TESTING SIMILARITY COEFFICIENTS FOR ANALYSIS OF THE FOSSIL RECORD USING CLUSTERING METHODS: THE PALAEOZOIC FLORA AS A STUDY CASE

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ABSTRACT

This paper reports a global methodological approach based on the similarity and clustering methods of the Palaeozoic plant fossil record using a comparative approach between two similarity measures: the Jaccard and Raup-Crick Coefficients. The results show that although the Raup-Crick Coefficients clearly have the potential for providing more robust results, the consequences of the extinction processes are better reflected in the similarity analysis based on the Jaccard Coefficients. On the other hand, the cluster analysis based on UPGMA algorithm shows four robust clusters and reveals new evidence for the singularity of Mississippian flora. Finally, the results obtained reveal that similarity and cluster analysis are powerful tools to interpret the consequence of the processes modifying the taxonomic composition of the several analyzed Palaeozoic time units.

Key words: Evolutionary innovations, extinction processes, multivariate analysis, Palaeozoic, fossil record, similarity.

RESUMEN

Este artículo divulga una aproximación metodológica global basada en los métodos de similitud y agrupamiento del registro paleozoico de las plantas vasculares mediante un análisis comparativo entre dos medidas de similitud: el índice de Jaccard y el de Raup-Crick. Los resultados demuestran que aunque los coeficientes de Raup-Crick presentan claramente un mayor potencial para proporcionar resultados más robustos, las consecuencias de los procesos de extinción se reflejan mejor en los análisis de similitud basados en los coeficientes de Jaccard. Por otra parte, el análisis de agrupamiento basado en el algoritmo UPGMA revela cuatro clusters robustos junto con nueva evidencias de la singularidad de la flora del Misisípico. Finalmente, los resultados obtenidos revelan que los análisis de similitud y agrupamiento son poderosas herramientas para interpretar las consecuencias de los procesos que modifican la composición taxonómica de las distintas unidades de tiempo analizadas del Paleozoico.

Palabras clave: Innovación evolutiva, procesos de extinción, análisis multivariable, Paleozoico, registro fósil, similitud.

INTRODUCTION

In the second half of the past century, several authors published a series of articles which today comprise the most recent history of palaeontological and evolutionary science (Raup, 1972, 1975, 1978, 1985; Van Valen, 1972, 1973a, 1973b; Raup & Stanley, 1978; Sepkoski, 1978, 1979, 1984, 1987, 1993, 1994, 1997, 1998; Raup & Crick, 1979; Raup & Boyajian, 1988). The methodologies proposed in these papers are currently still in use, but undergoing continuous revision, in order to optimized the information obtained from the fossil record about evolutionary patterns and process.

In recent years, numerical and multivariate methods have played an important role in palaeontological analysis. These methods now go far beyond the diverse fields of morphological and phylogenetic analyses to embrace biostratigraphy, palaeobiogeography, and palaeoecology

(Sepkoski & Kendrick, 1993; Miller & Foote, 1996; Roth & Mosbrugger, 1996; Kramer & Konigsberg, 1999; Mertz *et al.*, 2000; Sepkoski *et al.*, 2000; Valentine & Jablonski, 2003; Marui *et al.*, 2004; Ruíz *et al.*, 2004; Palmqvist *et al.*, 2008; Figueirido *et al.*, 2009; Frobisch, 2009; among others). In this sense, recently published papers emphasise the use of clustering methods in palaeogeographical and palaeoecological applications to provide a better, detailed vision of the assemblages at specific times of the geologic time (Dimitrova & Cleal, 2007; Hilton & Cleal, 2007; Cleal, 2008a, 2008b; Coiffard *et al.*, 2008). Here I use similarity and clustering methods to bring a general vision of the Palaeozoic plant fossil record with a methodological comparative approach.

MATERIAL AND METHODS

DATA SOURCES

In agreement with several classic palaeobiological papers of the twentieth century, which use compiled data from the monographic literature (Newell, 1952; Simpson, 1953; Müller, 1961; Schindewolf, 1962; Valentine, 1969), the Palaeozoic plant fossil record has been analysed based on several classic monographic studies (Cleal, 1993a, 1993b; Stewart & Rothwell, 1993; Taylor & Taylor, 1993; Cleal & Thomas, 1994, 1999). This paper has been conducted at the family level; the taxa used are specified in Table S1. In accordance with recently published works (Kvaček *et al.*, 2006; Willis *et al.*, 2007; Jud *et al.*, 2008; Wagner & Álvarez-Vázquez, 2008), the taxonomy used in the present paper follows that of Cleal (1993a, 1993b) in "The Fossil Record 2". To minimize the taxonomic, sampling and rock record bias (Raymond & Metz, 1995; Foote, 1997; Lane & Benton, 2003; Wang & Bush, 2009), inherent to this methodology, several types of fossils were considered for each taxon in the sample (Benton, 1993; Taylor *et al.*, 2009) taking into account vegetative and reproductive structures in order to diminish the possible taphonomic effect regarding to the preservation bias; see Table S1 for details. Detailed information about this methodological bias can be consulted from Cascales-Miñana *et al.* (in press).

The data were codified in a primary double-entry matrix from floristic lists by placing the taxa in rows and the time units in columns, in agreement with Digby & Kempton (1987) and Kovach (1988). Recent articles have used the binary nomenclature to codify the data (Hilton & Cleal, 2007; Cleal, 2008a; Coiffard *et al.*, 2008). According to this methodology, each box of the matrix takes a value of one or zero when the taxa are either present or absent in a time unit. The present analysis includes nine time units of the geological time scale (Gradstein & Ogg, 2004). The time units have been named according to the International Commission on Stratigraphy's time-rock term, and the discussion has been written accordingly. Absolute ages have been extracted from Gradstein & Ogg (2004). For detailed absolute ages and information about the time units see Table 1.

Table 1. Temporal range of the analysis of Palaeozoic flora, time units and abbreviations. Absolute ages extracted from Gradstein & Ogg (2004).

Time Units	*Abbreviation*	*Ages (Myr)*	
Late Silurian	US	428.2	416.0
Early Devonian	LD	416.0	397.5
Middle Devonian	MD	397.5	385.3
Late Devonian	UD	385.3	359.2
Mississippian	LC	359.2	318.1
Pennsylvanian	UC	318.1	299.0
Early Permian	LP	299.0	270.6
Late Permian	UP	270.6	251.0
Early Triassic	LT	251.0	245.0

SIMILARITY AND CLUSTER ANALYSIS

Traditionally, Jaccard Coefficients have been regarded as the most reliable similarity coefficient for presence-absence data which are a measure of the proportion of elements (taxa) that two objects (time units) have in common (Shi, 1993; Cleal & Shute, 1995; Thomas, 2007). Nevertheless, problems arise when the Jaccard coefficients are used to compare two samples when one has considerably more taxa than the other (Hammer & Harper, 2006). One alternative is to use the Raup-Crick Coefficient, which is calculated using a "Monte-Carlo" randomization procedure, to determine how often a comparable level of similarity occurs in two hundred randomly replicated samples of the same size (Raup & Crick, 1979). This statistical probabilistic index is the confidence level associated with a unilateral randomization test, which involves, for each pair of time units compared (Maridet *et al.*, 2007). The general procedure cited by the literature specify that when a couple of time units appear characterized by a very high Raup-Crick index value (say, $RC > 0.95$) show a significant similarity between their studied taxonomic composition (they non-randomly share too many taxa in common); in contrast, a couple of time units characterized by a very low Raup-Crick index value (say, $RC < 0.05$) show a significant difference between their studied taxonomic composition (they non-randomly share too few taxa in common), which can be interpreted as a measure of the robustness (Costeur *et al.*, 2004; Maridet *et al.*, 2007; Costeur & Legendre, 2008). Therefore, for each pair of time units, the associated null distribution of the number of shared families was estimated by generating 10,000 successive random resamplings from the common pool of families without taking into account the observed probabilities of taxa occurrence. In other words, it provides an estimate of the likelihood of the observed similarity between the two samples occurring through a random selection from a single-parent pool. Shi (1993), in his classic paper about the comparative analysis of several similarity coefficients, did not test the reliability of Raup-Crick Coefficients because, as it was commented by Cleal (2008b), the laborious computing tasks required at that time made its practical use difficult. In the present-day, modern software packages enable such calculations to be done in seconds, and now Raup-Crick Coefficients are a very powerful tool for palaeobotanical and palaeobiological analyses, like that attempted here.

In light of these views, this study has been performed based on the Jaccard and Raup-Crick Coefficients as a comparative approach. Initially, several clustering methods including Unweighted Pair-Group Mean Average (UPGMA), Single Linkage Clustering Algorithm (SLCA) and Ward's Method were employed. The Ward´s method was used to contrast the cluster results based on similarity measures and to avoid possible methodological bias due to this algorithm is founded on the Euclidean distance (Hammer & Harper, 2006); nevertheless, preliminary results revealed a strong variation in the cophenetic correlation values between the several algorithms performed (Table 2). In this paper, similarity coefficients were clustered using the UPGMA algorithm, because this clustering method showed the best cophenetic correlation values independently of the similarity measures used (Table 2). The results are illustrated using the traditional type of dendrograms. Clustering was stratigraphically constrained, and only stratigraphically-adjacent time units were clustered during the agglomerative procedure. Although this might impose a preordained pattern on the output, according to the literature, bootstrapping in fact reveals that a stratigraphically-constrained cluster analysis provides a more robust reflection of the data structure than unconstrained clustering. The raw similarity data of the several clusters are available from the supporting information (Tables 3 and 4). These were all performed using the PAST software package (Hammer *et al.*, 2001).

Table 2. Cophenetic correlation values (*r*) of the several algorithms employed.

Algorithm	*Jaccard*	*Raup-Crick*	*Euclidean distance*
Unweighted Pair-Group Mean Average	0.8911	0.8107	
Single Linkage Clustering Algorithm	0.8676	0.7556	
Ward's Method			0.7825

Table 3. Similarity matrix based on the Jaccard Coefficients.

	US	LD	MD	UD	LC	UC	LP	UP	LT
US	1.0000								
LD	0.5000	1.0000							
MD	0.1539	0.2857	1.0000						
UD	0.1053	0.1429	0.5790	1.0000					
LC	0.0000	0.0278	0.1944	0.2564	1.0000				
UC	0.0000	0.0196	0.0741	0.1035	0.3750	1.0000			
LP	0.0000	0.0270	0.0476	0.0870	0.2353	0.5294	1.0000		
UP	0.0000	0.0000	0.0244	0.0667	0.1091	0.2667	0.5122	1.0000	
LT	0.0000	0.0000	0.0370	0.0625	0.0444	0.0877	0.1429	0.2778	1.0000

Table 4. Similarity matrix based on the Raup-Crick Coefficients.

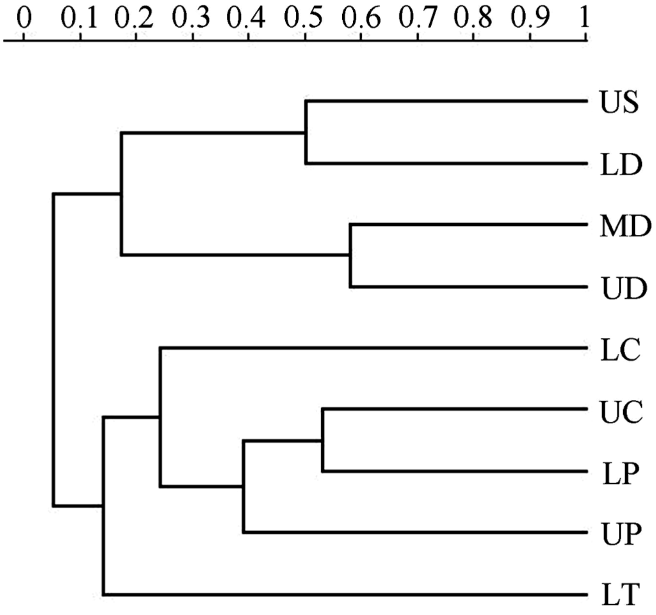
	US	LD	MD	UD	LC	UC	LP	UP	LT
US	1.0000								
LD	1.0000	1.0000							
MD	0.9625	0.9925	1.0000						
UD	0.8900	0.8925	1.0000	1.0000					
LC	0.0925	0.0800	0.8300	0.8700	1.0000				
UC	0.0325	0.0200	0.0350	0.0000	0.8050	1.0000			
LP	0.0800	0.0975	0.0125	0.0175	0.2350	1.0000	1.0000		
UP	0.0850	0.0200	0.0025	0.0050	0.0000	0.1550	1.0000	1.0000	
LT	0.2075	0.1125	0.1225	0.0900	0.0025	0.0075	0.2525	0.9600	1.0000

RESULTS AND DISCUSSION

The multivariate analysis based on the similarity and clustering methods appears in figure 1. In general terms, the results based on the Jaccard Coefficients show a pattern in which similarity decreases non proportionally toward more modern intervals (Table 3). The similarity measures demonstrate how the chronological consecutive intervals of one same period show lower similarity values than the intervals of different periods. This fact can be observed, for example, in the cluster formed by the Pennsylvanian and the Early Permian. In this cluster, the taxonomic composition of the Pennsylvanian is more analogous with the Permian flora than with the Mississippian (Fig. 1a).

On the other hand and irrespectively of the chosen similarity coefficient, the data representation does not reveal a major difference from the cluster groups. Nevertheless, the Raup-Crick Coefficients better adjust the clustered groups. Only a few changes can be observed at the end of the Palaeozoic where the UPGMA algorithm reveals a major affinity between the Late Permian and the Early Triassic when the Raup-Crick Coefficients are used. The cluster results obtained using the Raup-Crick Coefficients clearly demonstrate that there are four groups of time units which represent robust clusters (Fig. 1b). These groups are in accordance with the different interpretations of the plant fossils cited in the literature and they represent an easy, global vision of the Palaeozoic plant fossil record.

a) Jaccard Similarity Coefficients



b) Raup-Crick Similarity Coefficients

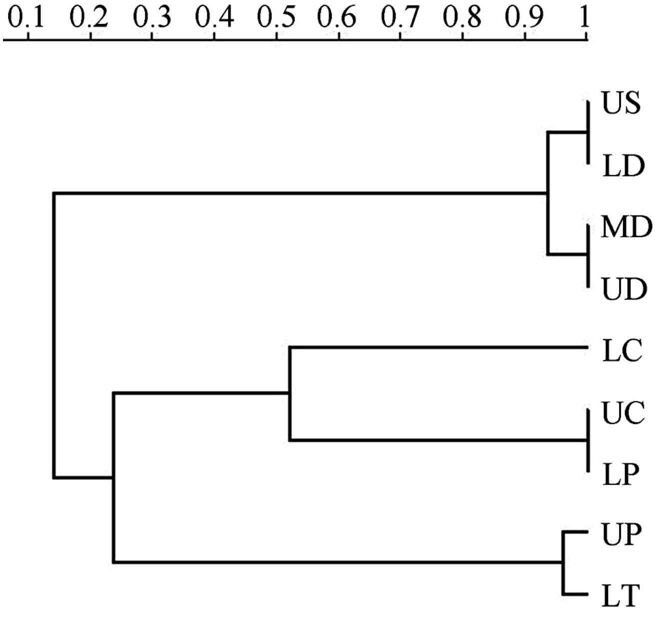


Figure 1. Cluster analyses of the Palaeozoic plant fossil record analyzed. Details of the analytical method used are given in the text (see Material and Methods). **a**, Cluster analysis based on the Jaccard Coefficients. Raw data is given in Table 3. **b**, Cluster analysis based on the Raup-Crick Coefficients. Raw data is given in Table 4.

The first group of the dendrogram corresponds to the time units of the Late Silurian and the Early Devonian, and it is during this interval that the first origination and radiation of vascular land plants take place. This cluster contains the early evolutionary trends of vascular plants, which constitutes a special time in plant life history. Some of these taxa, rhyniophytes for instance, are characterized by terminal sporangia and dichotomous branching (Cleal & Thomas, 1994; Roth-Nebelsick *et al.*, 2000), whereas others, like zosterophylls and trimerophytes, have sporangia that aggregate into terminal spikes (Edwards, 1969; Banks & Niklas, 1989) and a trifurcating branching pattern (Niklas & Banks, 1985; Rothwell, 1999), respectively. Previous works (Gensel & Andrews, 1984; McGhee, 1996; Godderis & Joachimski, 2004; Cascales-Miñana & Ruiz-Sánchez, 2009) reveal, as others in the literature have, that the plant fossil record which included these taxa groups considerably reduced in the Middle Devonian until these taxa totally disappeared at the end of the Devonian. Among other considerations, this fact could explain the robustness of this cluster.

The second cluster corresponds to the Middle and the Late Devonian. This section on the geologic time scale is a very important episode of plant life history, and is characterized not only by the increased size of the vascular forms of lycophytes which developed into the arborescent habit (Gensel & Berry, 2001), but also by the origin and consolidation of the progymnosperm groups (Gensel & Andrews, 1984; Cleal & Thomas, 1999). Progymnosperms have an important effect on plant evolution because they develop large, secondary-thickened, gymnosperm-like axes which allow many of them to reach arborescent proportions (Fairon-Demaret & Leponce, 2001; Scheckler & Galtier, 2003). Note, however, that their free-spore reproductive habit was pteridophytic (Marshall, 1996). These plants were the first true trees on the Earth, and they represent the phylogenetic intermediates between the early vascular pteridophytes and seed plants. All these evolutionary innovations emphasize the particular character of this cluster.

Interestingly, the Mississippian is a time unit whose taxonomic composition is not shared with the other time units analysed as this interval is only linked to time intervals with very low coefficient values (Fig. 1). This fact could be explained as result of the extinction processes and the evolutionary dynamics, that is, processes which would lead to many taxa of the Mississippian not being recorded in the subsequent intervals. This context can be observed in the similarity measures based on the Jaccard and Raup-Crick Coefficients (Tables 3 and 4). Among other interpretations, the results suggest that the taxa which originated in the Devonian radiation underwent a fast diversification process. Nevertheless, not all the groups achieved the same evolutionary success in terms of prolonged duration (Rothwell, 1996; Cascales-Miñana & Ruiz-Sánchez, 2008b), but generated a taxonomic turnover process that is reflected in the similarity and clustering methods in terms of Mississippian flora.

The fourth cluster is formed by the Pennsylvanian and the Early Permian (Fig. 1). The vast majority of the diversity of the exclusive vascular plant groups, for example some types of seed ferns or pteridosperms, date back to the end of the Carboniferous. The literature offers considerable evidence that a palaeoclimatic change was the main cause of extinction (Phillips & Peppers, 1984; Cecil, 1990; Kosanke & Cecil, 1996). The results of the similarity and clustering methods mark a sloped change between the Mississippian and the Pennsylvanian. The clustering methods support several published ideas about this topic (Phillips & Peppers, 1984; Phillips & Cecil, 1985; Phillips *et al.*, 1985; DiMichele *et al.*, 1987; DiMichele & Phillips, 2002; Shute & Cleal, 2002) and offer a plausible explanation of this observation: it is likely that the two humid periods documented in the Carboniferous would not have been of equal magnitude in water regime terms, and such was the extent of this scenario that a gradual drying of habitats would have taken place. This could be one of the main causes behind both the turnover of the structural plans and the reduced plant fossil record representation of the arborescent forms of Lycophytes.

The last cluster, made up of the Late Permian and the Early Triassic, and performed with the Raup-Crick Coefficients, does not correlate in the dendrogram based on the Jaccard Coefficients. Nevertheless, both coefficients are in agreement with the differences between the two Permian time units. The Permian mass extinction event is probably the most significant of life history and probably affected virtually all marine invertebrates (Sepkoski, 1988; Benton, 1995). Nevertheless, previous studies (Cascales-Miñana & Ruiz-Sánchez, 2007, 2008a, 2009) only reflect a gradual reduction of diversity from the end of the Mississippian, which is based on the change of the vegetation mainly dominated by lycophytes, sphenophytes, filicophytes and pteridosperms to other forms of vegetation dominated by cycads, ginkgos and conifers in the Palaeozoic-Mesozoic transition (Knoll, 1984; Knoll & Niklas, 1987; Jablonski & Sepkoski, 1996; Willis & McElwain, 2002).

All these considerations reveal that the saltational changes illustrated by the similarity measures, irrespectively of the chosen coefficients, are a result of the differential taxonomic composition among the time units. This fact could be explained by either the appearance of evolutionary innovations or the changes brought about by extinctions together with the geologic constraints associated with these methods. Thus, together with the rock-record bias, the evolutionary innovations and the ecological context are some of the factors that condition the taxonomic composition. Nevertheless, extinction events may have affected the several lineages unequally. In my opinion, the taxonomic changes caused by these processes would be reflected in the measures of similarity among the intervals both before and after these events. Based on the Jaccard Coefficients, this fact is reflected as important variations of similarity among the time units in the Devonian-Carboniferous transition (Table 3). The effects of the extinction events can also be observed in the Mississippian-Pennsylvanian transition when a considerable number of taxa extinguished. It is possibly for these reasons that the Carboniferous time unit does not appear enclosed in a single cluster. On the other hand, the cluster formed by the primitive flora at the end of the Silurian and in the Early Devonian is quite far from the rest of the intervals (Fig. 1a), but it is also important to note that, this flora is very close to the cluster formed by the Middle and Late Devonian (Fig. 1b). This observation is probably related to the plant fossil record composition and to the declivity of the primitive structural plans of vascular plants, as previously mentioned. Finally, the special case of Mississippian flora, where many taxa are not recorded in the subsequent intervals, emphasizes the fact that the similarity based on Jaccard Coefficients among the several time units obtains its minimum value when the last taxon of the oldest interval extinguishes.

CONCLUDING REMARKS

This study uses cluster analyses with two similarity measures, on the one hand, the descriptive binary similarity measure of the Jaccard's index and the other hand, the probabilistic similarity measure of Raup-Crick, to show the palaeofloristic composition of the Palaeozoic fossil record from a cluster viewpoint. It is universally accepted that the palaeofloristic structure has not remained constant through Palaeozoic times. Accordingly, the cluster analyses presented herein reveal significant discontinuities in terms of taxonomic composition, especially between Mississippian flora and the several floras of the subsequent time units. Nevertheless, a special mention requires the deep disruption observed, with both coefficients, between the Early and Middle Devonian.

Previous studies (Cleal & Shute, 1995; Thomas, 2007) have used cluster analyses with Jaccard Coefficients. The present study has confirmed that cluster analysis is a powerful tool for such work, but the Raup-Crick Similarity Coefficients may provide a better pattern resolution within the data. Along these lines, although the cluster analyses were performed with both similarity measures and they essentially provide similar results, the Raup-Crick Coefficients clearly have the potential for providing more robust results, whereas the consequence of the extinction processes appears to be better reflected in the Jaccard Coefficients-based analysis.

This study provides new evidence of the importance of using more than one type of similarity coefficients and comparing the results with both measures to obtain a better interpretation of the fossil record data. On the other hand, due to the controversial character of taxonomic data, which present an inevitable subjective basis, and the nature of the taxonomic process that are in constant revision, in concordance with recent ideas about the influence of the taxonomy in the palaeobiological works (Valentine & May, 1996; Robeck *et al.*, 2000; Adrain & Westrop, 2003; Alroy, 2003; Lane *et al.*, 2005), this type of approaches would need be re-examined in the future in agreement with new hierarchic systems taking into account new discoveries and new taxonomic classifications.

Finally, the results presented here demonstrate that the similarity measures are an excellent indicator of the processes that modify the taxonomic composition of the plant record. Furthermore, the results also show that analysing the plant fossil record with similarity and clustering methods proves a powerful tool to interpret plant life history from a synthetic viewpoint.

SUPPORTING INFORMATION

Table S1. Families and the main predominant types of fossil compiled to codify the binary matrix of the analysis. Families appear in alphabetic order. For more details, see the consulted sources in Material and Methods.

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Table S1. Families and main predominant types of fossil compilated to codify the binary matrix of the analyses. The families appear by alphabetic order. For more detail see consulted sources in Material and Methods.

FAMILY	TYPE OF FOSSIL	REFERENCES
Aneurophytaceae	Fertile parts	Bonamo & Banks, 1967
	Stems	Lang, 1926
Arberiaceae	Foliages	Delevoryas & Person, 1975
		Vakhrameev *et al.*, 1978
	Pollen organ	Delevoryas & Gould, 1971
	Fructifications	Anderson & Anderson, 1985
Archaeocalamitaceae	Fructifications	Scott *et al.*, 1985
	Stems	Ischenko, 1965
		Novik, 1968
Archaeopteridaceae	Foliages	Allen & Marshall, 1986
	Reproductive structures	Chaloner, 1968
Asterothecaceae	Axes	Pfefferkorn, 1976
	Fructifications	Phillips, 1980
Biscalithecaceae	Fronds	Galtier, 1978
	Sporangia	Galtier & Scott, 1979
Botryopteridaceae	Fructifications	Galtier, 1967
		Galtier, 1971
		Scott *et al.*, 1985
Bowmanitaceae	Sterile foliages	Remy, 1961
		Remy & Spassov, 1959
	Strobilies	Remy, 1961
		Remy & Spassov, 1959
Buriadiaceae	Fructifications	Pant & Nautiyal, 1967
Calamopityaceae	Fructifications	Galtier & Rowe, 1989
		Walton, 1949b
	Foliages	Walton, 1931
	Stem	Long, 1964
Calamostachyaceae	Sterile foliages	Kerp, 1984
		Stockmans & Willière, 1953
Callistophytaceae	Stems	Phillips, 1980
	Pollen organ	Phillips, 1980
Cardiolepidiaceae	Foliages fragments	Meyen, 1983
	Fructifications	Meyen, 1983, 1988
Caudatocarpaceae	Reproductive structures	Brack-Hanes, 1981
Cecropsidaceae	Leaves	Stubblefield & Rothwell, 1989
Chaloneriaceae	Cones	Chaloner, 1958
		Crookall, 1966
	Reproductive structures	Pigg & Rothwell, 1983
Cheirostrobaceae	Reproductive structures	Scott, 1898
Cladoxylaceae	Reproductive structures	Long, 1968a
		Schweitzer, 1972, 1973
	Vegetative organs	Long, 1968a
		Schweitzer, 1972, 1973
Cordaitanthaceae	Foliages	Mei, 1984
	Seeds	Long, 1977
Corynepteridaceae	Fertile foliages	Galtier & Scott, 1979
	Fructifications	Scott *et al.*, 1985
	Sterile foliages	Stockmans & Willière, 1955
Crossothecaceae	Foliages	Brousmiche, 1983
Cycadaceae	Leaves	Leary, 1990
	Pollen cones	Taylor, 1969
	Seeds	Leary, 1990
Cyclodendraceae	Sterile stems	Rayner, 1985
Cyclostigmaceae	Fertile structures	Chaloner, 1968
Diaphorodendraceae	Stems	DiMichele & Bateman, 1992
	Axes	DiMichele & Bateman, 1992
Dicranophyllaceae	Foliages	Meyen & Smoller, 1986
		Stockmans & Willière, 1953
	Fructifications	Meyen & Smoller, 1986
		Renault, 1890
Drepanophycaceae	Sterile axes	Stubblefield & Banks, 1978
		Kräusel & Weyland, 1937
Echinostachyaceae	Reproductive structures	Grauvogel-Stamm, 1978
Eleutherophyllaceae	Reproductive structures	Josten, 1983
		Zimmermann, 1930
	Vegetative organs	Josten, 1983
		Zimmermann, 1930
Elkinsiaceae	Fructifications	Walton, 1949a
	Reproductive structures	Rothwell *et al.*, 1989
	Seeds	Long, 1961b
Emplectopteridaceae	Fronds	Halle, 1927
	Fructifications	Li & Yao, 1983
	Leaves	Asama, 1962
	Seeds	Halle, 1932
Emporiaceae	Reproductive structures	Mapes & Rothwell, 1991
Eospermaceae	Seeds	Long, 1961a
		Barnard, 1959
Equisetaceae	Foliar whorls	Escapa & Cúneo, 2006
	Esterile stems	Kon'no, 1973
	Fertile structures	Escapa & Cúneo, 2006
		Kon'no, 1962

FAMILY	TYPE OF FOSSIL	REFERENCES
Eviostachyaceae	Fructifications	Leclercq, 1957
Ferugliocladaceae	Reproductive structures	Archangelsky & Cúneo, 1987
Flemingitaceae	Megaspores	Chaloner, 1953
	Stems	Zhao *et al*., 1980
Genomospermaceae	Reproductive structures	Long, 1959
Gleicheniaceae	Sporangia	Ash, 1969 Halle, 1927
	Vegetative organs	Ash, 1969 Halle, 1927
Gondwanostachyaceae	Foliages	Townrow, 1956
Horneophytaceae	Sporangia	El-Saadway & Lacey, 1979
Ibykaceae	Stems	Bertrand, 1913 Skog & Banks, 1973
Isoetaceae	Reproductive structures	Stubblefield & Rothwell, 1981
Lagenostomaceae	Fronds	Shadle & Stidd, 1975
	Seeds	Long, 1975
Lepidocarpaceae	Fructifications	Tian & Guo, 1987
Lycopodiaceae	Sterile axes	Kräusel & Weyland, 1937
Majonicaceae	Reproductive structures	Clement-Westerhof, 1987 Stoneley, 1958
Marattiaceae	Fertile pinnules	Zhao-Hua *et al*., 2000
	Fronds	Hill *et al*., 1985 Hill & Camus, 1986
	Sporangia	Hill *et al*., 1985
Miadesmiaceae	Sterile fragments	Bertrand, 1895
Nilsoniaceae	Leaves	Kimura & Okubo, 1985
Noeggerathiaceae	Fertile structures	Hirmer, 1941
	Foliages	Gothan, 1931
Osmundaceae	Fronds	Kidston & Gwynne-Vaughan, 1908a, 1908b
Peltaspermaceae	Foliages	Kerp & Naugolnykh, 1996 Bouroz & Doubinger, 1977
Physostomaceae	Seeds	Gordon, 1910 Leisman, 1964 Oliver, 1909
Pinakodendraceae	Reproductive structures	Kidston, 1911 Rousseau, 1933
	Vegetative organs	Kidston, 1911 Rousseau, 1933
Pleuromeiaceae	Reproductive structures	Grauvogel-Stamm & Duringer, 1983
Podocarpaceae	Foliages	Carpentier, 1935 Townrow, 1967
	Fructifications	Townrow, 1967

FAMILY	TYPE OF FOSSIL	REFERENCES
Potoniaceae	Foliages	Bouroz & Doubinger, 1977 Wagner *et al*., 1983
	Fronds	Stidd *et al*., 1975
	Fructifications	Stockmans & Willière, 1953
	Seeds	Phillips, 1980
	Spores	Stidd, 1978
Protokalonaceae	Stems	Barnard & Long, 1975
	Branches	Barnard & Long, 1975
Protolepidodendraceae	Sterile stems	Lemoigne & Brown, 1980
	Fructifications	Smith, 1962
Protopityaceae	Fructifications	Smith, 1962
Psalixochlaenaceae	Fronds	Holmes, 1981
	Fertile parts	Holmes, 1981
	Sporangia	Good, 1981
	Vegetative axes	Long, 1976
Pseudoborniaceae	Stems	Mamay, 1962 Schweitzer, 1967
	Leaves	Mamay, 1962 Schweitzer, 1967
Rhacophytaceae	Fertile structures	Wagner, 1984
	Pollen grains	Utting & Neves, 1970
Rhyniaceae	Sporangia	Edwards *et al*., 1992
	Stems	Edwards & Richardson, 2004 Li, 1982
Rufloriaceae	Foliages	Meyen, 1982
	Fructifications	Gorelova *et al*., 1973
Selaginellaceae	Reproductive structures	Fairon-Demaret, 1977
Sermeyaceae	Sporangia	Eggert & Delevoryas, 1967
Sigillariostrobaceae	Specimens	Long, 1968b
	Sterile stems	Feng *et al*., 1977
Spenceritaceae	Reproductive structures	Leisman & Stidd, 1967
	Spores	Kubart, 1910
Sporangiostrobaceae	Reproductive structures	Wagner, 1983
Stauropteridaceae	Reproductive structures	Cichan & Taylor, 1982 Erwin & Rothwell, 1989
	Vegetative organs	Cichan & Taylor, 1982 Erwin & Rothwell, 1989
Takhtajanodoxaceae	Reproductive structures	Thomas & Brack-Hanes, 1984
Tchernoviaceae	Fructifications	Meyen, 1982
	Sterile foliages	Radchenko, 1967
Tedeleaceae	Fructifications	Barthel, 1976 Meyen, 1987 Scott *et al*., 1985

FAMILY	TYPE OF FOSSIL	REFERENCES
Tingiostachyaceae	Foliages	Halle, 1927 Stockmans & Mathieu, 1939
	Reproductive structures	Stockmans & Mathieu, 1957
	Sterile foliages	Feng *et al.*, 1977 Kon'no *et al.*, 1971
	Sterile fragments	Tidwell, 1967
Trichopityaceae	Foliages	Cridland & Morris, 1963 Meyen, 1987
Trigonocarpaceae	Foliage	Wagner *et al.*, 1983
	Seeds	Taylor & Eggert, 1967
	Stems	Barthel, 1976
Trimerophytaceae	Sporangia	Croft & Lang, 1942
	Stems	Gerrienne, 1983 Kaspar *et al.*, 1988
Ullmanniaceae	Reproductive structures	Clement-Westerhof, 1988
Umkomasiaceae	Foliages	Meyen, 1979
Urnatopteridaceae	Foliages	Kerp & Fichter, 1985 Stockmans & Willière, 1953
Utrechtiaceae	Reproductive structures	Mapes & Rothwell, 1991
Vojnovskyaceae	Leaves	Vakhrameev *et al.*, 1978
Voltziaceae	Reproductive structures	Clement-Westerhof, 1988
Zosterophyllaceae	Sporangia	Edwards, 1972, 1975
	Stems	Hueber, 1971, 1972
Zygopteridaceae	Fertile structures	Scott *et al.*, 1984
	Fructifications	Scott *et al.*, 1985
	Stems	Galtier & Scott, 1979 Scott & Galtier, 1985
	Sterile foliages	Scott *et al.*, 1985