Popa 2009
Scotland	Bearreraig-M	Bateman et al. 2000, Dower et al. 2004
	Sutherland-U	van Konijnenburg-van Cittert and van der Burgh 1989, 1996
Serbia	Stara Planina-L	Haas et al. 2011
Sweden	Scania-L	Ahlberg et al. 2003
Switzerland	Basel-U	Gee et al 2003, Jank et al. 2006
United Kingdom	Stonesfield-M	Cleal and Rees 2003
	Yorkshire-M	Harris 1953, Van Konijnenburg-van Cittert and Morgans 1999

Multivariate methods were used for all studied localities.

2.1) Large amounts of data can be grouped according to their similarity (Hammer et al. 2001) using cluster analysis with Ward's method (Euclidean distance). In this method the clusters with lowest variance within groups are combined in pairs (Hammer & Harper 2006, Hatvani et al. 2011). Segregation may result from different factors such as the age of the floras, palaeogeographic region, or environmental factors. All of these factors, together with error caused by sampling or other human influences, should be taken into consideration in interpreting the results (Cascales-Miñana 2010, Kovács et al. 2012).

2.2) The data were also ordered along a continuum of taxonomical content (Hammer & Harper 2006). The results of such ordination can be interpreted as influenced by environmental factors. Among the ordination methods, PCA (principal component analysis) (Spicer & Hill 1979) has often been used in palaeontology. The axes are virtually combined from the presence and absence of all taxa occurring. The localities are placed in a low-dimensional space in a way that highly preserves the original distances between them. In this study the method could not be used for the basic data because the matrix is undetermined (the number of taxa significantly exceeds the number of localities). The localities can be compared by PCA if α diversity is used.

Correspondence analysis (CA) is widely used in grouping data having similar properties (e.g. Coiffard et al. 2008, Barbacka 2011) but we did not apply it here. CA maximizes the correspondence and not the variance among localities. CA values are calculated from variance and covariance matrixes, which would require abundance data; as mentioned, in the literature only presence-absence information is given.

2.3) Non-metric multidimensional scaling (NMDS) was used to illustrate the relationships between localities based on their degree of similarity. NMDS uses rank orders and can therefore be applied to a variety of types of data. The objective of this method is to reduce information from multiple dimensions (in our study, multiple localities) to two or three, so that they can be visualized and interpreted. NMDS is not an eigenvalue-eigenvector technique like principal components analysis or correspondence analysis. This means that an NMDS ordination can be rotated or centred to any desired configuration (Rabinowitz 1975, Holland 2008).

We chose to use three-dimensional visualisation for this study.

Table 4. Alpha diversity of different groups at different localities/units, normed against maximum diversity of the given group

	Hepa-tophytes	Lycophy-tes	Horsetails	Ferns	Seed Ferns	Cycads	Bennet-tites	Gink-gophytes	Conifers
Scoresby-L	1.000	0.500	0.625	0.533	0.273	0.281	0.125	0.474	0.464
Veneto-L	0.000	0.000	0.375	0.367	0.273	0.031	0.450	0.105	0.679
Franken-L	0.000	0.000	0.250	0.300	0.091	0.094	0.000	0.158	0.321
Stonesfield-M	0.000	0.000	0.000	0.133	0.227	0.063	0.100	0.053	0.214
Holy Cross-L	0.000	0.500	0.625	0.700	0.318	0.469	0.075	0.579	0.464
Stara Planina-L	0.000	0.000	0.125	0.300	0.136	0.219	0.100	0.211	0.071
Reșița-L	0.200	0.500	0.250	0.667	0.455	0.219	0.400	0.474	0.286
Scania-L	0.000	1.000	0.500	0.833	1.000	0.656	0.350	0.368	0.500
Vendée-L	0.000	0.000	0.000	0.133	0.273	0.156	0.200	0.053	0.357
Mecsek-L	0.000	0.000	0.500	0.433	0.273	0.219	0.075	0.263	0.536
Yorkshire-M	1.000	0.500	1.000	1.000	0.591	1.000	1.000	1.000	1.000
Brent-M	0.000	0.000	0.125	0.400	0.000	0.094	0.100	0.211	0.000
Bearreraig-M	0.000	0.000	0.125	0.167	0.000	0.063	0.050	0.000	0.036
Andoya-M	0.000	0.000	0.000	0.033	0.045	0.000	0.025	0.105	0.143
Grojec-M	0.000	0.000	0.500	0.667	0.091	0.156	0.075	0.053	0.107
Sardegna-M	0.000	0.000	0.000	0.200	0.091	0.094	0.425	0.000	0.214
Causses-M	0.000	0.000	0.375	0.067	0.000	0.000	0.000	0.000	0.107
Mamers-M	0.000	0.000	0.250	0.000	0.045	0.000	0.300	0.000	0.071
Sutherland-U	0.000	0.000	0.375	0.733	0.318	0.469	0.250	0.000	0.500
Basel-U	0.000	0.000	0.125	0.000	0.000	0.000	0.025	0.000	0.214
Jura-U	0.000	0.000	0.000	0.167	0.182	0.281	0.225	0.000	0.714
Wólka-U	0.000	0.000	0.000	0.000	0.091	0.000	0.000	0.000	0.143
Solnhofen-U	0.000	0.500	0.125	0.100	0.045	0.000	0.075	0.316	0.750

RESULTS AND DISCUSSION

ALPHA DIVERSITY

The dataset includes 770 macrofossil plant taxa from 25 units (46 localities) of the European Jurassic. Only 181 (23.5%) of the 770 taxa occurred at more than one locality; 76.5% of them are specific to single localities or groups of localities.

The two most widespread species were *Cladophlebis denticulata* and *C. haiburnensis*, present at eight localities. Of the 65 ginkgophyte taxa present in the European Jurassic, only five occurred at more than two localities.

The analysed localities greatly differ in the degree of diversity of their floral composition (Fig. 1). Most diverse is the flora from Yorkshire (Middle Jurassic, 197 taxa), where all plant groups are represented by a large number of taxa. Five localities (Andoya-M, Basel-U, Bearreraig-M, Causses-M, Wólka-U) showed ca 10 or fewer species.

As shown in Figure 2A and B, the number of taxa decreased by 22.7% (species level) and 21.3% (genus level) going from the Early to Middle Jurassic, and continuously from the Middle to Late Jurassic by 12.9% (species) and 15.9% (genera). The decrease in taxa corresponds to a decrease in the number of known fossiliferous sites in the Late Jurassic. This trend may be explained by an increase of sea level followed by transgression, particularly significant from the Middle Jurassic, which reduced the extent of emerged land in Europe (e.g. Pieńkowski et al. 2008) and consequently the terrestrial habitats. However, the numerical ratio of species/genera which defines average diversity in particular epochs does not decrease proportionally with time, but is highest in the Early Jurassic (3.7), followed by the Late Jurassic (3.1), and lowest in the Middle Jurassic (2.8).
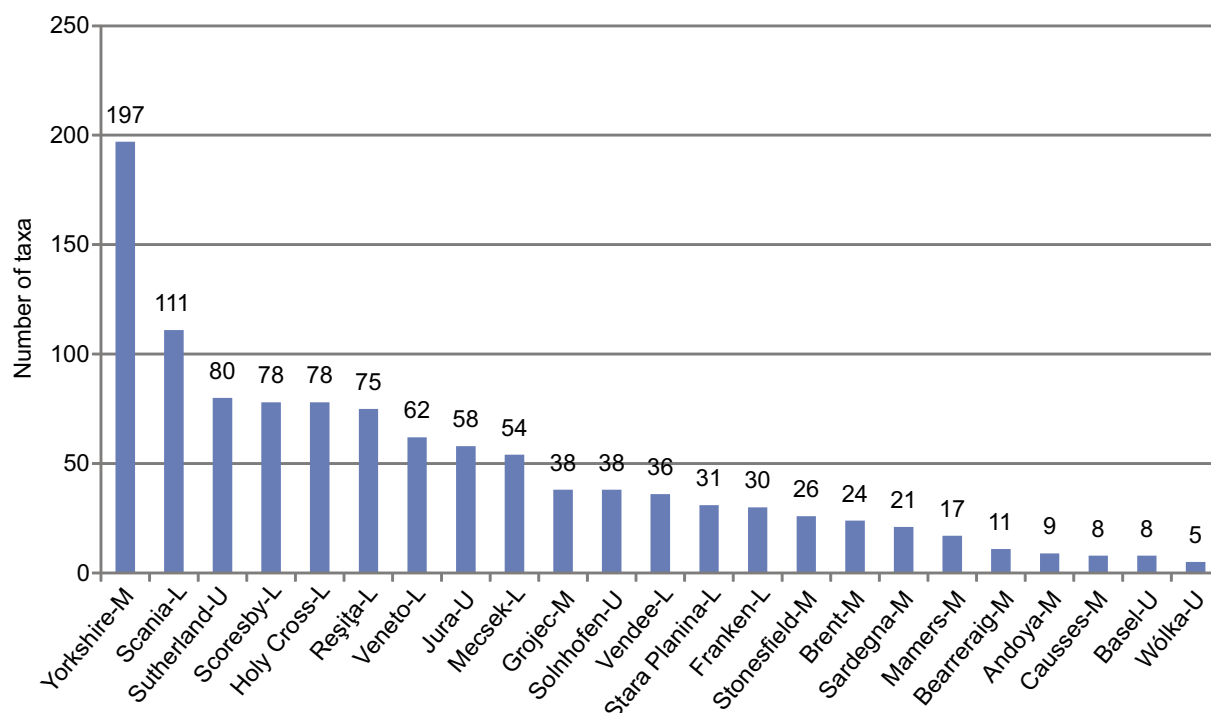
Fig. 1. Diversity of the studied localities

That last ratio is remarkable, because the most diverse flora (Yorkshire) is Middle Jurassic in age. On the other hand, half of the localities/ areas yielding Jurassic plant fossils are Early Jurassic in age. However, this alone cannot explain the conspicuously high diversity of the Early Jurassic (e.g. at Reşiţa, Scania, Scoresby Sound) presented on Figure 1.

Almost all higher plant groups were found in most localities and during the entire Jurassic. Usually the highest diversity was among ferns (11 units) and conifers (10 units), while bennettitaleans were the most diverse at only three localities. The distribution and diversity of the higher plant groups also depended on the type of locality. The most diversified and abundant floras come from large units like Yorkshire-M, Scoresby-L, Franken-L, and Scania-L, which have been studied in detail and over an extended period. Smaller localities such as Grojec-M, Mecsek-L, Reşiţa-L, Sardegna-M, and Solnhofen-U also yielded a rich and diverse flora. Several small plant associations such as Basel-U, Causses-M, Jura-U, Mamers-M, Veneto-L, and Wólka-U are characterised by a low number of taxa. Those are generally allochthonous and deposited in lagoonal sedimentary basins. It is possible that plant remains from these localities were exposed to damage, destruction, and selection during transport prior to their burial in the marine environment.
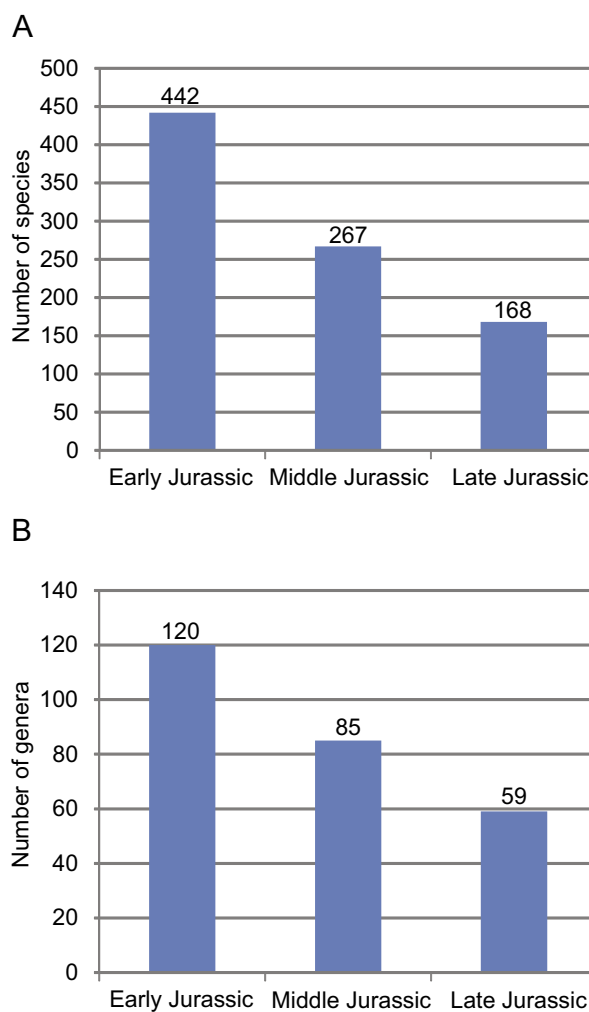

Fig. 2. **A** – Number of species in particular epochs. **B** – Number of genera in particular epochs
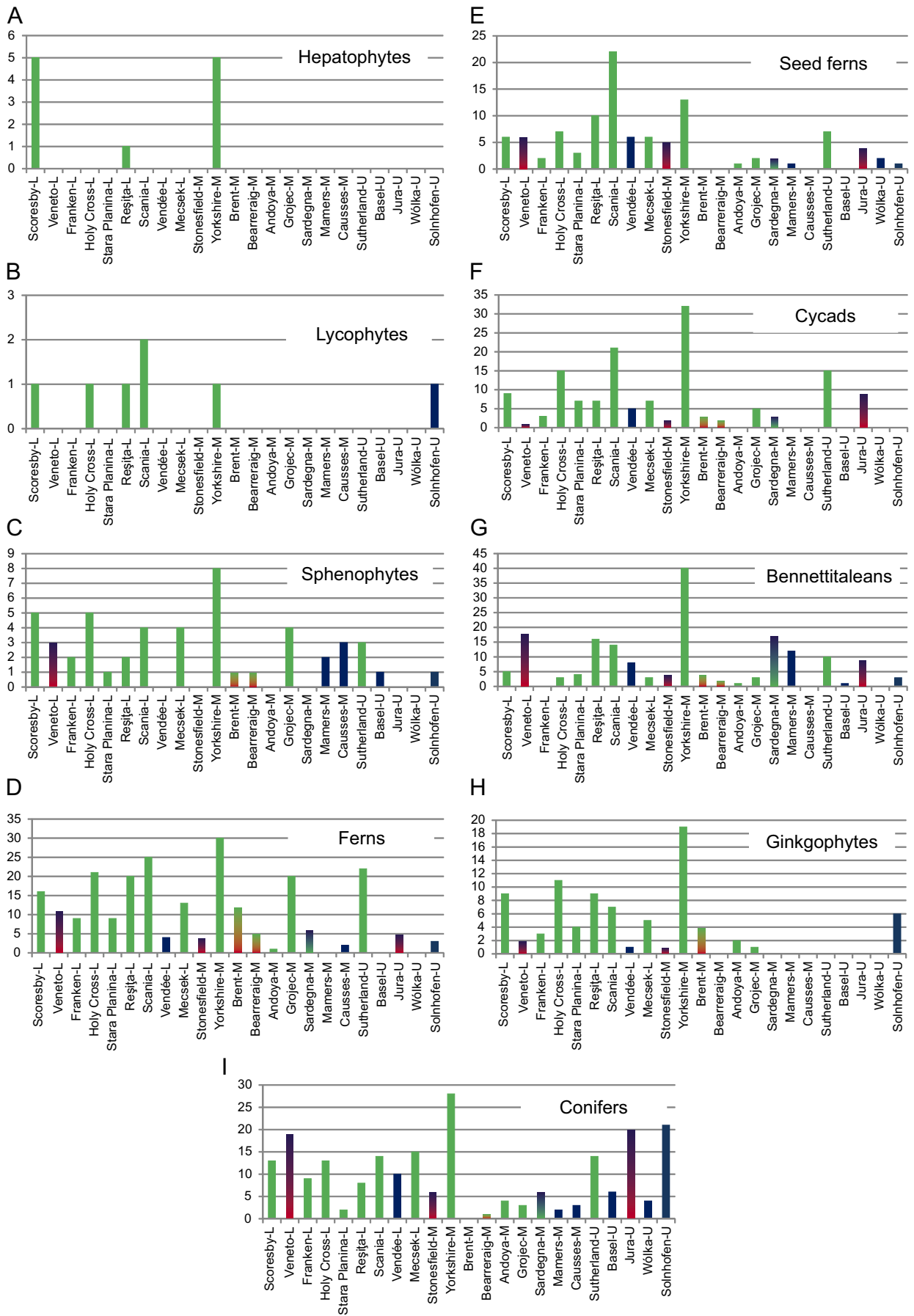
Fig. 3. Number of recorded taxa belonging to major plant groups, by time and environment. Green – delta and fluvial, blue – coastal and lagoon, blue-green – coastal, fluvial. Grouping by cluster analysis: blue-red – allochthonous coastal lagoonal, green-red – allochthonous fluvial and delta

Bryophytes and lycophytes are the rarest plant groups (Fig. 3A, B). They were described mostly from Early Jurassic floras (e.g. Holy Cross-L, Reşiţa-L, Scania-L, Scoresby-L) and from the Yorkshire Middle Jurassic locality. The low diversity of these groups might be due to factors such as their low fossilization potential and difficulties in correct identification due to their small size. Sphenophytes as well as ginkgophytes were common and diverse during the whole Jurassic (Fig. 3C, H); their diversity decreased slightly in the Middle and Late Jurassic, but this might also reflect the general decrease in species diversity from the Middle to Late Jurassic. The distribution of ferns is quite constant through the Jurassic, differing in diversity between localities, with a slight decrease towards the Late Jurassic (Fig. 3D). The distribution of cycads and bennettitaleans also remains quite constant throughout the Jurassic (Fig. 3F, G). Seed ferns show a significant reduction through time, with the highest diversity in Scania-L (Fig. 3E).

Conifers show a significant reduction of taxa number in the Middle Jurassic but increase in diversity during the Late Jurassic (Fig. 3I).

Based on the relative abundance of the higher plant groups within the different floras, the localities can be divided into five categories. Category A, including Basel-U, Causses-M, and Wólka-U, (Fig. 4A) is characterised by a low number of plant groups (2–3) but significantly more diverse conifers. These localities are usually poor in taxa and are formed in a lagoonal setting. This suggests transport of plants at least from the coastal zone to the site of deposition. Category B, including Andoya-M, Jura-U, and Solnhofen-U (Fig. 4B), shows similar lagoonal deposition and very diverse conifers, but other plant groups are also represented (5–7).

Category C (Fig. 4C) includes two localities (Mamers-M, Sardegna-M) in which bennettitaleans are the most diverse group, associated with conifers, seed ferns and ferns or horsetails (4–5 plant groups).

Category D (Fig. 4D) is characterised by very diverse ferns and low occurrence of higher plant groups (5–7). This group contains Bearreraig-M, Brent-M, and Grojec-M, all Middle Jurassic in age. This grouping is in line with Abbink et al.'s (2004) inference, on the basis of palynological results from the Callovian, of cooler and more humid conditions.

The last two categories, E and F (Fig. 4E, F), are characterised by the presence of numerous higher plant groups but with lower taxonomical variability within the various groups; no group shows much higher diversity than the other groups in these floras. Category E has 6–7 higher plant groups, with almost equally diverse conifers, ferns, cycads, and bennettitaleans. The floras in this group are those of Franken-L, Mecsek-L, Stonesfield-M, Veneto-L, and Vendée-L.

In category F the 7–9 higher plant groups are represented by relatively equal numbers of taxa. This group includes Holy Cross-L, Reşiţa-L, Scania-L, Scoresby-L, Stara Planina-L, Sutherland-U, and Yorkshire-M.

It seems that high diversity of one of the higher plant groups (Fig. 4A–D) limits both the diversity and number of the other groups, while uniform variability within plant groups is associated with an increase of the number of groups in a given environment (Fig. 4E, F).

The trends depicted in Figure 4A–F can be explained by the correlations for certain plant groups (Fig. 5). The correlation is highest between cycads and ferns (0.85) and lowest between bennettitaleans and sphenophytes (0.5). The correlation is also low between seed ferns and sphenophytes (0.53), conifers and ginkgophytes (0.55), and conifers and ferns (0.57).

MULTIVARIATE ANALYSES

Multivariate analyses were performed at the level of higher plant groups based on their diversity. Both PCA (Fig. 6) and visualisation by NMDS (Fig. 10) show a strong horseshoe effect which is generally caused by the nonlinear connection between the variables (Podani & Miklos 2002). This is common in ecological samples (Rees et al. 2000), where environmental factors often influence the plot. The position of the localities in Figure 6 is determined by their taxonomical composition at the level of major plant groups. The PCA biplot shows which groups affected the differentiation of localities and to what degree. The vectors show the reversed direction and significance (length) of this effect.

In PCA (Fig. 6) the localities with lagoonal and coastal settings occupy the right upper quarter of the plot, while those of fluvial or deltaic types occupy the right lower quarter. The first component explains 73% of the variance

and the second explains 12%, indicating that the method is reliable.

Along the PC1 axis all plant groups are negatively correlated. The first component is determined mainly by the ferns (loading: −0.5), cycads (loading: −0.47), and bennettitaleans (loading: −0.48). Along the PC2 axis the bennettitalean group is positively correlated and the most important (loading +0.73), together with ferns having similar absolute values but different signs (loading −0.57). The small loading values indicate low explanatory power of
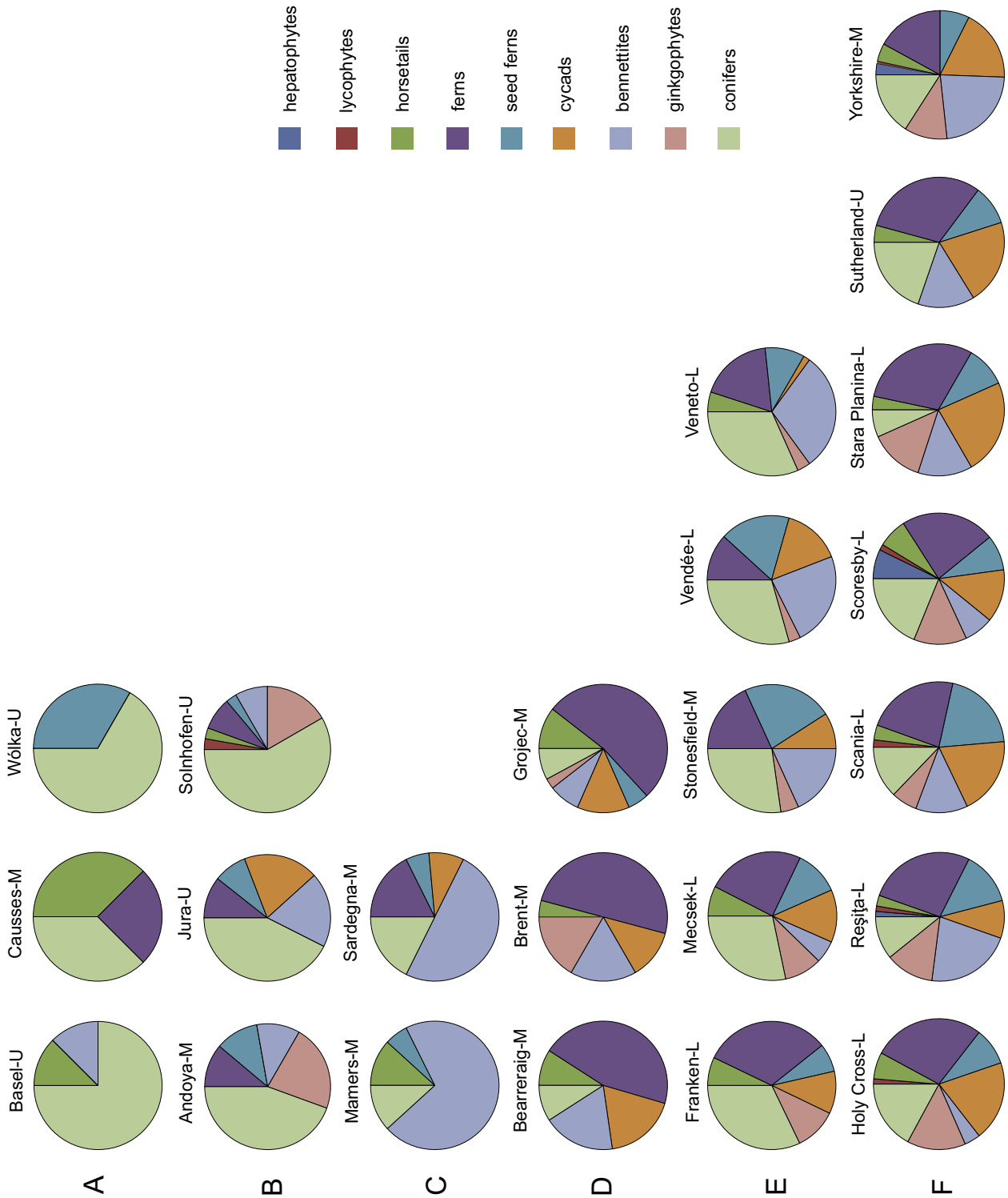

Fig. 4. Grouping of localities by diversity. **A** – with maximum diversity of conifers and low number of other plant groups, **B** – with maximum diversity of conifers but with other more diverse plant groups, **C** – with maximum diversity of bennettitaleans, **D** – with maximum diversity of ferns, **E** – with high number of plant groups but with conifers being most diverse, **F** – with high number of plant groups, rather equally represented
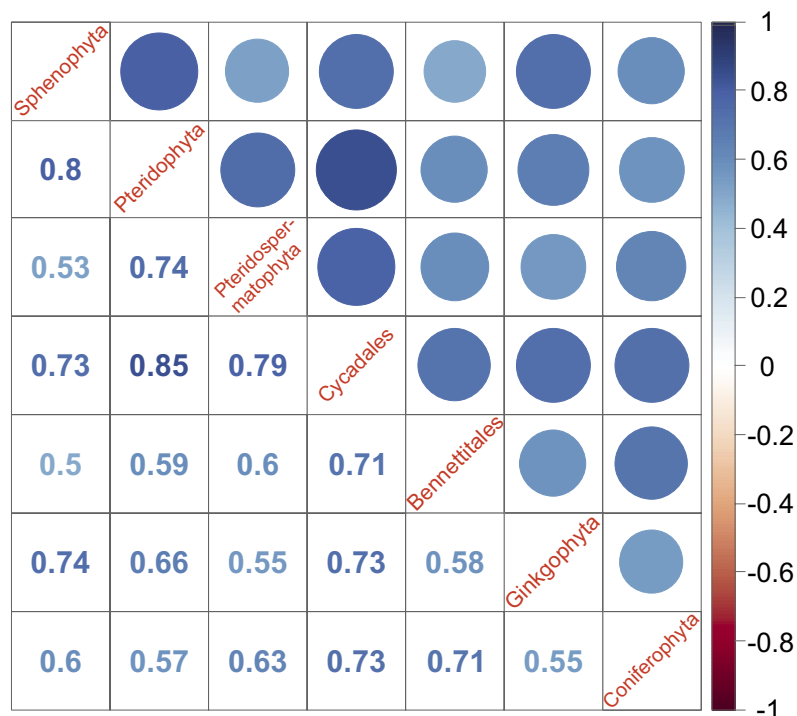
Fig. 5. Correlation values of plant groups during the Jurassic in Europe (the size and colour intensity of the circles represent the strength of the correlation)
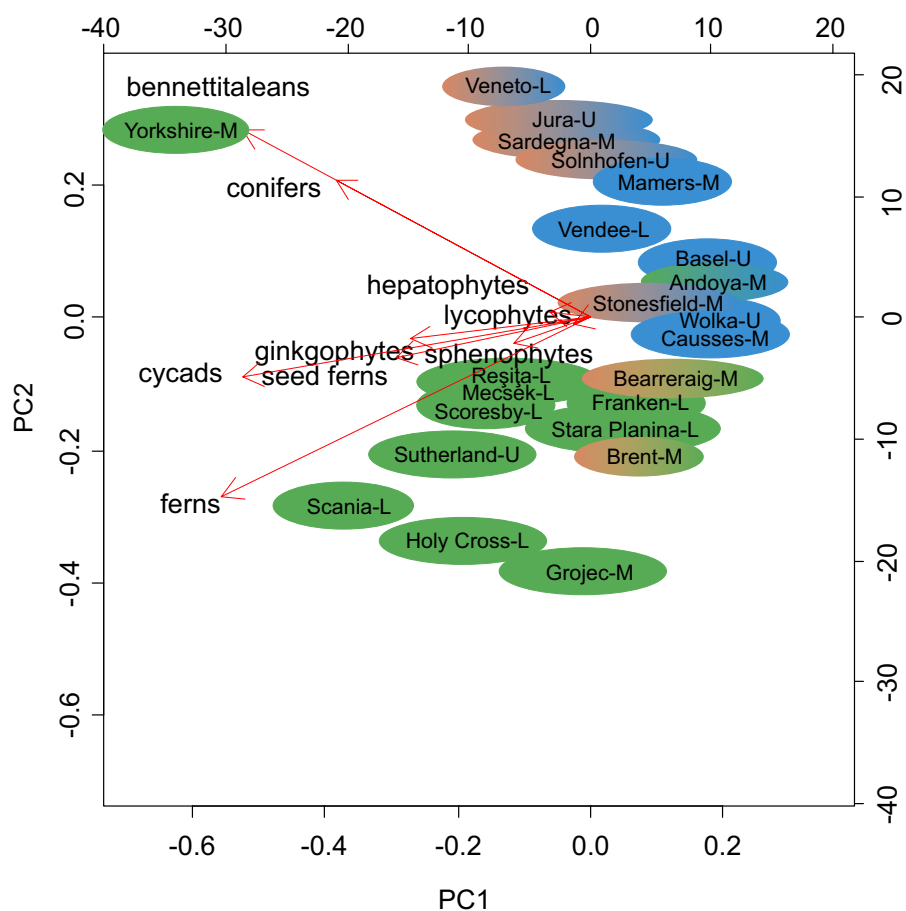

Fig. 6. PCA biplot calculated from plant group diversity of all localities. Arrows indicate the trend of the plant groups in forming axes PC1 and PC2. Locality colours correspond to depositional environment: green – delta and fluvial, blue – coastal and lagoon, blue-green – coastal and fluvial. Grouping by cluster analysis: blue-red – allochthonous coastal lagoonal, green-red – allochthonous fluvial and delta
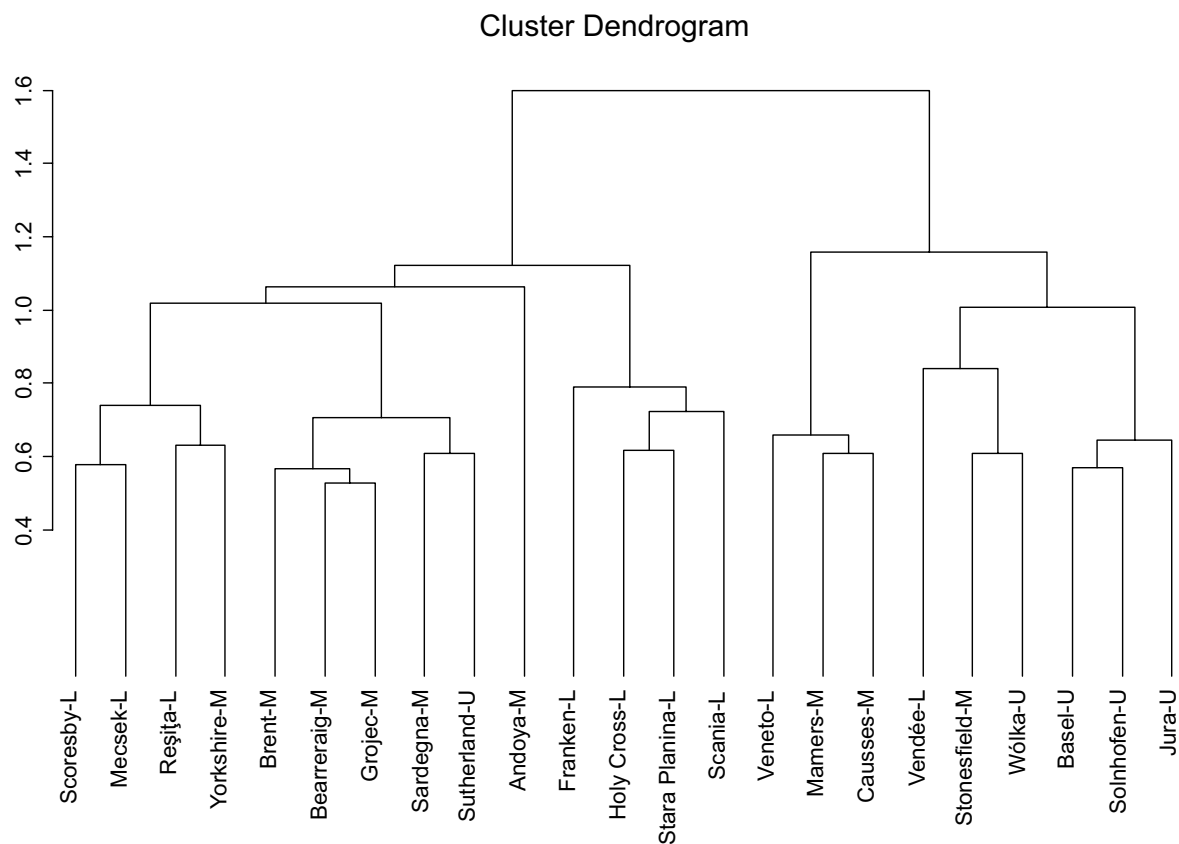
Cluster Dendrogram

Fig. 7. Cluster dendrogram calculated with Ward's method, based on genus data

groups such as hepatophytes, lycophytes, and sphenophytes (loadings under 0.1).

Yorkshire-M is most highly influenced by bennettitaleans (40 taxa), followed by the Veneto-L flora (with 18 taxa). In Sardegna-M (17) and Mamers-M (12) the ferns are extremely rare, having a high impact in the negative region of the PCA plot.

The negative correlation of PC2 is affected mainly by the ferns. Relatively high fern diversity characterises Holy Cross-L (21 taxa) and Grojec-M (20 taxa), and also Scania-L (25 taxa), Sutherland-U (22), and Scoresby-L (16), which were fern-dominated.

CLUSTER ANALYSES

Ward's cluster analysis was done for genus and species levels. The analysis based on genera allowed us to compare localities in which the state of preservation prevents determination to species. Analyses on genus level also lessen the possibility of error resulting from incorrect classification.

In the genus cluster (based on presence-absence) the localities are organized in two major clades corresponding to their palaeoenvironmental distribution (Fig. 7). The first clade

(left) groups all localities with fluvio-deltaic depositional settings. The second clade (right) groups all localities of lagoonal, archipelago of spongy reefs, or island environments with marine influences (xerophytic plants, salt trails visible on cuticle structures). Some outcrops (Causses-M, Mamers-M) are lagoonal or correspond to paralic basins (Barale 1981, Bernier et al. 2014). Some floras such as Solnhofen-U (Barthel et al. 1990), Wólka-U (archipelago of spongy reefs and islands), and Veneto-L (preserved in the marine Calcari Grigi Formation) were formed in marine settings and preserved in limestone with few taxa (Bartiromo & Barone Lumaga 2009). The allochthonous floras (unknown depositional environment) tend towards fluvio-deltaic or lagoonal types of environment.

Cluster analysis based on species shows a different pattern of similarity between particular localities (Fig. 8). In contrast to the cladogram at genus level, environment is not the most important factor; a set of different factors seems to influence the grouping of localities.

The error of this analysis is rather large. In the genera dataset, 40% of the genera are recorded from only one locality, while in the species dataset the singletons comprise 67%.
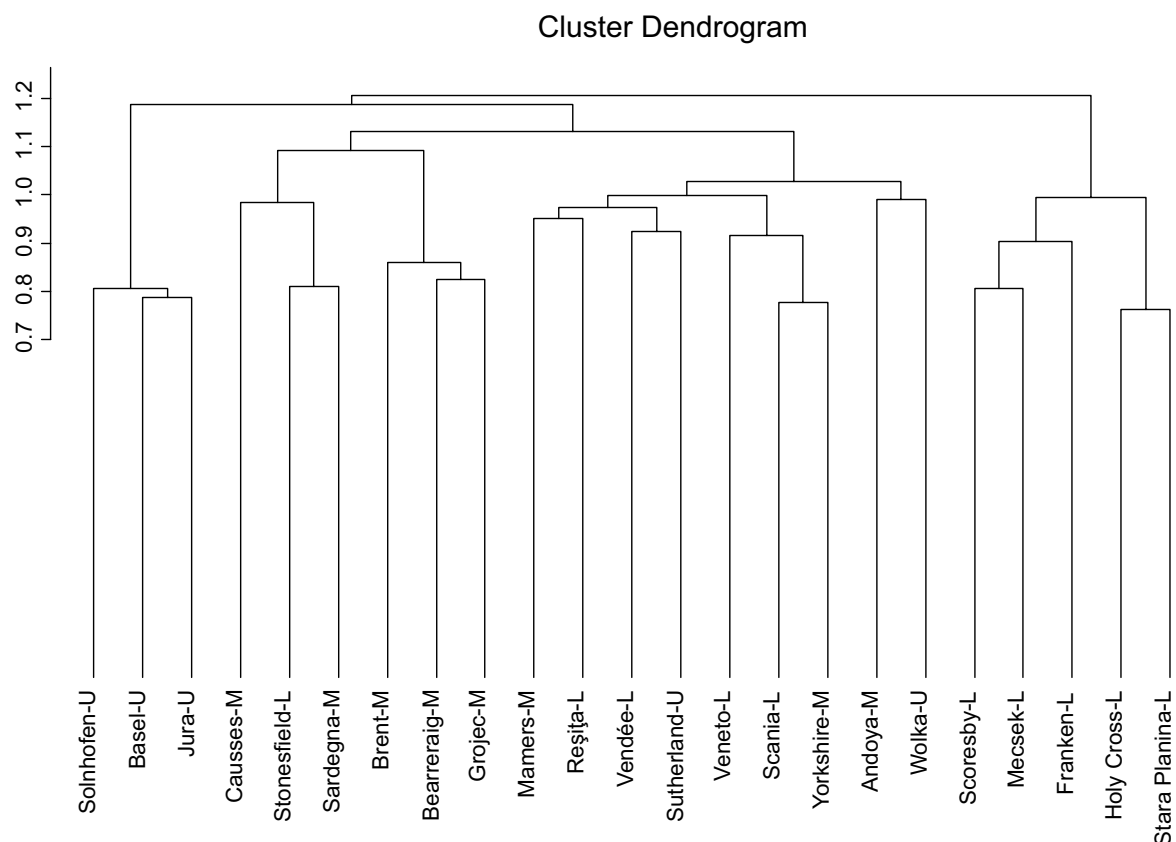
Cluster Dendrogram

Fig. 8. Cluster dendrogram calculated with Ward's method, based on species data

The analysis for species highlights similarity between sites, while the cluster analyses for genera points up differences between localities. The large number of singletons is a serious source of error, making the data difficult to compare.

Table 5 presents a correlation analysis showing very low correlations and a very low linear connection between localities.

The highest correlation is between Stara Planina-L and Holy Cross-L. The correlations are also high between Holy Cross-L and Franken-L and between Scoresby-L and Mecsek-L. These localities are grouped together in the cladogram (right clade); this may be explained by their location on the stable European continental platform (Csontos & Vörös 2004). Additionally, all of them are Early Jurassic in age.

The other clade (right middle) contains localities of mixed age, which are correlated with Yorkshire-M (Scania-L, Vendée-L, Veneto-L) and are grouped with localities whose correlations are minimal (Reşiţa-L, Andoya-M). This is probably due to their high numbers of species not typical for European Jurassic floras and derived from neighbouring areas such as Reşiţa-L, which has numerous elements in

common with Iranian and Afghan floras (Popa 1998, Popa & Van Konijnenburg-van Cittert 2006, Vakhrameev 1991).

The floral composition of Andoya-M and Basel-U shows a high percentage of singleton taxa.

The third cluster (left middle in Fig. 8) has Bearreraig-M, Brent-M, and Grojec-M fern-dominated floras; the three other points (Causses-M, Sardegna-M, Stonesfield-M) correlate mostly with Brent-M or Grojec-M. All of them are middle Jurassic in age.

The left-clade groups (Basel-U, Jura-U, Solnhofen-U) are conifer-dominated and deposited in deep marine environments, preserved in laminated marls.

Our three-dimensional NMDS (Fig. 9) visualises the relationships between all localities, displaying information in a distance matrix. The localities form two separate groups which correspond to the predominant type of depositional environment in a given territory. Those with coastal-lagoonal landscape (e.g. Andoya-M, Basel-U, Causses-M, Mamers-M, Solnhofen-U, Vendée-L, Wólka-U) are grouped together with allochthonous floras from Jura-U, Stonesfield-M, and Veneto-L, similar to the groupings in the PCA and in the genus
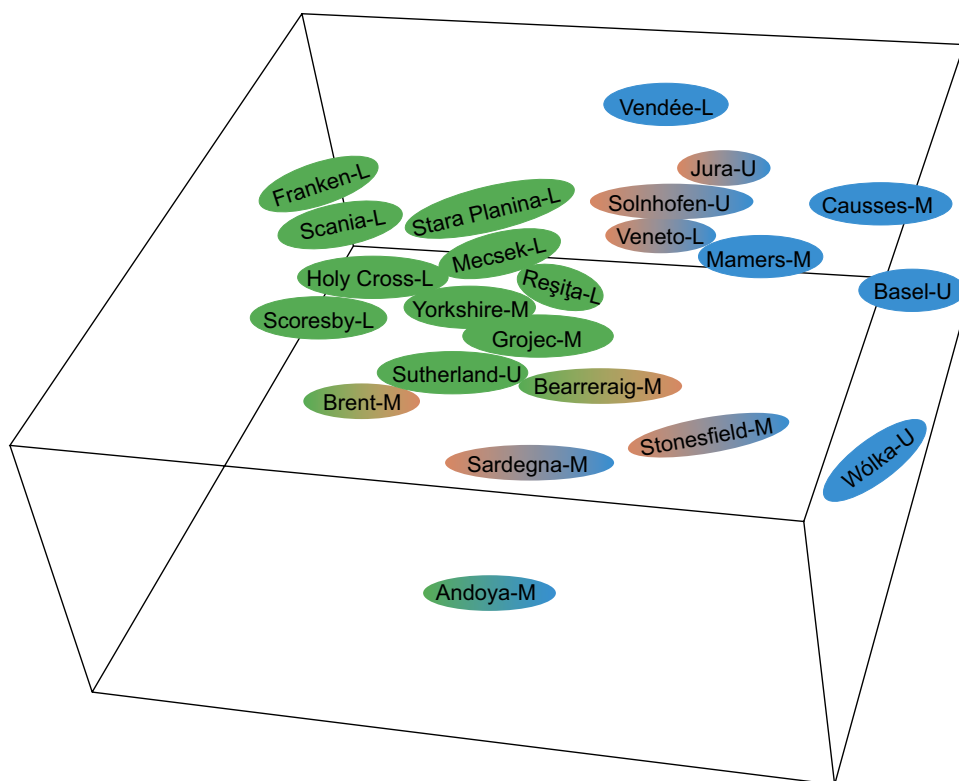
Table 5. Correlation analysis between localities: white cells – very low correlation, yellow – higher correlation, pink cells – highest correlation (relative values)

	Causses-M	Mamers-M	Scoresby-L	Veneto-L	Franken-L	Stonesfield-M	Holy Cross-L	Stara Planina-L	Reşiţa-L	Scania-L	Vendée-L	Mecsek-L	Yorkshire-M	Brent-M	Bearreraig-M	Andoya-M	Grojec-M	Sardegna-M	Sutherland-U	Basel-U	Jura-U	Wólka-U
Mamers-M	-0.02																					
Scoresby-L	-0.04	-0.05																				
Veneto-L	0.02	-0.05	-0.09																			
Franken-L	-0.02	-0.03	0.11	-0.06																		
Stonesfield-M	0.05	-0.03	-0.06	0.00	-0.04																	
Holy Cross-L	-0.04	-0.02	0.07	-0.01	0.20	-0.04																
Stara Planina-L	-0.02	-0.03	0.02	0.01	0.06	0.03	0.24															
Reşiţa-L	-0.03	-0.05	-0.01	-0.07	0.07	0.01	-0.01	0.00														
Scania-L	-0.01	-0.06	-0.02	-0.10	0.05	-0.04	0.03	-0.01	-0.05													
Vendée-L	-0.02	-0.03	-0.04	-0.07	0.02	-0.04	-0.06	-0.02	-0.05	-0.06												
Mecsek-L	-0.03	-0.01	-0.19	-0.06	-0.13	0.03	-0.19	-0.10	-0.10	-0.06	-0.06											
Yorkshire-M	0.06	0.07	0.16	0.15	0.09	0.05	0.08	0.02	0.08	0.23	0.11	0.03										
Brent-M	0.05	-0.03	0.01	0.00	0.00	0.05	0.06	0.00	-0.01	-0.08	-0.04	0.07	0.18									
Bearreraig-M	-0.01	-0.02	-0.04	0.00	-0.02	0.04	-0.01	0.09	0.07	-0.05	-0.03	0.09	0.08	0.17								
Andoya-M	-0.01	-0.02	-0.04	0.01	-0.02	-0.02	0.04	-0.02	-0.04	-0.05	-0.02	-0.03	-0.04	-0.02	-0.01							
Grojec-M	0.04	-0.04	0.00	-0.05	0.05	0.06	0.06	0.07	0.02	-0.04	-0.05	0.15	0.04	0.13	0.17	0.03						
Sardegna-M	0.06	-0.03	0.00	0.04	-0.03	0.19	0.07	0.09	0.00	-0.03	-0.04	0.05	0.08	0.15	0.05	0.06	0.00					
Sutherland-U	0.01	-0.05	-0.08	-0.07	-0.07	-0.02	0.05	0.06	-0.04	-0.12	-0.08	-0.03	-0.05	0.08	0.10	0.00	0.08	0.07				
Basel-U	-0.01	-0.02	-0.04	-0.03	-0.02	0.05	-0.04	-0.02	-0.03	-0.04	0.10	-0.03	-0.06	-0.02	-0.01	-0.01	-0.02	-0.02	0.01			
Jura-U	0.02	0.02	-0.10	-0.09	-0.06	-0.03	-0.10	-0.06	-0.08	-0.12	0.05	-0.08	-0.16	-0.05	-0.04	-0.03	-0.04	-0.02	-0.08	0.21		
Wólka-U	-0.01	-0.01	-0.03	-0.02	-0.02	-0.02	-0.03	-0.02	-0.03	-0.03	-0.02	0.04	0.03	-0.01	-0.01	-0.01	-0.02	-0.01	-0.03	-0.01	0.04	
Solnhofen-U	-0.02	-0.03	-0.08	-0.02	-0.05	-0.04	-0.04	-0.02	-0.05	-0.09	-0.02	-0.01	-0.12	-0.04	-0.03	0.03	-0.02	0.04	-0.06	0.21	0.18	-0.02

Fig. 9. 3D NMDS plot based on genus data. Colours indicate depositional environments: green – delta and fluvial, blue – coastal and lagoonal, blue-green – coastal and fluvial. Grouping by cluster analysis: blue-red – allochthonous coastal and lagoonal, green-red – allochthonous fluvial and delta

cladogram (Figs 6, 7 respectively). These localities are clearly separated from the floras of deltaic and fluvial environments.

INTERPRETATION AND DISCUSSION

A comparison of many different localities dispersed in such a large area as Europe is bound to be affected by certain biases. One of the most important of them is the fact that the majority of the big fossil assemblages were collected over a long time interval (several years or decades), often from several sites in the same area or from different fossiliferous horizons. On the other hand, a finding of lower diversity of plant assemblages may be due to the small area of the locality, a low number of fossiliferous layers, and/or limited opportunities to sample. These kinds of problems are well known in palaeobotanical studies (Cleal & Rees 2003).

Due to the palaeobiogeographic distribution of the emerged land (Csontos & Vörös 2004), most terrestrial European fossil assemblages are Early Jurassic in age (27 localities studied, comprising 59% of all studied floras). All of them are relatively diverse. The Middle Jurassic is represented by nine localities/

units (20% of all those studied); among them, Yorkshire-M is the richest of all European Jurassic localities (197 taxa), having nearly twice as many taxa as the richest Early Jurassic locality (Scania-L) and five times as many as the subsequent Middle Jurassic flora from Grojec-M (see Fig. 1). From all the remaining seven Middle Jurassic localities/units (15% of all those studied) fewer than 40 taxa were reported altogether. Ten localities are Late Jurassic in age. Basel-U in Switzerland and Wólka-U in Poland show very low plant diversity, with less than ten taxa. More diverse are the French Jura-U unit (three localities: Armaille, Creys, Orbagnoux) with 58 species, and Sutherland-U (Scotland) with 80 species.

The cluster analyses clearly indicate that time is the factor that least influences the floristic composition of Europe's Jurassic localities. Neither in the genus nor in the species cladograms were the localities grouped by age.

At genus level the principal factor affecting taxonomical composition is the type of environment. Based on the depositional settings of the localities, three types of depositional environments were distinguished: fluvial; deltaic, representing riparian vegetation; and lagoonal,

most probably representing coastal environments (references in Table 2).

The results from multivariate analyses clearly separate the floras of fluvial and deltaic habitats from those of lagoonal or coastal vegetation. Such differentiation can be explained by the stress effect observed in plant assemblages from marine-influenced environments (xerophytic conditions). The poorer plant content of marine deposits might also be caused by taphonomic selection during transport from emerged land to the deep-sea environments where they fossilized (e.g. Wólka-U).

It is noticeable that in most localities in lagoonal depositional settings, which suggest a coastal influence on the vegetation, one of the higher plant groups is more diverse than others. This is the case of the conifers found in Andoya-M, Basel-U, Causses-M, Solnhofen-U, and Wólka-U, or the bennettitaleans in Mamers-M and Sardegna-M (conifers are also well represented in these latter floras). The rest of the "lagoon" localities, although more variable in plant groups, have considerably less diverse ferns.

In delta and fluvial depositional environments the ferns are very diverse, sometimes more diverse than all other plant groups, while the diversity of ginkgophytes varies widely between localities. Conifers are usually less diverse than in lagoon environments (see Fig. 4 A–E).

Cluster analysis at species level does not differentiate localities by environment as much as it links them by common species which can be very widespread and highly tolerant. This analysis rather shows similarities in alpha diversity and also correlations between numbers of common species.

Alpha diversity analysis showed the plant groups to have unequal distributions in particular localities. Sphenophytes are not recorded at seven localities (see Fig. 3C). Six of these localities were conifer-dominated and had small amounts of ferns, except for Sardegna-M which was fern-dominated. The presence of ferns would suggest wet conditions but sphenophytes did not develop there. The total lack of sphenophytes in the Stonesfield-M flora has been explained by the absence of marshy conditions (Cleal & Rees 2003).

At some small localities with allochthonous flora the absence of certain plant groups might be explained by taphonomic processes.

For example, ferns are highly diverse at almost every locality (Fig. 3D). Most widely distributed are *Cladophlebis denticulata* and *C. haiburnensis* (8 localities), *Todites princeps* and *T. williamsoni* (7 localities), *Clathropteris meniscoides*, *Phlebopteris angustiloba*, and *P. polypodioides* (6 localities); other species of *Thaumatopteris*, *Dictyophyllum*, and *Phlebopteris* occur at five localities. Such a wide distribution of ferns may be explained in part by the higher number of deltaic and fluvial environments, always favourable for ferns.

A lack of sphenophytes and ferns may be connected with conditions or with the energy of transport. Delicate fronds can hardly withstand long-distance transport in water. This would also explain why palynological samples of Jurassic terrestrial sediments contain frequent fern spores (Abbink et al. 2004, Götz et al. 2011).

Seed ferns were very common elements during the whole Jurassic (Fig. 3E) but they were missing from a few low-diversity localities with allochthonous flora. At genus level the seed ferns are not very diverse even though the 18 seed fern genera contain 73 species. High diversity of seed ferns can be explained by their ability to occupy various palaeoecological habitats, from mires (where they can be coal generators) to flood plains and levees, sometimes even as mangroves or as climbers and lianas (Harris 1932a, Harris 1964, Popa 1997b). This evolutionary strength is therefore expressed systematically.

The genera *Sagenopteris* and *Pachypteris* are most widespread among the seed ferns, both recorded from 12 localities, but in fact only 8 species of *Sagenopteris* and 12 species of *Pachypteris* were reported from Europe. Most of them occur at only one locality.

At genus level the most frequent is *Brachyphyllum* (18 localities), probably due to its wide environmental tolerance (Vakhrameev 1970, 1991, Alvin 1982, Hesselbo et al. 2003, Greb et al. 2006, Wang et al. 2005, Popa & Van Konijnenburg-van Cittert 2006, Barbacka 2011). Also widespread are *Nilssonia*, *Otozamites* (14 localities), *Pterophyllum*, *Neocalamites*, *Baiera*, *Pagiophyllum* (10 localities), and *Elatocladus*, *Podozamites*, and *Equisetites* (9 localities). Most of these are associated with deltaic and fluvial environments which offered variable and good conditions for diversification of floras (Popa 2009, Barbacka 2011).

In both cluster analysis and the NMDS matrix it can be seen that allochthonous floras with uncertain environmental settings are attributable to a depositional setting based on their composition. This may be helpful in general discussions on their depositional settings. Thus, the palaeoenvironment related to the French Late and Early Jurassic localities may be determined as lagoon, while Bearreraig-M, Brent-M, Sutherland-U, and Veneto-L probably originated from fluvial/deltaic surroundings.

CONCLUSIONS

– The Jurassic floras of Europe are continuous in transitions between epochs; they often show similarity independently of time.

– Particular epochs differ in dominant plant groups but not greatly.

– The most diverse flora comes from the Middle Jurassic (Yorkshire, 197 taxa) although the Middle Jurassic is represented by the fewest localities.

– It seems that during the entire Jurassic the growth and depositional environment was the factor most influencing the floral composition.

– The basic known types of environment were characterised by the dominance of particular plant groups.

– Statistical methods are helpful in segregating and interpreting large datasets. Especially interesting here is the clear differentiation of allochthonous localities by habitat conditions.

ACKNOWLEDGMENTS

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