Quantitative analysis of Triassic-Jurassic pollen and spores for paleoenvironmental and paleoclimate reconstructions

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Zhang, Jianguang: Quantitative analysis of Triassic-Jurassic pollen and spores for paleoenvironmental and paleoclimate reconstructions

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Declaration of authorship

Ich erkläre hiermit, die vorliegende Dissertation ohne Hilfe Dritter und nur mit den angegebenen Quellen und Hilfsmitteln angefertigt zu haben. Alle Stellen, die aus Quellen übernommen wurden, sind als solche kenntlich gemacht worden. Diese Arbeit hat in dieser oder ähnlicher Form noch keiner Prüfungsbehörde vorgelegen. Die schriftliche Fassung stimmt mit der elektronischen Fassung überein.

I hereby certify that the complete work to this PhD thesis was done by myself and only with the use of the referenced literature and the described methods.

Darmstadt

Jianguang Zhang

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Preface

For most of the Mesozoic dispersed sporomorphs, the quantitative application of Eco-Plant (The Eco-group classification based on the growth-form of plants) is limited, because either their assignment to a specific eco-group remains uncertain or the botanical affinities to plant taxa are unclear. Therefore, it is first important to identify their botanical affinities, because otherwise, their Eco-Plant implications are not reliable. Based on a newly created database for sporomorphs, this study tries to link the dispersed Mesozoic sporomorph genera of Bryophytes, Pteridophytes, and Gymnosperms to their closest parent plants and Eco-Plant model.

Chapter 1 introduces this thesis by giving an overview of the study motivations and the study aims.

Chapter 2 introduces a new online database ***Sporopollen*** (http://www.sporopollen.com). It organizes a huge data set (about 3 million entries) and makes the sporomorph assignment to the botanical affinities and Eco-Plant implications more reliable.

Chapter 3 (published article) with the help of the database, dispersed Mesozoic sporomorph genera of Bryophytes, Pteridophytes, and Gymnosperms are reviewed by comparing the unique outline and structure/sculpture of the sporomorph wall with that of modern plants and *in situ* fossil plants. They are linked to their closest parent plants and the Eco-Plant model at the family or order level. The reasons that some sporomorphs can not be linked to any parent plant and Eco-Plant model are also discussed.

Zhang, J., Lenz, O.K., Wang, Y., Hornung, J., 2021. The Eco-Plant model and its implication on Mesozoic dispersed sporomorphs for Bryophytes, Pteridophytes, and Gymnosperms. Review of Palaeobotany and Palynology. https://doi.org/10.1016/j.revpalbo.2021.104503

Chapter 4 (published article) based on the reviewed result in **Chapter 3,** a new interface (http://www.sporopollen.com/sporemesozoicsegs.php?opencode=paper1) was created to quickly link the dispersed sporomorphs to past vegetation patterns and climatic changes.

Zhang, J., Lenz, O.K., Wang, P., Gao, Y., Hornung, J., 2021. Database-based Eco-Plant analysis for Mesozoic dispersed sporomorphs. MethodsX 8, 101329. https://doi.org/10.1016/j.mex.2021.101329

Chapter 5 (published article) using the Eco-Plant model and the sporomorphs from a 10 m thick lignite bed from the Upper Triassic Haojiagou Formation (Rhaetian), the palaeovegetation and palaeoenvironment near the Triassic-Jurassic boundary are discussed. This represents a case study to validate and show the potential of the outcomes from this study.

Zhang, J., Lenz, O.K., Hornung, J., Wang, P., Ebert, M., Hinderer, M., 2020. Palynology and the Eco-Plant model of peat-forming wetlands of the Upper Triassic Haojiagou Formation in the Junggar Basin, Xinjiang, NW China. Palaeogeography, Palaeoclimatology, Palaeoecology 556, 109888. https://doi.org/10.1016/j.palaeo.2020.109888

Chapter 6 presents a summary of the results obtained during this study.

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Abbreviations

CA	Correspondence analysis.
*.csv file	CSV is a simple file format used to store tabular data, such as a spreadsheet or database. For detail see: https://www.computerhope.com/issues/ch001356.htm
DCA	Detrended correspondence analysis.
DRD	Dataset relation diagram.
Eco-Plant model	The Ecogroup classification based on the growth-form of plants.
EPH	Eco-Plant model that assesses the effect of humidity.
EPT	Eco-Plant model that assesses the effect of temperature.
ESEM	Environmental scanning electron microscope.
H2O2	Hydrogen peroxide.
HCl	Hydrochloric acid.
HF	Hydrofluoric acid.
HJG	Haojiagou.
HNO3	Nitric acid.
KOH	Potassium hydroxide.
LM	Light microscope.
MAT	Mean annual air temperature.
MySQL	An open-source relational database management system. "My", the name of co-founder Michael Widenius's daughter, and "SQL", the abbreviation for Structured Query Language.
PCA	Principal component analysis.
PHP	Hypertext Preprocessor: a general-purpose scripting language that is especially suited to web development.
PZ	Palynozone.
SD	Units of average standard deviation of species turnover.
SEG model	The Sporomorph Ecogroup Model of Abbink et al (2004b).
SEM	Scanning Electron Microscope.
TEM	Transmission electron microscope.
UPGMA	Unweighted pair-group average.

Abstract

The eco-group classification based on the growth-form of plants (Eco-Plant model) is widely used for extant, Cenozoic, Mesozoic, and Paleozoic palaeoenvironmental reconstructions. However, for most Mesozoic dispersed sporomorphs, the application of the Eco-Plant model is limited, because either their assignment to a specific eco-group remains uncertain or the botanical affinities to plant taxa are unclear. A new database ***Sporopollen*** (http://www.sporopollen.com) focused mainly on Mesozoic sporomorphs is created. Currently, it has collected **100,610** sporomorph pictures, **59, 498** plant pictures, **31, 922** sporomorph descriptions. At the same time, from **63, 035** references, it has collected **2, 215, 162** occurrences for both sporomorph and non-sporomorph fossils. The collected plant data include **32, 972** genera from **946** families. The collected sporomorph pictures include **5, 857** genera.

With the help of the database, **861** dispersed Mesozoic sporomorph genera of Bryophytes, Pteridophytes, and Gymnosperms are reviewed by comparing the unique outline and structure/sculpture of the sporomorph wall with that of modern plants and *in situ* fossil plants. The results show that **474** of them can be linked to their closest parent plants and Eco-Plant model at family or order level, but **387** of them can not because of the lack of detailed ultrastructure descriptions. The use of a light microscope (LM) for determination is one of the main reasons that some dispersed sporomorphs cannot be linked precisely to their parent plants. The presented eco-groups for disperse Mesozoic sporomorphs provide the possibility to identify detailed vegetation and palaeoenvironmental change in the Mesozoic, especially in the context of climate change.

A new interface (http://www.sporopollen.com/sporemesozoicsegs.php?opencode=paper1) was created based on the reviewed result to quickly link the dispersed sporomorphs to past vegetation patterns and climatic changes. Users can upload their data to the database and in return get quick results. It can automatically link all of the Mesozoic and Cenozoic sporomorphs to their possible parent plants at phylum, order, or family level. It can also automatically link all of the Triassic and Jurassic sporomorphs to the Eco-Plant model to assess the effect of humidity (EPH) and the effect of temperature (EPT).

By using 30 sporomorph samples from a 10 m thick lignite bed from the Upper Triassic Haojiagou Formation (Rhaetian) as an example, the palaeovegetation and palaeoenvironment of a peat-forming wetland near the Triassic-Jurassic boundary are discussed with the help of the Eco-Plant model. The results show that the palynoflora contains both Eurasian and Gondwanan elements, and is dominated by the spores and pollen of Bennettitales, Corystospermales, Ginkgoales, and Gleicheniales. At the Triassic/Jurassic boundary (Hettangian), the palynoflora significantly changes as Cyatheales spores become the dominant elements. We analyse assemblages in terms of an Eco-Plant model, which assigns the parent plants of the palynomorphs into five groups based on humidity and four groups based on temperature, and uses multivariate statistical analyses to infer palaeoclimate and palaeoenvironmental conditions. Results suggest that the palaeoclimate of the Rhaetian was generally wet and subtropical with short seasonal drought periods. Our analysis shows that an Eco-Plant model may be a useful tool to reveal past vegetation patterns and climate changes, applicable to other Mesozoic assemblages.

1. Introduction

1.1 Motivations

1.1.1 Mesozoic sporomorphs

The words “sporomorph” and “sporopollen” are synonymously used as umbrella terms for pollen and spores or, more specifically even, only to pollen and the spores of embryo-producing (embryophytic) plants. Spores are part of the lifecycles of lower plants such as bryophytes and pteridophytic vascular plants, while pollen is part of the lifecycles of seed-producing plants such as gymnosperms and angiosperms (Jansonius and Mcgregor, 1996a).

Several special characters of sporomorphs make them important for palaeoenvironment reconstruction and stratigraphy. Firstly, sporomorphs are small. A miospore is a sporomorph that has a size of less than 200 µm, while a macrospore has a size of more than 200 µm (Traverse, 2007). Normally, pollen and spores are between 20 to 100 µm in size (Zhou and Yang, 2007). Secondly, sporomorphs are abundant. **Table 1-1** presents the pollen production of flowers and trees. It is reported that a hectare of *Picea* can produce 7,500 tons of pollen during each season (Zhou and Yang, 2007). Thirdly, sporomorphs are resistant. The wall of a sporomorph is among the most, probably the most chemically inert of the major naturally occurring organic compounds (Traverse, 2007). Fourthly, sporomorphs are diverse. Different plants produce different pollen or spores so that they can be used to recover their mother plants in palaeoenvironment reconstruction. Finally, sporomorphs show a fast evolution. Various taxa represent preserved parts of the life cycles of various organisms that, during one or more periods of Earth history, were comparatively fast-evolving (Traverse, 2007). Therefore, they can be used for stratigraphic analysis.

Table 1-1 Grain numbers of the pollen production for a flower and a tree

A flower	
Typha	174,000,000
Corylus avellana	2,550,000
Tilia cordata	43,000
A tree	
Pinus	350,000,000
Fagus	20,450,000,000

In the last decades, illustrations, descriptions, and definitions of Mesozoic dispersed sporomorphs are well studied e. g ., Jiang et al. (2016), Huang (2008), Liu (2003), Shang (2011), Song et al. (1999), Song et al. (2000), Shu and Norris (1999), the 6 volumes book series of *Synopsis der Gattungen der Sporae dispersae* (Potonié, 1956, 1958, 1960, 1966, 1970; Potonié and Kremp, 1970), and the 26 volumes book series of *Catalog of fossil spores and pollen* (Ames and Spackman, 1985; Ames et al., 1976; Kremp and Ames, 1959, 1961b, 1962a, b, 1965a, b; Kremp et al., 1957a, b; Kremp et al., 1958, 1959, 1960a, b; Kremp et al., 1966; Kremp et al., 1967, 1968; Traverse and Ames, 1968, 1969, 1971, 1979; Traverse et al., 1973a, 1974, 1975; Traverse et al., 1969). However, for the Mesozoic, sporomorph assemblages cannot reflect the composition of plant communities as successful as for the Quaternary, because for most of the Mesozoic dispersed sporomorphs, their botanical affinities are still missing. As more and more sporomorphs of *in situ* fossils (e.g., Balme, 1995; van Konijnenburg-van Cittert, 1971), and of extant plants (e.g., Gosling et al., 2013; Hesse et al., 2009; Li et al., 2011) have been well studied and described, it is possible to link dispersed sporomorphs convincingly to their parent plants. Therefore, a systematic review is needed to effectively accelerate a scientific solution on the debates focusing on linking sporomorphs to parent plants.

1.1.2 Eco-Plant model

Quantitative analysis of sporomorphs provides the possibility of constructing environmental models for each time-successive depositional sequence (Abbink, 1998). The Eco-group classification based on the growth-form of plants (Eco-Plant) was established by the pioneering work of Warming (1895) and Schimper (1898). They analyzed diverse plant associations with relation to principal climatic elements such as water, heat, light, and air. The Eco-Plant model has been widely used for extant (e.g., Baeza et al., 2010; Godin, 2017; Sheremetov and Sheremetova, 2017; Veisberg, 2017), Cenozoic (e.g., Bozukov et al., 2009; Yang et al., 2013; Yurtsev, 2001), Mesozoic (e.g., Hill, 2017; Vakhrameev, 1991), and Paleozoic palaeoenvironmental reconstructions (e.g., Bashforth et al., 2014; Wang, 1999b). It is also applied by palynologists for palaeoenvironmental reconstructions using dispersed sporomorphs from the Cenozoic (e.g., Aranbarri et al., 2014; Kern et al., 2012; Popescu et al., 2006; Suc and Fauquette, 2012) and Mesozoic (e.g., Césari and Colombi, 2016; Hochuli and Vigran, 2010; Mueller et al., 2016; Roghi et al., 2010; Visscher and van der Zwan, 1981; Wang et al., 2013; Wang et al., 2005; Zhao et al., 2014).

For the analysis of palaeoenvironmental and palaeoclimate variations, an Eco-Plant model is used. It assesses the effect of humidity (EPH) and the effect of temperature (EPT) that has also been used by other authors for Mesozoic records (e.g., Hill, 2017; Vakhrameev, 1991).

EPH separates the palynomorphs and their parent plants into five groups (Zhang et al., 2020):

a) *Hydrophytes* are aquatic plants that are completely or mostly submerged in water as well as being amphibious plants that grow both in water and in excessively wet habitats along the shorelines of reservoirs, in areas of shallow water, and swamps.

b) *Hygrophytes* are plants that are living in excessively wet habitats with high air and soil moisture but usually no water stagnation on the surface, such as the lower tiers of wet forests, or open habitats with constantly wet soils and wet air.

c) *Mesophytes* are plants that have some ability to resist periods of drought or to regulate their water metabolism in moist areas such as dry meadows or pine forests.

d) *Xerophytes* are plants that can resist long periods of drought and are living in stony steppes and dry rock outcrops.

e) *Euryphytes* are plants that are adapted to great variations in humidity.

EPT categorizes the palynomorphs and their parent plants into four groups (Zhang et al., 2020):

a) Megathermic plants inhabiting regions such as tropics and subtropics with a mean annual air temperature (MAT) above 20 °C.

b) Mesothermic plants inhabiting regions such as warm temperate zones with a MAT between 14 to 20 °C.

c) Microthermic plants inhabiting regions such as the cool temperate zone, the subarctic zone, or elevated areas with a MAT below 14 °C.

d) Eurythermic plants that can tolerate a wide range of temperatures.

The Sporomorph Eco-group Model (SEG model) of Abbink et al. (2004b) is also commonly used for Mesozoic palaeoenvironmental reconstructions of Europe and some parts of China (e.g., Abbink et al., 2001; Abbink et al., 2004a; Abbink et al., 2004b; Heunisch et al., 2010; Li and Wang, 2016; Li et al., 2016). It represents a simplified Eco-Plant model. According to hydrologic and temperature conditions in the Eco-Plant model, plants are classified into different EPH and EPT groups due to their climatic preferences. In contrast, in the SEG model, plants are classified as belonging to a wetter, drier, warmer, or cooler group. Besides, in the SEG model, due to uncertain botanical affinities of some sporomorphs, several plants indicating a different climate and environment are categorized in the same group. For example, in the Eco-Plant model, Ginkgoales are classified as mesophytes and mesothermic plants, but Bennettitales as hygrophytes and megathermic plants (see below). In contrast, in the SEG model, Ginkgoales, Cycadales, and Bennettitales are all included in the same group of the "Lowland SEG" and indicate a "drier" and "warmer" climate, since the pollen of Ginkgoales, Cycadales, and Bennettitales can usually only be distinguished under the scanning electron microscope (SEM) and transmission electron microscope (TEM) (Abbink et al., 2004b). Therefore, for the studies in this thesis, the Eco-Plant has been chosen since it allows for more detailed and precise statements on palaeoclimate than the SEG model.

However, for most of the Mesozoic dispersed sporomorphs, the application of Eco-Plant is limited, because either their assignment to a specific eco-group remains uncertain or the botanical affinities to plant taxa are unclear. Therefore, it is first important to identify their botanical affinities, because otherwise, their Eco-Plant implications are not reliable. Therefore, a systematic review is urgently needed for the Mesozoic dispersed sporomorphs related with Bryophytes, Gymnosperms, and Pteridophytes and linked them to their possible parent plants as well as Eco-Plant.

1.1.3 Sporomorph database

Sporomorphs are well dispersed and preserved in near-shore marine and continental sediments. Their distribution and abundance are excellent proxies for reconstructing terrestrial palaeoenvironments since they allow the identification of past vegetation communities (Traverse, 2007; Vincens et al., 2007). Consequently, serveral global and regional sporomorph database systems have been created to assist palynologists in palaeoenvironment studies (Bradshaw, 2007; Gajewski, 2008; Vincens et al., 2007; Whitmore et al., 2005), stratigraphic studies (Campbell and Mcandrews, 1992; Grimm, 1987; White et al., 2009) and sample identification (Bush and Weng, 2007; Han et al., 2014). Nevertheless, most databases such as PalDat (www.paldat.org) are related to recent or Cenozoic sporomorphs. There are some Mesozoic databases such as Palynodata (White et al., 2009) and *Strats-Pc* (Jansonius and Mcgregor, 1996b). However, these mainly focus on stratigraphic and not on palaeoenvironment/palaeoclimate analysis. Therefore, a robust database system is needed to collect illustrations, descriptions, occurrences, and taxonomy of sporomorphs. Different user-friendly interfaces are needed for data query both on a map and in datasets, sporomorph identification, palaeoenvironment/palaeoclimate reconstruction, and stratigraphic analysis.

1.2 Aims

The aims of this PhD thesis are:

- The collection of illustrations, descriptions, occurrences, and taxonomy of sporomorphs in a new database system as the basis for the detailed identification of their parent plants.

- The linkage of sporomorphs to their possible parent plants and the Eco-Plant model based on literature and the unique outline and structure/sculpture of the sporomorph wall.

- The application of the Eco-Plant model as a tool to reveal vegetation patterns and climate changes in a case section near the Triassic/Jurassic boundary.

- The discussion of the vegetation patterns and climate changes at the Triassic/Jurassic boundary.

2. *Sporopollen*, a new database for Mesozoic sporomorphs

Abstract

Most sporomorph database systems are related to recent or Cenozoic sporomorphs. The new database ***Sporopollen*** (http://www.sporopollen.com) presented here focuses on Mesozoic sporomorphs. It is created using MySQL as the database server and Hypertext Preprocessor (PHP) to create the dynamic website. It collects illustrations, descriptions, occurrences, and the taxonomy of sporomorphs. Different user-friendly interfaces are created for data queries on a map and in datasets, sporomorph identification, and stratigraphic analysis. Based on the literature, sporomorphs are also linked to their parent plants.

2.1 Introduction

Sporomorphs are well dispersed and preserved in near-shore marine and continental sediments. Their distribution and abundance are good proxies for reconstructing terrestrial palaeoenvironments since they allow the identification of past vegetation communities (Traverse, 2007; Vincens et al., 2007). Consequently, several global and regional sporomorph database systems have been created to assist palynologists in palaeoenvironment studies (Bradshaw, 2007; Gajewski, 2008; Vincens et al., 2007; Whitmore et al., 2005), stratigraphic studies (Campbell and Mcandrews, 1992; Grimm, 1987; White et al., 2009) and sample identification (Bush and Weng, 2007; Han et al., 2014). Nevertheless, most databases such as PalDat (www.paldat.org) are related to recent or Cenozoic sporomorphs. There are some Mesozoic databases such as Palynodata (White et al., 2009) and *Strats-Pc* (Jansonius and Mcgregor, 1996b). However, these mainly focus on stratigraphic rather than palaeoenvironment/palaeoclimate analysis. A new database system is required that focuses on Mesozoic sporomorphs and provides an efficient and reliable platform, which (a) quickly reveals stratigraphic information for a sporomorph genus or assemblage and (b) quickly reconstructs the palaeoenvironment for a sporomorph assemblage.

2.2 Materials and methods

2.2.1 General Design

An online database system ***Sporopollen*** (http://www.sporopollen.com) is created using MySQL (Schwartz et al., 2012) as the database server and Hypertext Preprocessor (PHP) (Rochkind and Adams, 2013) to create the dynamic website (see **Appendix 4-1** and **4-2**).

2.2.2 Data Collection

The collected data are incorporated in several independent datasets (**Figure 2-1**). Each column in a dataset is called a field. The first row in a dataset is used to store the field names which give a hint about the stored data. The other rows in a dataset are used to store the data including, for example, illustrations, descriptions, palaeoenvironmental proxies, and taxonomy of sporomorphs and their parent plants. One such row is also called a record. The fossil occurrences for both sporomorphs and non-sporomorphs are also collected. Different datasets can be linked to each other by the same fields if they have. Each dataset collects specific data, as follows:

2.2.2.1 Reference

All data collected from published resources are cited. Detailed reference information (year, title, author, journal/publisher, volume, issue, and pages) is included in the dataset *Reference* (**Table 2-1**). The attribute *Reference No* is the unique archive number, which identifies each reference in the whole database system.

Therefore, another dataset, such as *Occurrences*, does not need to include detailed reference information. By the attribute *Reference No*, the reference of each record in another dataset can be traced by linking the dataset to the dataset *Reference* (**Figure 2-1**, **Table 2-1**, and **Table 2-5**).

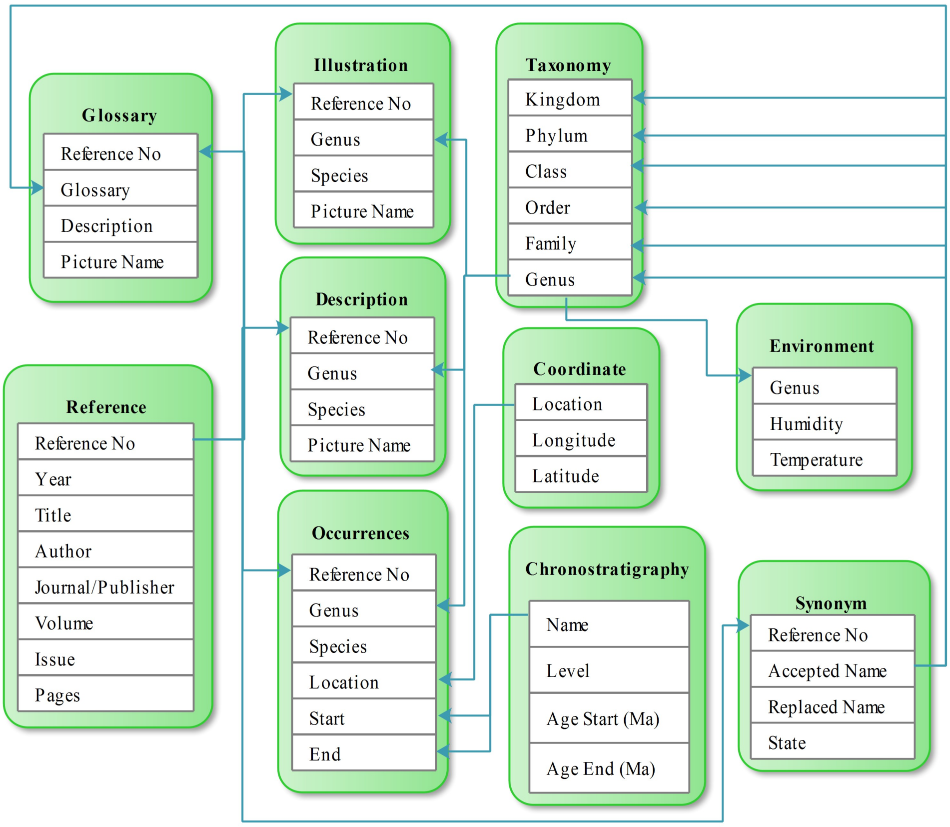


Figure 2-1 Dataset relation diagram (DRD) of database design.

Note: Each green box resembles a dataset, in which each white box resembles the field storing different data. Different datasets can be connected by the same fields (see the blue lines). For example, the datasets Description and Reference can be connected as a united dataset by the field of Reference No. In this way, the literature for a genus description can be easily traced.

2.2.2.2 Images

Descriptions and illustrations of plant or sporomorph species collected from the published literature are saved as images with the unique file name. They are separately stored in the dataset *Illustration* (**Table 2-2**) as well as the dataset *Description* (**Table 2-3**). Both the datasets include the fields of *Genus* and *Species*. The detailed reference information is stored in the datasets of *Reference*. Only the *Reference No* is included in these datasets. The field of *Picture Name* stores the file name of each description or illustration, by which the file can be traced.

2.2.2.3 Chronostratigraphic chart

Absolute ages of stratigraphic units are based on the International Chronostratigraphic Chart 2020 (Cohen et al., 2013) and are included in the dataset *Chronostratigraphy*. Four different units (levels) are used: era, period, epoch and age (**Table 2-4**).

2.2.2.4 Occurrences and Coordinates

Locality and stratigraphic range information for taxa are included in the dataset *Occurrences* (**Table 2-5**). Each locality is transformed into coordinate information according to Google Earth and included in the dataset *Coordinate* (**Table 2-6**). Linking the datasets *Occurrences* and *Coordinate* by their mutual field of *Location*, the spatial distribution of a taxon can be transformed into the coordinate system for easy visualization on maps.

Table 2-1 Part of the dataset *Reference* collecting reference details.

Reference No	Year	Title	Author	Journal/Publisher	Volume	Issue	Pages
13549	1983	The palynology of the Aalenian (Middle Jurassic) sediments of Jackdaw Quarry, Gloucestershire, England	Riding, J.B.	Mercian Geologist	9	2	111-187
9785	1957	Catalog of fossil spores and pollen Volume 1: Cretaceous and Tertiary Spores and Pollen	G. O. W. Kremp, H. T. Ames and H. Grebe	University Park, Pennsylvania			182
1043	1971	Catalog of fossil spores and pollen Volume 33: Cretaceous Pollen and Spores	A. Traverse and H. T. Ames	University Park, Pennsylvania			263
13549	1983	The palynology of the Aalenian (Middle Jurassic) sediments of Jackdaw Quarry, Gloucestershire, England.	Riding,J.B.	Mercian Geologist	9	2	111-187
4342	1955	Die Sporae dispersae des Ruhrkarbons, ihre Morphographie und Stratigraphie mit Ausblicken auf Arten anderer Gebiete und Zeitabschnitte	Potonié, R. and Kremp, G.O.W.	Palaeontographica	98		1-136
8732	2006	A classification for extant ferns	Smith, A. R. et al	Taxon	55	3	705-731
…	…	…	…	…			

Note: The attribute *Reference No* is the unique archive number, which identifies each reference in the whole database system. The other datasets do not need to include detailed reference information. Only include *Reference No* is enough to trace the reference.

Table 2-2 Part of the dataset *Illustration* containing illustrations for plants or sporomorphs.

Reference No	Genus	Species	Picture Name
9785	*Abies*	*concolipites*	Abies concolipites 2192812.jpg
…	…	…	…

Note: The detailed reference information is stored in the datasets of *Reference*. Each reference has a unique *Reference No* in the datasets of *Reference* which is also included in this dataset.

Table 2-3 Part of the dataset *Description* containing descriptions for plants or sporomorphs.

Reference No	Genus	Species	Picture Name
1043	*Appendicisporites*	*erdtmanii*	215_3(2014_4_11 12_25_31).jpg
…	…	…	…

Note: The detailed reference information is stored in the datasets of *Reference*. Each reference has a unique *Reference No* in the datasets of *Reference* which is also included in this dataset.

Table 2-4 Part of the dataset *Chronostratigraphy* for transferring stratigraphic units into absolute ages.

Name	Level	Age start (Ma)	Age end (Ma)
Aalenian	Age	174.1	170.3
Middle Jurassic	Epoch	174.1	163.5
Jurassic	Period	201.3	145.0
Mesozoic	Era	252.17	66.0
…		…	…

Note: Absolute ages of stratigraphic units are based on the International Chronostratigraphic Chart 2020.

Table 2-5 Part of the dataset *Occurrences* containing distributional details for plants or sporomorphs.

Reference No	Genus	Species	Location	Start	End
13549	*Classopollis*	*classoides*	Gloucestershire, England	Aalenian	Aalenian
…	…	…	…	…	…

Note: The detailed reference information is stored in the datasets of *Reference*. Each reference has a unique *Reference No* in the datasets of *Reference* which is also included in this dataset.

Table 2-6 Part of the dataset *Coordinate* for transferring location to coordinate.

Location	longitude	latitude
Gloucestershire, England	-2.238104°	51.864384°
…	…	…

Table 2-7 Part of the dataset *Glossary*.

Reference No	Glossary	Description	Picture Name
4342	Kyrtome	A more or less arcuate fold or band in the interradial areas outside the laesurae of trilete spores.	Kyrtome 20110821922.jpg
…	…	…	…

Note: The detailed reference information is stored in the datasets of *Reference*. Each reference has a unique *Reference No* in the datasets of *Reference* which is also included in this dataset.

Table 2-8 Part of the dataset *Synonym*.

Reference No	Accepted Name	Replaced Name
8732	Cyatheaceae	Alsophilaceae
…	…	…

Note: The detailed reference information is stored in the datasets of *Reference*. Each reference has a unique *Reference No* in the datasets of *Reference* which is also included in this dataset.

Table 2-9 Part of the dataset *Taxonomy*.

Kingdom	Phylum	Class	Order	Family	Genus
Plantae	Gymnospermae		Araucariales	Araucariaceae	*Araucariacites*
Plantae	Gymnospermae		Araucariales	Podocarpaceae	*Podocarpidites*
Plantae	Gymnospermae		Araucariales	Podocarpaceae	*Microcachryidites*
Plantae	Gymnospermae		Caytoniales	Caytoniaceae	*Vitreisporites*
Plantae	Gymnospermae		Corystospermales	Umkomasiaceae	*Alisporites*
Plantae	Gymnospermae		Cheirolepidiales	Cheirolepidiaceae	*Classopollis*
Plantae	Pteridophyta	Polypodiopsida	Cyatheales	Cyatheaceae	*Cyathidites*
Plantae	Pteridophyta	Polypodiopsida	Cyatheales	Cibotiaceae	*Cyatheacidites*
Plantae	Pteridophyta	Polypodiopsida	Gleicheniales	Gleicheniaceae	*Gleicheniidites*
Plantae	Pteridophyta	Polypodiopsida	Gleicheniales	Matoniaceae	*Matonisporites*
Plantae	Pteridophyta	Polypodiopsida	Osmundales	Osmundaceae	*Baculatisporites*
Plantae	Pteridophyta	Polypodiopsida	Polypodiales	Dennstaedtiaceae	*Leptolepidites*
Plantae	Pteridophyta	Polypodiopsida	Salviniales	Marsileaceae	*Crybelosporites*
Plantae	Pteridophyta	Polypodiopsida	Schizaeales	Lygodiaceae	*Concavissimisporites*
Plantae	Pteridophyta	Polypodiopsida	Schizaeales	Anemiaceae	*Cicatricosisporites*
Plantae	Pteridophyta	Lycopsida	Selaginellales	Selaginellaceae	*Ceratosporites*
…	…	…	…	…	…

Note: Based on literature and the unique outline and structure/sculpture of the sporomorph wall, the dispersed sporomorphs are compared with the modern and in situ fossil sporomorphs to link them to their closest parent plant (Zhang et al., 2021b).

2.2.2.5 Glossary, Synonym and Taxonomy

The sporomorph and plant glossary, synonym and systematic scheme mainly follow Balme (1995), Smith et al (2006), Punt et al (2007), Traverse (2007), Hesse et al (2009), Taylor et al (2009), Christenhusz et al (2011) and Byng et al (2016). The glossary descriptions and information for illustrations are included in the dataset *Glossary* (**Table 2-7**), the published synonyms for both plants and sporomorphs in the dataset *Synonym* (**Table 2-8**), and the plant systematic schemes in the dataset *Taxonomy* (**Table 2-9**). The systematic scheme of each genus of a dispersed sporomorph is also included in the dataset *Taxonomy*. Based on literature and the unique outline and structure/sculpture of the sporomorph wall, the dispersed sporomorphs are compared with the modern and in situ fossil sporomorphs to link them to their closest parent plant (Zhang et al., 2021b).

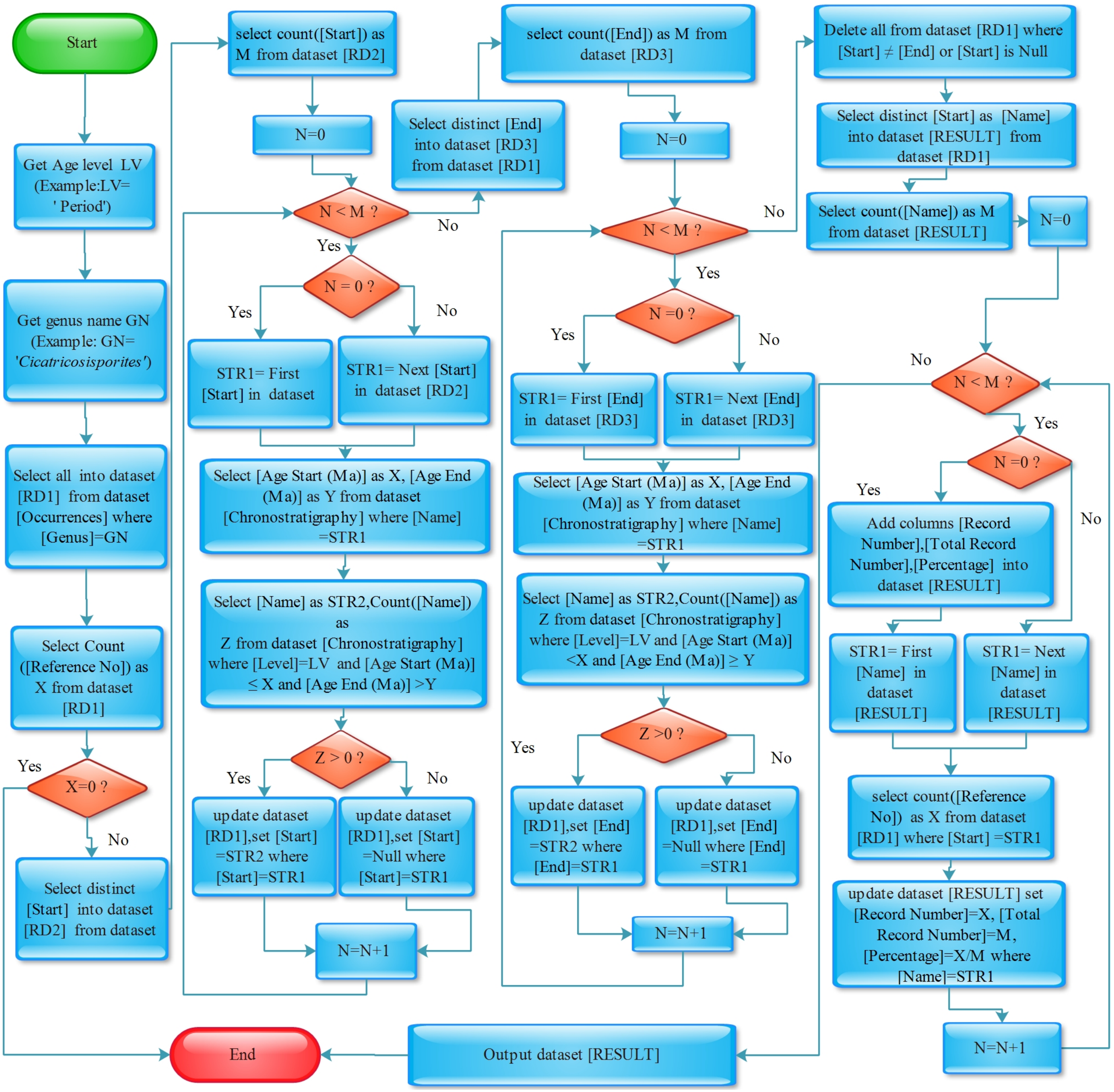


Figure 2-2 Flow chart of stratigraphic distribution estimation for a genus

Note: Dataset names and attribute names are in square brackets, e.g. [Reference No]. LV is the optional level, e.g. period; GN is the analyzed genus name, e.g. *Cicatricosisporites*; X, Y, Z, M, N, STR1, and STR2 are variables; RD1, RD2, and RD3 are temporary datasets; RESULT is the result dataset.

2.2.3 Algorithms

Different algorithms are used to upload, retrieve, filter, update and analyze data. The stratigraphic distribution of all taxa in the database can quickly be calculated separately at era, period, epoch, and age level. Data included in the dataset *Chronostratigraphy* (**Table 2-4**) and *Occurrences* (**Table 2-5**) are automatically retrieved and used. **Figure 2-2** presents the flow chart of the algorithm to get the stratigraphic distribution at different levels. **Table 2-10** presents the results for the fern genus *Cicatricosisporites* and **Figure 2-3** depicts the respective age distribution plot at four different age levels.

Table 2-10 The stratigraphic distribution pattern of the fern spore genus *Cicatricosisporites* at period level

Name	Record Number	Total Record Number	Percentage
Carboniferous	4	7820	0.051%
Permian	1	7820	0.013%
Triassic	664	7820	8.491%
Jurassic	383	7820	4.898%
Cretaceous	5582	7820	71.381%
Paleogene	985	7820	12.596%
Neogene	160	7820	2.046%
Quaternary	41	7820	0.524%

Note: 7820 records of *Cicatricosisporites* have been collected at the period level. Percentage= Record Number/ Total Record Number. For example, 5582 records of *Cicatricosisporites* have been collected from Cretaceous, so that 71.381% of records are from Cretaceous indicating the acme of *Cicatricosisporites* is Cretaceous. See **Figure 2-3** for detailed workflows and **Figure 2-4** for the age distribution plot based on it.

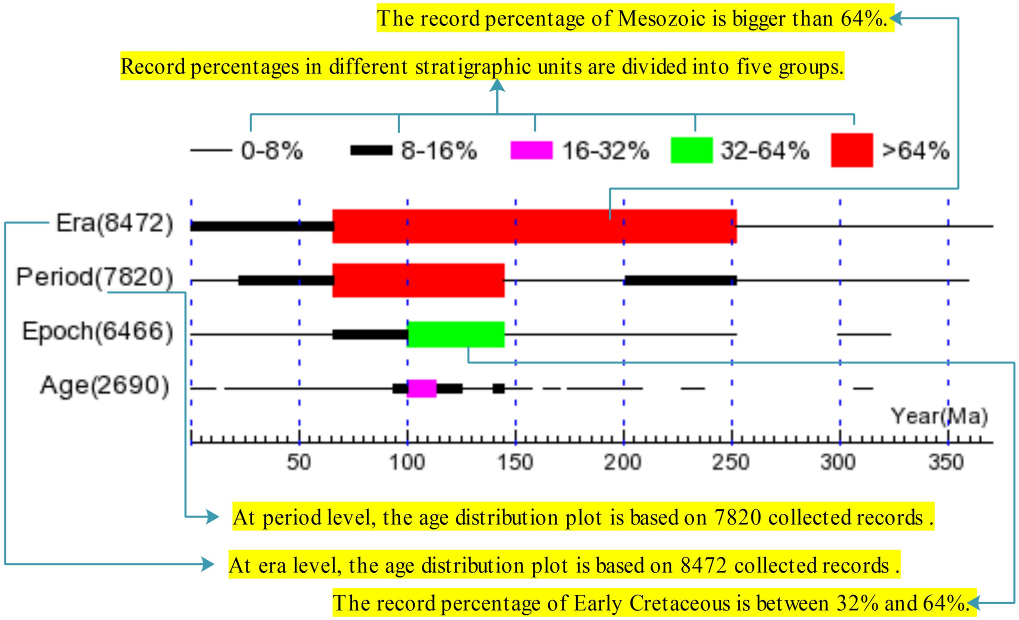
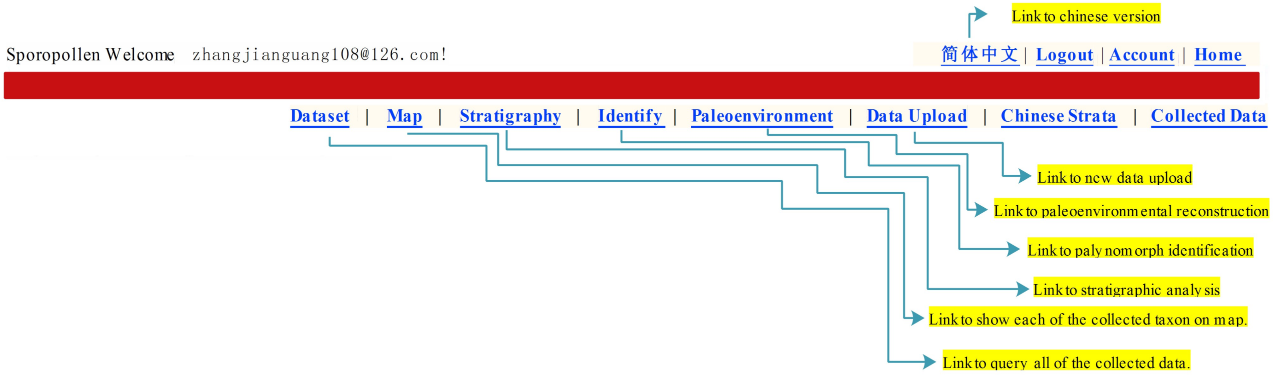


Figure 2-3 Age distribution plots for the fern *Cicatricosisporites* at era, period, epoch, and age levels

2.3 Interfaces

Currently, ***Sporopollen*** has collected 100,610 sporomorph pictures, 59,498 plant pictures, 31,922 sporomorph descriptions. At the same time, from 63,035 references, it has collected 2,215,162 occurrences for both sporomorph and non-sporomorph fossils. The collected plant data include 32, 972 genera from 946 families. The collected sporomorph pictures include 5,857 genera. To help users quickly get the data and also to protect the data, different interfaces are designed. An interface is part of the online webpage where interactions between users and this database occur. It allows effective operation and control of the database from the user end, whilst the database simultaneously feeds back information. It makes users easy, efficient, and enjoyable (user-friendly) to operate this database without knowing the tables, algorithms, and PHP codes that build up this database.


Sporopollen Welcome zhangjianguang108@126.com!

Link to chinese version

Link to new data upload

Link to paleoenvironmental reconstruction

Link to palynomorph identification

Link to stratigraphic analysis

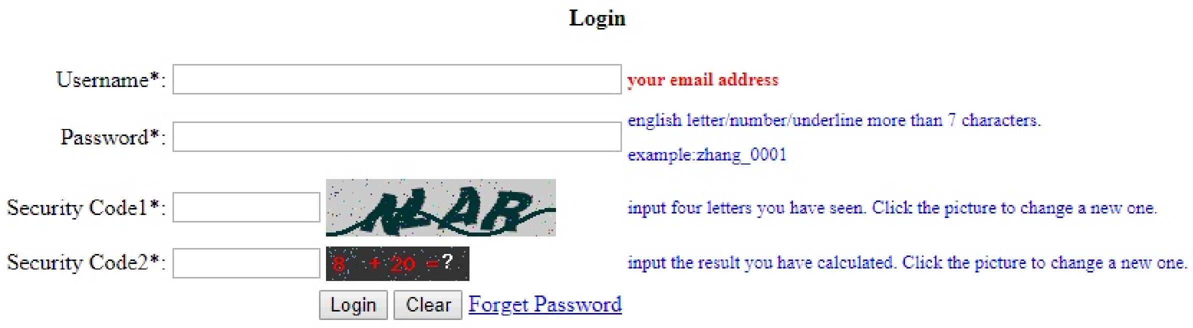
Link to show each of the collected taxon on map.

Link to query all of the collected data.

Figure 2-4 The account line and menu line for all of the webpages accessed by a login account.

Note: All current webpages support both Chinese and English. Click the button in Chinese on the up top of each webpage will switch from the English version to the Chinese version and vice versa. The blue characters under the red ribbon are menus that can guide the users to the specific interfaces.

For each webpage, the first line (account line) is mainly used to show the account information. If it is accessed by a login account, the account name will show up. It supports both Chinese and English. Click the button in Chinese will switch from the English version to the Chinese version and vice versa. Click the button *Logout* will log out the account safely. Click the button *Account* will get the account detail. Click the button *Home* will guide the user to the homepage of the website (**Figure 2-4**). If it is accessed by an anonymous account, the account name will not show up. The button *Account* will change to the button *Login* which will guide the user to the interface for login (**Figure 2-5**). The button *Logout* will change to the button *Register* which will guide the user to the interface for registration (**Figure 2-6**). The third line (menu line) is used for different menus which always use the characters in blue (**Figure 2-4**). Click different menus will guide the user to different interfaces. Under the menu line, different interfaces are created. Some important interfaces are described as following:


Login

Username*: your email address

Password*: english letter/number/underline more than 7 characters. example:zhang_0001

Security Code1*: input four letters you have seen. Click the picture to change a new one.

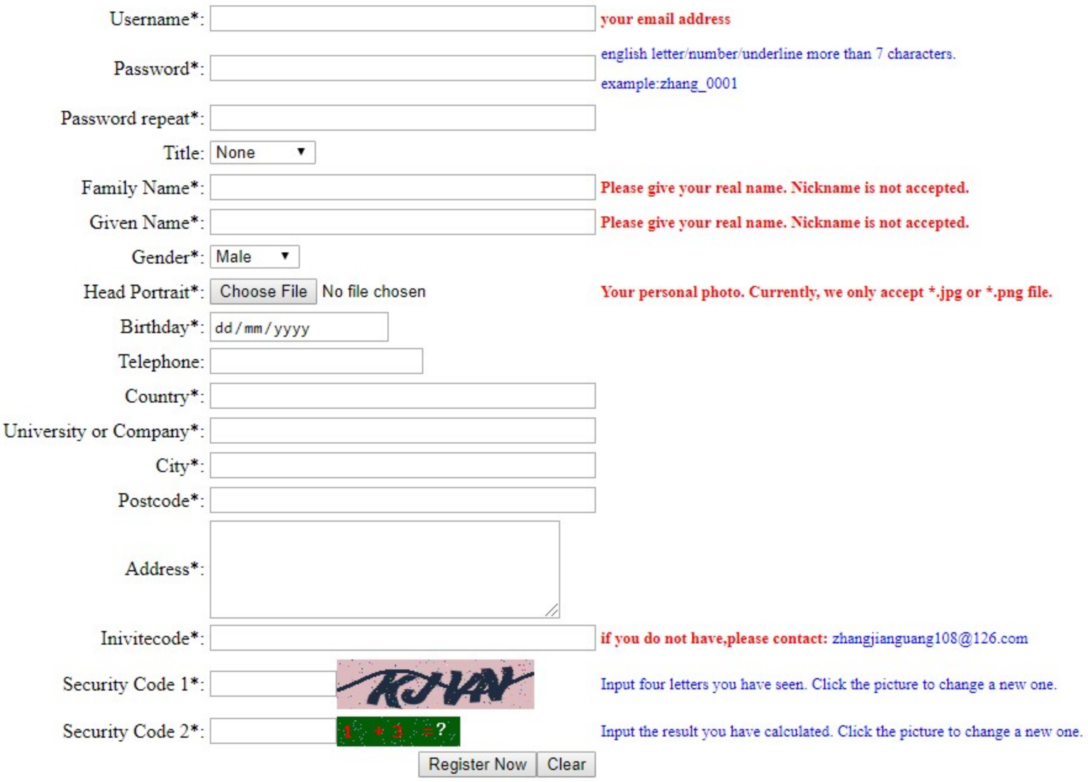
Security Code2*: input the result you have calculated. Click the picture to change a new one.

Figure 2-5 User interface for login: users who have an account must log in with their username and password.

Note: This interface is available at: http://www.sporopollen.com/sporelogin.php. The fields marked with the asterisk means they are required and should not be kept blank. Two security codes are used to defend against the robotic algorithms.

2.3.1 User organization interfaces

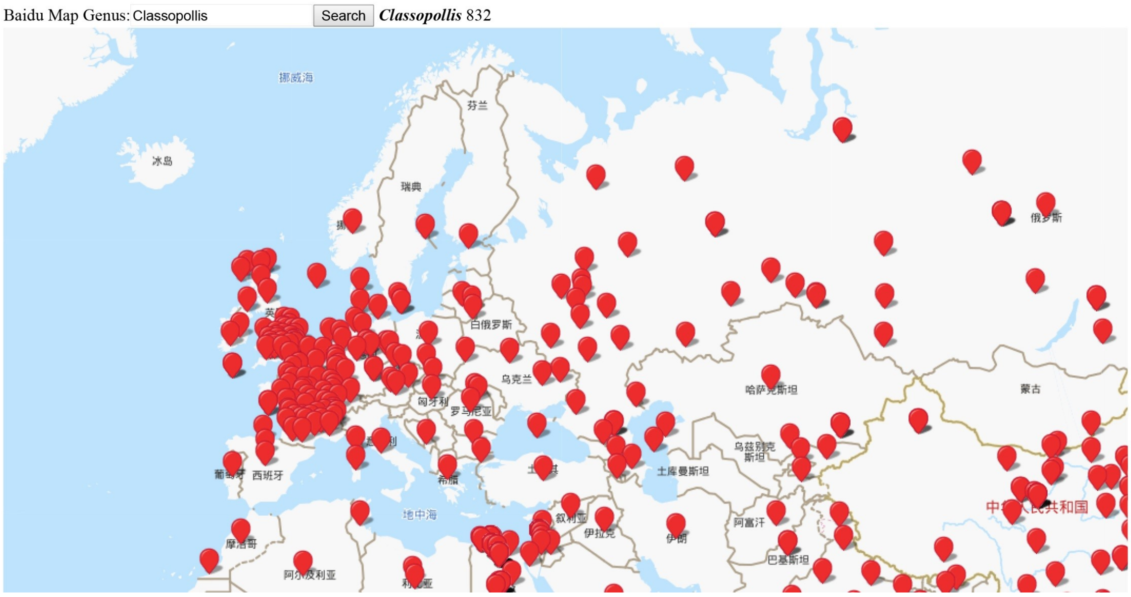
The full access to the collected data is only for scientific study for the peers who help to collect the data or who may contribute to this database. Users must log in with their username and password (**Figure 2-5**). New users need to get an invite code that can be used to create a new account (**Figure 2-6**). When they request an invite code, they must agree that all the data they submitted for a new account are allowed to be stored in this database. The collected information is used to identify the scientists and for possible scientific communication.



Username*: your email address
Password*: english letter/number/underline more than 7 characters. example:zhang_0001
Password repeat*:
Title: None
Family Name*: Please give your real name. Nickname is not accepted.
Given Name*: Please give your real name. Nickname is not accepted.
Gender*: Male
Head Portrait*: Choose File No file chosen Your personal photo. Currently, we only accept *.jpg or *.png file.
Birthday*: dd/mm/yyyy
Telephone:
Country*:
University or Company*:
City*:
Postcode*:
Address*:
Inivitecode*: if you do not have,please contact: zhangjianguang108@126.com
Security Code 1*: Input four letters you have seen. Click the picture to change a new one.
Security Code 2*: Input the result you have calculated. Click the picture to change a new one.

Figure 2-6 User interface for registration.

Note: This interface is available at: http://www.sporopollen.com/sporeregist.php. Any potential user must send an email to zhangjianguang108@126.com to get an invitecode. The fields marked with the asterisk means they are required and should not be kept blank. The collected information is used to identify the scientists and for possible scientific communication. Anonymous login is forbidden. When users request an invitecode, they must agree that all the data they submitted are allowed to be stored in this database. Two security codes are used to defend against the robotic algorithms.



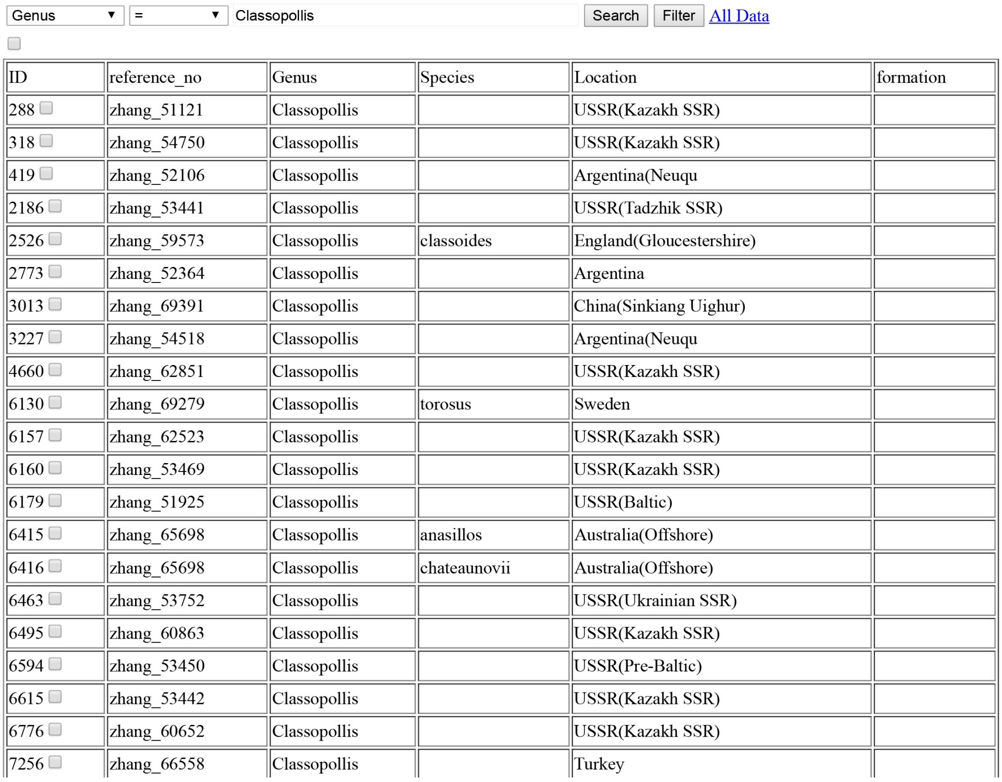
Baidu Map Genus: Classopollis *Classopollis* 832

Figure 2-7 Distribution of *Classopollis* queried on map.

Note: This interface is available at: http://www.sporopollen.com/sporemap.php?map=baidu&type=genus. It is designed to help users to find the occurrences on a map for a genus. Each red spot represents a location where the fossil is reported. Here is an example to find the occurrences of the genus *Classopollis*. 832 occurrences are collected in the database. Each red spot represents an occurrence.

2.3.2 Data query interfaces

Sporopollen provides some interfaces to query the occurrences of the collected fossils in the form of Map (**Figure 2-7**). Both Baidu map and Google map are available. The fossil can either be a genus name or a species name. Click the menu *Map* (**Figure 2-4**) will pop up the selection which guides the users to the specific interface. ***Sporopollen*** also provides some interfaces to query the collected data in the form of a dataset (**Figure 2-8**). All of the datasets in this database can be queried. Click the menu *Dataset* (**Figure 2-4**) will pop up the selection which guides the users to the specific interface.



ID	reference_no	Genus	Species	Location	formation
288 ☐	zhang_51121	Classopollis		USSR(Kazakh SSR)	
318 ☐	zhang_54750	Classopollis		USSR(Kazakh SSR)	
419 ☐	zhang_52106	Classopollis		Argentina(Neuqu	
2186 ☐	zhang_53441	Classopollis		USSR(Tadzhik SSR)	
2526 ☐	zhang_59573	Classopollis	classoides	England(Gloucestershire)	
2773 ☐	zhang_52364	Classopollis		Argentina	
3013 ☐	zhang_69391	Classopollis		China(Sinkiang Uighur)	
3227 ☐	zhang_54518	Classopollis		Argentina(Neuqu	
4660 ☐	zhang_62851	Classopollis		USSR(Kazakh SSR)	
6130 ☐	zhang_69279	Classopollis	torosus	Sweden	
6157 ☐	zhang_62523	Classopollis		USSR(Kazakh SSR)	
6160 ☐	zhang_53469	Classopollis		USSR(Kazakh SSR)	
6179 ☐	zhang_51925	Classopollis		USSR(Baltic)	
6415 ☐	zhang_65698	Classopollis	anasillos	Australia(Offshore)	
6416 ☐	zhang_65698	Classopollis	chateaunovii	Australia(Offshore)	
6463 ☐	zhang_53752	Classopollis		USSR(Ukrainian SSR)	
6495 ☐	zhang_60863	Classopollis		USSR(Kazakh SSR)	
6594 ☐	zhang_53450	Classopollis		USSR(Pre-Baltic)	
6615 ☐	zhang_53442	Classopollis		USSR(Kazakh SSR)	
6776 ☐	zhang_60652	Classopollis		USSR(Kazakh SSR)	
7256 ☐	zhang_66558	Classopollis		Turkey	

Figure 2-8 Distribution of *Classopollis* queried in Dataset.

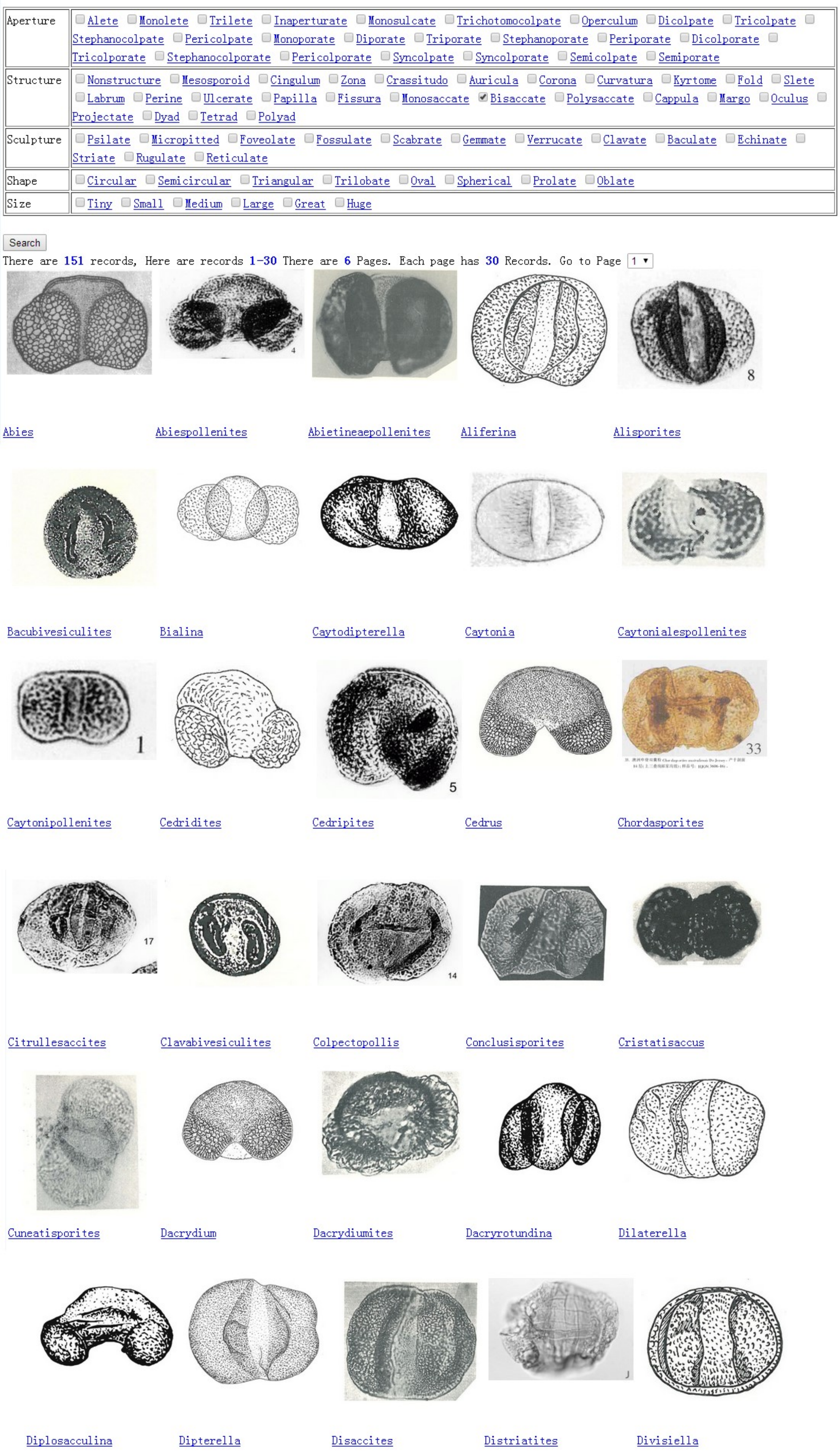
Note: This interface is designed to help users to find the occurrences in a dataset for a genus. It is available at: http://www.sporopollen.com/sporequery.php?table=occurrence. Here is an example to find the occurrences of the genus *Classopollis*. By the *Reference NO*, users can also get the reference detail for each record in the dataset *Reference* (see **Table 2-1**).

2.3.3 Spores and pollen identification interfaces

Potonie's Turmal System (Potonié, 1956, 1958, 1960, 1966, 1970; Potonié and Kremp, 1970), which arranges all sporomorphs by their aperture, structure, sculpture, shape, and size characters, is used to help users to identify sporomorph (**Figure 2-9**). The interface can be visited with a logged account at http://www.sporopollen.com/sporeidentify.php?operate=pollenidentifygenus.

2.3.4 Stratigraphic analysis interfaces

Based on the abundances for different stratigraphic units, age distribution plots can be automatically created for both a single genus/species (**Figure 2-10**) and a genus-group/species-group (**Figure 2-11**) separately at era, period, epoch, and age levels. It can give age distribution plots for both sporomorph and non-sporomorph taxa.



Aperture	☐ Alete ☐ Monolete ☐ Trilete ☐ Inaperturate ☐ Monosulcate ☐ Trichotomocolpate ☐ Operculum ☐ Dicolpate ☐ Tricolpate ☐ Stephanocolpate ☐ Pericolpate ☐ Monoporate ☐ Diporate ☐ Triporate ☐ Stephanoporate ☐ Periporate ☐ Dicolporate ☐ Tricolporate ☐ Stephanocolporate ☐ Pericolporate ☐ Syncolpate ☐ Syncolporate ☐ Semicolpate ☐ Semiporate
Structure	☐ Nonstructure ☐ Mesosporoid ☐ Cingulum ☐ Zona ☐ Crassitudo ☐ Auricula ☐ Corona ☐ Curvatura ☐ Kyrtome ☐ Fold ☐ Slete ☐ Labrum ☐ Perine ☐ Ulcerate ☐ Papilla ☐ Fissura ☐ Monosaccate ☑ Bisaccate ☐ Polysaccate ☐ Cappula ☐ Margo ☐ Oculus ☐ Projectate ☐ Dyad ☐ Tetrad ☐ Polyad
Sculpture	☐ Psilate ☐ Micropitted ☐ Foveolate ☐ Fossulate ☐ Scabrate ☐ Gemmate ☐ Verrucate ☐ Clavate ☐ Baculate ☐ Echinate ☐ Striate ☐ Rugulate ☐ Reticulate
Shape	☐ Circular ☐ Semicircular ☐ Triangular ☐ Trilobate ☐ Oval ☐ Spherical ☐ Prolate ☐ Oblate
Size	☐ Tiny ☐ Small ☐ Medium ☐ Large ☐ Great ☐ Huge

There are 151 records, Here are records 1-30 There are 6 Pages. Each page has 30 Records. Go to Page 1

Figure 2-9 Sporomorph identification interface: here is an example of identifying the bisaccate pollen.

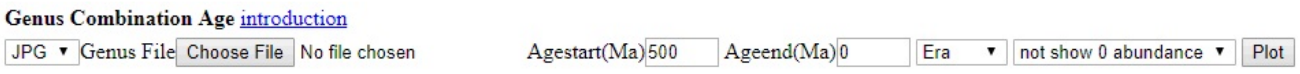
Note: This interface is available at: http://www.sporopollen.com/sporeidentify.php?operate=pollenidentifygenus. Aperture, structure, sculpture, shape, and size are categorized into several groups. By selecting the groups and clicking the Search button the user will get the result. Multiple selections are allowed.


Genus Age introduction

JPG Genus Cicatricosisporites Agestart(Ma) 375 Ageend(Ma) 0

Figure 2-10 Interface of age distribution plot for a single genus.

Note: This interface is available at: http://www.sporopollen.com/sporeexample.php?opterate=GenusAge. It is designed to help users to get the age distribution plot for a genus. Here is an example to show the distribution plot of the genus *Cicatricosisporites*. **Figure 2-3** is the result. Click the link of *introduction* will get the manual for this interface. Click the button of *Plot* will get the result as a JPG file.


Genus Combination Age introduction

JPG Genus File No file chosen Agestart(Ma) 500 Ageend(Ma) 0 Era not show 0 abundance

Figure 2-11 Interface of age distribution plot for a genus-group: currently, only *.csv files are accepted.

Note: This interface is available at: http://www.sporopollen.com/sporeanalyse.php?opterate=GenusCombinationAge. It is designed to help users to get the age distribution plot for a genus-group. Click the link of *introduction* will get the manual for this interface. Users need to upload the genus-group to this database by click the button of *Choose File*. Currently, only CSV file is accepted. Click the button of *Plot* will get the result as a JPG file. The example CSV file can be downloaded without login at: http://www.sporopollen.com/sporeexample.php?opterate=GenusCombinationAge

2.3.5 Spores and pollen affinity interfaces

Spores and pollen affinity can be queried taxonomically from kingdom to genus with open access. When the taxonomical rank is a genus, the related references will also show up (**Figure 2-12**). Currently, the literature includes Chinese, German, and English. Many German or Chinese references do not have an English title so that they are kept originally.


Abiespollenites

Plant Sporopollen Description

Kingdom: Plantae **Phylum:**Gymnospermae **Order:**Pinales **Family:**Pinaceae **Genus:**Abiespollenites

Pinaceae *Abiespollenites* **松辽盆地白垩纪石油地层孢粉学** 179
Pinaceae *Abiespollenites* **Versuch der Einordnung der fossilen Sporae dispersae in das phylogenetische System der Pflanzenfamilien** 137
Pinaceae *Abiespollenites* **Middle Miocene palynoflora of the Legnica lignite deposit complex, Lower Silesia, Poland** 23
Pinaceae *Abiespollenites* **The Eco-Plant model and its implication on Mesozoic dispersed sporomorphs for Bryophytes, Pteridophytes, and Gymnosperms** 20
Pinus armandi type pollen Organ Comparison
Pinaceae *Abiespollenites* **中国孢粉化石:中生代孢粉** 428 Abies LM Microscope
Pinaceae *Abiespollenites* **中国孢粉化石:晚白垩世和第三纪孢粉** 205 Abies LM Microscope
Pinaceae *Abiespollenites* **Catalog of fossil spores and pollen Volume 21: Early and Late Tertiary Spores and Pollen** 40 Abies LM Microscope

Figure 2-12 Interface of quickly get the plant affinities and related literature for the sporomorph genus.

Note: At http://www.sporopollen.com/sporeidentify.php?operate=taxonomy&taxonomy=Abiespollenites this interface is available with open access. All of the dispersed sporomorphs collected in this database can be queried by inserting the taxon in the white box and clicking the Search button beside it. Here is an example to show the affinity of ***Abiespollenites*** and the related references. Click the title of the references in blue will guide the user to the reference detail.

2.4 Summary

The online database ***Sporopollen*** (http://www.sporopollen.com) collects illustrations, descriptions, occurrences, and taxonomy of sporomorphs. Different user-friendly interfaces are created for data queries both on a map and in datasets, sporomorph identification, and stratigraphic analysis. Based on the literature, sporomorphs are linked to their parent plants. The age distribution plot for a sporomorph taxon or assemblage can be quickly used to reveal their stratigraphic distributions. Currently, full access to the database is only used for scientific study. It also provides some interfaces for open access, e.g., for all of the dispersed sporomorphs collected in this database, their plant affinities and related literature can be queried by an interface with open access at: http://www.sporopollen.com/sporeidentify.php?operate=taxonomy&taxonomy=Abiespollenites.

3. The Eco-Plant model and its implication on Mesozoic dispersed sporomorphs for Bryophytes, Pteridophytes, and Gymnosperms

Published article

Zhang, J., Lenz, O.K., Wang, Y., Hornung, J., 2021. The Eco-Plant model and its implication on Mesozoic dispersed sporomorphs for Bryophytes, Pteridophytes, and Gymnosperms. Review of Palaeobotany and Palynology.

https://doi.org/10.1016/j.revpalbo.2021.104503

Abstract

The ecogroup classification based on the growth-form of plants (Eco-Plant model) is widely used for extant, Cenozoic, Mesozoic, and Paleozoic palaeoenvironmental reconstructions. However, for most Mesozoic dispersed sporomorphs, the application of the Eco-Plant model is limited because either their assignment to a specific ecogroup remains uncertain or the botanical affinities to plant taxa are unclear. By comparing the unique outline and structure/sculpture of the wall of dispersed sporomorph to the sporomorph wall of modern plants and fossil plants, 861 dispersed Mesozoic sporomorph genera of Bryophytes, Pteridophytes, and Gymnosperms are reviewed. Finally, 474 of them can be linked to their closest parent plants and Eco-Plant model at family or order level. Based on the demands of the parent plants to different humidity conditions, the Eco-Plant model separates between hydrophytes, hygrophytes, mesophytes, xerophytes, and euryphytes. Additionally, due to different temperature demands a separation in megathermic, mesothermic, microthermic, and eurythermic plants is possible. In the Mesozoic, both spore-producing and pollen-producing plants are adapted to different kinds of humidity. The concept to use the spore/pollen ratio to reflect the hygrophytes/xerophytes ratio is therefore questionable. The presented ecogroups for dispersed Mesozoic sporomorphs now allow identifying at least relative plant, palaeoenvironmental and paleoclimate changes in Mesozoic sedimentary records.

3.1 Introduction

The ecogroup classification based on the growth-form of plants (Eco-Plant model), established by the pioneering work of Warming (1895) and Schimper (1898), who analyzed diverse plant associations with relation to the principal climatic elements such as water, heat, light, and air, is widely used for extant (e.g., Baeza et al., 2010; Godin, 2017; Sheremetov and Sheremetova, 2017; Veisberg, 2017), Cenozoic (e.g., Bozukov et al., 2009; Yang et al., 2013; Yurtsev, 2001), Mesozoic (e.g., Hill, 2017; Vakhrameev, 1991), and Paleozoic palaeoenvironmental reconstructions (e.g., Bashforth et al., 2014; Wang, 1999b). The Eco-Plant model is also used by palynologists for dispersed sporomorphs from the Cenozoic (e.g., Aranbarri et al., 2014; Kern et al., 2012; Popescu et al., 2006; Suc and Fauquette, 2012) and Mesozoic (e.g., Césari and Colombi, 2016; Hochuli and Vigran, 2010; Mueller et al., 2016; Roghi et al., 2010; Visscher and van der Zwan, 1981; Wang et al., 2013; Wang et al., 2005; Zhang et al., 2020; Zhao et al., 2014) for palaeoenvironmental reconstructions. The sporomorph ecogroup model (SEG model) of Abbink et al. (2004b) is also commonly used to reconstruct the palaeoenvironment and its changes of Mesozoic records in Europe and some parts of China (e.g., Abbink et al., 2001; Abbink et al., 2004a; Abbink et al., 2004b; Heunisch et al., 2010; Li and Wang, 2016; Li et al., 2016). The SEG model represents a simplified Eco-Plant model. According to hydrologic and temperature conditions, the Eco-Plant model classifies plants into different EPH (the effect of humidity) and EPT (the effect of temperature) groups due to their climatic preferences (Zhang et al., 2020). In contrast, in the SEG model, plants are classified as belonging to a wetter, drier, warmer, or cooler group. Additionally, in the SEG model (Abbink et al., 2004b), due to uncertain botanical affinities of some palynomorphs, several plants indicating a different climate and environment are categorized in the same group. For example, in the Eco-Plant model, GINKGOALES Gorozhankin are classified as mesophytes and mesothermic plants, but BENNETTITALES

Engler as hygrophytes and megathermic plants (Zhang et al., 2020). In contrast, in the SEG model, GINKGOALES Gorozhankin, CYCADALES Persoon ex Berchtold et Presl, and BENNETTITALES Engler are all included in the same group of the "Lowland SEG" and indicate a "drier" and "warmer" climate, since the pollen of GINKGOALES Gorozhankin, CYCADALES Persoon ex Berchtold et Presl, and BENNETTITALES Engler can usually only be distinguished under scanning electron microscopy (SEM) or transmission electron microscopy (TEM) (Abbink et al., 2004b). Therefore, the Eco-Plant model allows for more detailed and precise statements on palaeoclimate than the SEG model. However, for most Mesozoic dispersed sporomorphs, the application of the Eco-Plant model is limited, because either their assignment to a specific ecogroup remains uncertain or the botanical affinities to plant taxa are unclear. Therefore, it is most important to identify their botanical affinities, because otherwise, their Eco-Plant model implications are not reliable (Zhang et al., 2020). In the last decades, dispersed sporomorphs (e.g., Song et al., 1999; Song et al., 2000; Traverse, 2007), *in situ* sporomorphs of fossils (e.g., Balme, 1995; van Konijnenburg-van Cittert, 1971), and sporomorphs of extant plants (e.g., Gosling et al., 2013; Hesse et al., 2009; Li et al., 2011) had been well studied and described, which provide data to link dispersed sporomorphs convincingly to their parent plants. Different authors have published compilations of fossil sporomorphs, which have been linked to plant taxa (e.g., Balme, 1995; Muller, 1981; Potonié, 1967; Song et al., 2004). However, a systematic review is needed to effectively accelerate a scientific solution on the debates focusing on linking sporomorphs to parent plants. Here, we focus especially on Mesozoic dispersed sporomorphs of Bryophytes, Gymnosperms, and Pteridophytes and link them to their possible parent plants and ecogroups.

3.2 Materials and methods

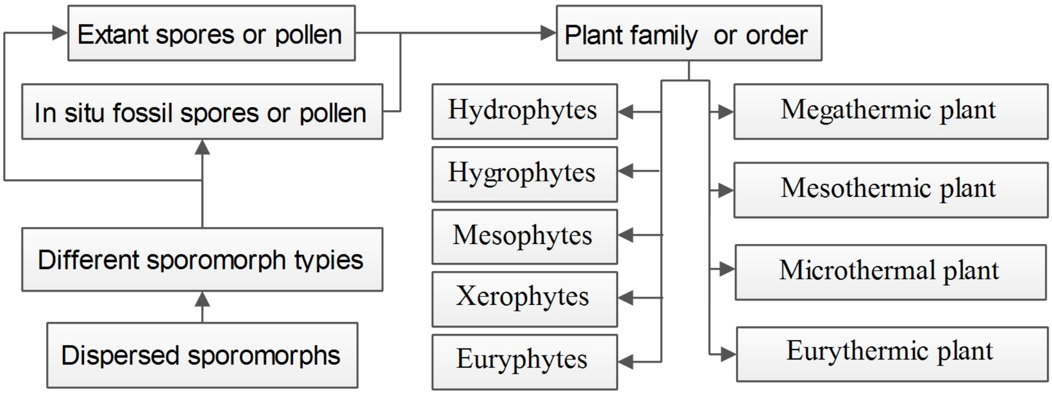


Figure 3-1 Flow chart of linking dispersed sporomorphs with plant categories related to Eco-Plant model

To discuss the Eco-Plant model for dispersed sporomorph genera of Bryophytes, Pteridophytes, and Gymnosperms from the Mesozoic, *in situ* sporomorphs from extant and fossil plants are categorized into different "sporomorph types" based on their unique outline, structure/sculpture of the sporomorph wall. The "sporomorph types" and plant taxa are completely different entities because they are characterized according to sporomorph morphology, including one or more species as taxonomic categories (De Klerk and Joosten, 2007; Joosten and de Klerk, 2002). We use one of the species names for *in situ* or extant spores or pollen to name the different "sporomorph types". The spores or pollen grains that belong to the same "sporomorph types" should share the same stable characters (***key characters***), which can be used to distinguish them from the other types. Each of the "sporomorph types" should come from a single plant family or order. By comparing the ***key characters*** of each type, dispersed sporomorphs are linked to their parent plants at the family or order level. The Eco-Plant model of the dispersed sporomorphs can therefore be discussed based on the related plant family or order (**Figure 3-1**). The dispersed sporomorph genera whose descriptions and illustrations do not fully meet the ***key characters*** of a specific sporomorph type or the ultrastructure is unclear so that can not be compared to the ***key characters*** of a specific sporomorph type ultrastructurally, but are most likely related to this type are followed by "[?]". Those which are accepted or supposed as synonyms by published studies are followed by "[S]". More *in situ* or extant sporomorphs are collected, but to limit the length of this paper we only list a part of them. For some sporomorph genera, the parent plants have been discussed by other authors in published studies. We cite the important studies in the "***Remarks***" part. As the reference is always provided, for simplification only the genus of the parent plants is listed in the "***Remarks***" part. For example, Dettmann (1963) stated that the dispersed spore ***Ceratosporites*** de Jersey et Paten is comparable to the spore of extant ***Selaginella** latifrons* Warburg, while Scafati et al. (2009) reported that ***Ceratosporites*** de Jersey et Paten is comparable to the spore of extant ***Selaginella** tenuispinulosa* Krasnova, but in this paper, we only describe that "***Ceratosporites*** de Jersey et Paten is comparable to the spore of extant ***Selaginella*** de Beauvois (Dettmann, 1963; Scafati et al., 2009)". All of the references, which are used for our study, including those which are not cited in this paper, can be found by choosing a sporomorph genus in the online database (http://www.sporopollen.com/sporefamilygenus.php) (Zhang et al., 2021a).

The sporomorph glossary used in this paper mainly follows Punt et al (2007) and Traverse (2007). The systematic scheme of extant plants is based on Christenhusz et al. (2011) for gymnosperms, Söderström et al. (2016) for hornworts and liverworts, Goffinet and Buck (2004) for mosses, and Schuettpelz et al. (2016) for lycophytes and ferns. The systematic scheme of fossil plants mainly follows Taylor et al. (2009). For figures, descriptions, and definitions of dispersed sporomorphs, we refer to Jiang et al. (2016), Huang (2008), Liu (2003), Shang (2011), Song et al. (1999), Song et al. (2000), Shu and Norris (1999), the 6 volumes book series of *Synopsis der Gattungen der Sporae dispersae* (Potonié, 1956, 1958, 1960, 1966, 1970; Potonié and Kremp, 1970), and the 26 volumes book series of *Catalog of fossil spores and pollen* (Ames and Spackman, 1985; Ames et al., 1976; Kremp and Ames, 1959, 1961b, 1962a, b, 1965a, b; Kremp et al., 1957a, b; Kremp et al., 1958, 1959, 1960a, b; Kremp et al., 1966; Kremp et al., 1967, 1968; Traverse and Ames, 1968, 1969, 1971, 1979; Traverse et al., 1973a, 1974, 1975; Traverse et al., 1969). Figures and descriptions of extant sporomorphs can mainly be found in Zhang et al. (2006), Wang and Dai (2010), Li et al. (2011), Tryon and Lugardon (1991), Hesse et al. (2009), Boros and Járai-Komlódi (1975), and Kramer and Green (1990). To easily find the figures and descriptions of the pollen and spores, which are mentioned in this paper, the references are given together with plate and figure numbers.

To manage all the information presented in the huge amount of literature data, it is necessary to store all the figures, descriptions, plant properties and related references in a database. Therefore, all information compiled in this paper was collected and organized in our database ***Sporopollen*** (http://www.sporopollen.com) (Zhang et al., 2021a).

For the analysis of palaeoenvironmental and palaeoclimate variations, this paper uses the Eco-Plant model modified by Zhang et al. (2020):

EPH (the effect of humidity) separates the palynomorphs and their parent plants into five groups:

a) *Hydrophytes* are aquatic plants that are completely or mostly submerged in water as well as being amphibious plants that grow both in water and in excessively wet habitats along the shorelines of reservoirs, in areas of shallow water, and swamps.

b) *Hygrophytes* are plants that are living in excessively wet habitats with high air and soil moisture but usually no water stagnation on the surface, such as the lower tiers of wet forests, or open habitats with constantly wet soils and wet air.

c) *Mesophytes* are plants that have some ability to resist periods of drought or to regulate their water metabolism in moist areas such as dry meadows or pine forests.

d) *Xerophytes* are plants that can resist long periods of drought and are living in stony steppes and dry rock outcrops.

e) *Euryphytes* are plants that adapt to great variations in humidity.

EPT (the effect of temperature) categorizes the palynomorphs and their parent plants into four groups:

a) *Megathermic* plants inhabiting regions such as tropics and subtropics with a mean annual air temperature (MAT) above 20 °C.

b) *Mesothermic* plants inhabiting regions such as warm temperate zones with a MAT between 14 to 20 °C.

c) *Microthermic* plants inhabiting regions such as the cool temperate zone, the subarctic zone, or elevated areas with a MAT below 14 °C.

d) *Eurythermic* plants that can tolerate a wide range of temperatures.

3.3 Results

Table 3-1 Mesozoic plants and their assignment to Eco-Plant model indicating humidity (EPH) as well as temperature (EPT) demands

Phylum	Family / Order	EPH	EPT
Bryophytes	Anthocerotaceae	hygrophytes	eurythermic
	Encalyptaceae	euryphytes	microthermic
	Naiaditaceae	hydrophytes	
	Notothyladaceae	hygrophytes	eurythermic
	Ricciaceae	hygrophytes	eurythermic
	Sphagnales	hydrophytes	eurythermic
Pteridophytes	Anemiaceae	mesophytes	megathermic
	Cyatheales	hygrophytes	megathermic
	Equisetales	hygrophytes	eurythermic
	Gleicheniales	mesophytes	megathermic
	Hymenophyllaceae	hygrophytes	eurythermic
	Isoetales	hydrophytes	eurythermic
	Lycopodiales	hygrophytes	eurythermic
	Lygodiaceae	hygrophytes	megathermic
	Marattiales	hygrophytes	megathermic
	Ophioglossaceae	mesophytes	eurythermic
	Osmundales	hygrophytes	eurythermic
	Polypodiaceae	mesophytes	megathermic
	Pteridaceae	euryphytes	eurythermic
	Salviniales	hydrophytes	megathermic
	Schizaeaceae	mesophytes	megathermic
	Selaginellaceae	euryphytes	eurythermic
Gymnospermae	Araucariaceae	hygrophytes	megathermic
	Bennettitales	hygrophytes	megathermic
	Caytoniaceae	hygrophytes	megathermic
	Cheirolepidiaceae	xerophytes	megathermic
	Corystospermales	mesophytes	megathermic
	Cupressaceae	euryphytes	eurythermic
	Cycadales	mesophytes	megathermic
	Czekanowskiales	mesophytes	mesothermic
	Ephedraceae	xerophyte	eurythermic
	Erdtmanithecaceae	xerophytes	eurythermic
	Ginkgoales	mesophytes	mesothermic
	Palissyaceae	hygrophytes	megathermic
	Peltaspermales	xerophytes	megathermic
	Pinaceae	mesophytes	microthermic
	Podocarpaceae	hygrophytes	megathermic
	Sciadopityaceae	hygrophytes	microthermic
	Voltziales	xerophytes	megathermic
	Welwitschiaceae	xerophytes	megathermic

In total, 861 dispersed Mesozoic sporomorphs genera of Bryophytes, Pteridophytes, and Gymnosperms, are reviewed. Among them, 474 can be linked to their closest parent plants at family or order level, 387 (**Appendix 3-1**) cannot because of the lack of detailed ultrastructure description. The ecogroups (EPH and EPT) of 40 plant families or orders whose fossil plants or dispersed sporomorphs can be found in the Mesozoic are listed in **Table 3-1**. The result can be downloaded online (http://www.sporopollen.com/sporefamilygenus.php). Below, dispersed sporomorph genera from the Mesozoic are linked to the different ecogroups:

3.3.1 Bryophytes

3.3.1.1 Family: ANTHOCEROTACEAE Dumortier

Species of extant ANTHOCEROTACEAE Dumortier can be found in tropical, subtropical, and temperate areas growing on the edge of forests or on moist soils (Verma et al., 2014; Zhang et al., 2006). They are hygrophytes and eurythermic plants.

***Anthoceros formosae* type isospore**

Extant spore: ***Anthoceros*** *cristatus* Stephani (Villarreal et al., 2015; p. 93, Pl. 1, Figs. A-B)
Extant spore: ***Anthoceros*** *formosae* Stephani (Zhang et al., 2006; p. 218, Pl. 76, Figs. 5-7)
Extant spore: ***Folioceros*** *fusciformis* (Montagne) Bharadwaj (Zhang et al., 2006; p. 219, Pl. 77, Figs. 1-6)

Key characters: This type of isospore is trilete, circular, generally 25-50 µm in size, with laesurae reaching the edge of the exospore. The exospore is scattered by irregular biform sculptures consisting of a broad base surmounted by one, or more than one relatively smaller spines or bacula.

Dispersed spores: The five dispersed isospore genera related to this type are ***Anthocerisporis*** Krutzsch, ***Bryosporis*** Mildenhall [?], ***Rudolphisporis*** Krutzsch, ***Saxosporis*** Krutzsch [?], and ***Saxosporites*** Nagy [?].

Remarks: ***Anthocerisporis*** Krutzsch, ***Rudolphisporis*** Krutzsch, ***Saxosporis*** Krutzsch, and ***Saxosporites*** Nagy are comparable to spores of extant ***Anthoceros*** Linnaeus (Ames and Spackman, 1985; Barreda et al., 2009; Huang et al., 2021; Potonié, 1966).

3.3.1.2 Family: ENCALYPTACEAE Schimper

Species of extant ENCALYPTACEAE Schimper (Goffinet and Buck, 2004) are mostly distributed in high mountain or glacial related regions (Gao et al., 1996; Horton, 1978). ***Bryobrittonia*** Williams occur most commonly in sandy or silty soils along streams or rivers where the substrate is constantly moist, while ***Encalypta*** Hedwig can be found in bogs, on arid ground, or rocks. They are euryphytes and microthermic plants.

***Encalypta ciliata* type isospore**

Extant spore: ***Encalypta*** *ciliata* Hedwig (Boros and Járai-Komlódi, 1975; p. 138, Figs. 1-8)
Extant spore: ***Encalypta*** *ciliata* Hedwig (Vitt and Hamilton, 1974; Pl. III, Figs. 18-19)
Extant spore: ***Encalypta*** *ciliata* Hedwig (Zhang et al., 2006; p. 230, Pl. 98, Figs. 4-6)

Key characters: This type of isospore is trilete, generally 30 - 40 µm in size, with indistinct laesurae. One of its faces exhibits a very characteristic central brochus with radial arms running to the equator.

Dispersed spore: The dispersed isospore genus related to this type is ***Staplinisporites*** Pocock.

Remarks: ***Staplinisporites*** Pocock is comparable to spores of extant ***Encalypta*** Hedwig (Cranwell and Srivastava, 2009; Dettmann, 1963; Potonié, 1966).

***Encalypta rhabdocarpa* type isospore**

Extant spore: ***Encalypta*** *rhabdocarpa* Schwägrichen (Zhang et al., 2006; p. 231, Pl. 99, Figs. 1-6)
Extant spore: ***Encalypta*** *spathulata* Müller (Zhang et al., 2006; p. 232, Pl. 100, Figs. 1-4)
Extant spore: ***Encalypta*** *vulgaris* (Hedwig) Hofmann (Vitt and Hamilton, 1974; Pl. VI, Figs. 32-37)

Key characters: This type of isospore is trilete, generally 25 - 40 µm in size, with indistinct laesurae. The sporoderm is covered by verrucae. On top of the verrucae, some irregular elements are often distributed.

Dispersed spore: The dispersed isospore genus related to this type is ***Encalyptaesporites*** Nagy.

Remarks: ***Encalyptaesporites*** Nagy is comparable to spores of extant ***Encalypta*** Hedwig (Ames and Spackman, 1985).

3.3.1.3 Family: NAIADITACEAE Schuster ex Katagiri et Hagborg

The family NAIADITACEAE Schuster ex Katagiri et Hagborg is a monogeneric family based on the fossil genus ***Naiadita*** Brodie from the Mesozoic (Katagiri and Hagborg, 2015). The abundance of fossil ***Naiadita*** Brodie, together with its mode of preservation suggests that it is a submerged fresh-water plant in a shallow lake (Harris, 1938; Hemsley, 1989). They are hydrophytes.

Naiadita lanceolata type isospore

In situ **spore:** ***Naiadita*** *lanceolata* Buckman (Hemsley, 1989; p. 92, Pl. I, Figs. 1-6; p. 94, Pl. II, Figs. 1-6)
In situ **spore:** ***Naiadita*** *lanceolata* Buckman (Harris, 1938; p. 46 Figs. 21.A-L; p. 47 Figs. 22.A-D)

Key characters: This type of isospore is more or less sub-triangular to circular in outline with an thin equatorial flange (zona) and a hilum (an irregular break) in the center of the proximal or distal face. The isospores can be 100 µm in size but sometimes rather smaller. The Y mark is invisible. The proximal face of the spore bears many small pointed spines whilst the distal face is covered with less densely spaced, but larger tuberculate to clavate projections.

Dispersed spores: The three dispersed isospore genera related to this type are ***Cooksonites*** Pocock [?], ***Coptospora*** Dettmann [?], and ***Couperisporites*** Pocock.

Remarks: ***Couperisporites*** Pocock is comparable to *in situ* spores of ***Naiadita*** Brodie (Dettmann, 1963; Potonié, 1966).

3.3.1.4 Family: NOTOTHYLADACEAE Müller ex Proskauer

Species of extant NOTOTHYLADACEAE Müller ex Proskauer (Söderström et al., 2016) can be found in moist soils from warm tropical regions to cold circumboreal regions (Boros and Járai-Komlódi, 1975; Zhang et al., 2006). They are hygrophytes and eurythermic plants.

Phaeoceros skottsbergii type isospore

Extant spore: ***Notothylas*** *levieri* Schiffner (Chantanaorrapint, 2015; p. 260, Figs. 27-28)
Extant spore: ***Notothylas*** *levieri* Schiffner (Zhang et al., 2006; p. 81, Figs. 3-6)
Extant spore: ***Phaeoceros*** *skottsbergii* Stephani (Warny et al., 2012; p. 241, Pl. 5, Figs. 5-6)

Key characters: This type of isospore is trilete, generally 25-50 µm in size. The exospore is considerably thick, and usually thicker in the distal rather than the proximal face. On the distal face, there is often a characteristic projection which can be a solid circle, a hollow circle, or concentric rings.

Dispersed spores: The ten dispersed isospore genera related to this type are ***Annulispora*** de Jersey, ***Dicyclosporis*** Schulz [S], ***Distalanulisporites*** Klaus [S], ***Distcyclosporis*** Schulz [S], ***Guyangspora*** Yu et Miao [?], ***Neochomotriletes*** Reinhardt [S], ***Parmulisporis*** Bai [?], ***Phaeocerosporites*** Nagy, ***Polycingulatisporites*** Simoncsics et Kedves [?], and ***Taurocusporites*** Stover [S].

Remarks: ***Annulispora*** de Jersey is comparable to spores of extant ***Notothylas*** Sullivant and ***Phaeoceros*** Proskauer(Zhang et al., 2020). ***Phaeocerosporites*** Nagy is comparable to spores of extant ***Phaeoceros*** Proskauer both in the order of magnitude and morphology (Ames and Spackman, 1985). ***Dicyclosporis*** Schulz, ***Distcyclosporis*** Schulz, and ***Distalanulisporites*** Klaus are synonyms of ***Annulispora*** de Jersey (McKellar, 1974; Potonié, 1966). ***Neochomotriletes*** Reinhardt and ***Taurocusporites*** Stover are synonyms of ***Polycingulatisporites*** Simoncsics et Kedves (Potonié, 1966, 1970). ***Annulispora*** de Jersey is distinguished from ***Polycingulatisporites*** Simoncsics et Kedves by possessing a single, distal, sub-circular ridge, whereas the latter genus is characterized by forms displaying two distal ridges that are concentrically situated with respect to the pole (McKellar, 1974).

***Paraphymatoceros diadematus* type isospore**

Extant spore: ***Notothylas*** *yunannensis* Peng & Zhu (Rattanamanee and Chantanaorrapint, 2015; p. 272, Pl. 1, Figs. C-D)

Extant spore: ***Paraphymatoceros*** *coriaceus* (Stephani) Stotler (Crandall-Stotler et al., 2008; p. 228, Pl. 5, Figs. 5-6)

Extant spore: ***Paraphymatoceros*** *diadematus* Hässel (Crandall-Stotler et al., 2008; p. 228, Pl. 5, Figs. 2-4)

Key characters: This type of isospore is trilete, generally 25-60 μm in size. The proximal face is divided into three flattened facets by laesurae. In the center of each facet, there is a hollow, which is often surrounded by a radial sculpture.

Dispersed spores: The five dispersed isospore genera related to this type are ***Asterisporites*** Venkatachala et Rawat [S], ***Foraminisporis*** Krutzsch, ***Nevesisporites*** de Jersey et Paten, ***Simeonospora*** Balme [S], and ***Trisolissporites*** Tschudy [S].

Remarks: ***Foraminisporis*** Krutzsch and ***Nevesisporites*** de Jersey et Paten are comparable to spores of extant ***Phaeoceros*** Proskauer and ***Notothylas*** Sullivant ex Gray (Dettmann, 1963; Nemejc and Pacltova, 1972; Potonié, 1966; Schrank, 2010). ***Asterisporites*** Venkatachala et Rawat, ***Simeonospora*** Balme, and ***Trisolissporites*** Tschudy are synonyms of ***Nevesisporites*** de Jersey et Paten (Song et al., 1999).

3.3.1.5 Family: RICCIACEAE Reichenbach

Species of extant RICCIACEAE Reichenbach (Söderström et al., 2016) can be found in warm tropical regions to cold circumboreal regions. Most of them live in wet environments and some of them float on water (Boros and Járai-Komlódi, 1975; Zhang et al., 2006). They are generally hygrophytes and eurythermic plants.

***Riccia frostii* type isospore**

Extant spore: ***Riccia*** *frostii* Austin (Boros and Járai-Komlódi, 1975; p. 51, Figs. 1-6)

Extant spore: ***Riccia*** *glauca* Linnaeus (Zhang et al., 2006; p. 140, Pl. 8, Fig. 3; p. 207 Pl. 75, Figs. 2-6)

In situ **spore:** ***Ricciopsis*** *sp.* (Volkheimer and Scafati, 2007; p. 127, Pl. 3, Fig. 3)

Key characters: This type of isospore is trilete, generally 50-90 μm in size, triangular, with a reticulate sculpture. On the equator there is an opening on each triangular corner. For some spore grains the thin equatorial flange (zona) is visible.

Dispersed spores: The five dispersed isospore genera related to this type are ***Ricciaesporites*** Nagy, ***Rouseisporites*** Pocock [S], ***Triporoletes*** Mtchedlishvili, ***Trochicola*** Srivastava [?], and ***Zlivisporis*** Pacltová [S].

Remarks: ***Ricciaesporites*** Nagy and ***Rouseisporites*** Pocock are comparable to spores of extant ***Riccia*** Linnaeus (Ames and Spackman, 1985; Dettmann, 1963). ***Rouseisporites*** Pocock and ***Zlivisporis*** Pacltová are synonyms of ***Triporoletes*** Mtchedlishvili (Song et al., 1999).

3.3.1.6 Family: SPHAGNACEAE Dumortier

Species of extant SPHAGNACEAE Dumortier (Goffinet and Buck, 2004) are nearly cosmopolitan, but most of them are found in circumboreal regions in bogs, wetlands, or swamp forests (Boros et al., 1993; Gao, 1994). They are generally hydrophytes and eurythermic plants.

***Sphagnum capillifolium* type isospore**

Extant spore: ***Sphagnum*** *capillifolium* (Ehrhart) Hedwig (Boros and Járai-Komlódi, 1975; p. 84, Figs. 1-6)

Extant spore: ***Sphagnum*** *cuspidatum* Ehrhart ex Hoffmann (Zhang et al., 2006; p. 144, Pl. 12, figure 1; p. 214, Pl. 82, Figs. 1,2)

Extant spore: ***Sphagnum*** *girgensohnii* Russow (Zhang et al., 2006; p. 144, Pl. 12, Fig. 2; p. 214, Pl. 82, Figs. 3-5)

Key characters: This type of isospore is trilete, generally 25-50 µm in size, oblate in the equatorial view, subtriangular in polar view, and has a smooth exospore. The perispore is provided with granula and verrucae of different sizes and shapes.

Dispersed spores: The nine dispersed isospore genera related to this type are ***Coralloseratisporis*** Timmermann [S], ***Distancoraesporis*** (Krutzsch) Srivastava, ***Distverrusporis*** Krutzsch, ***Duplozonosporis*** Döring et Krutzsch [S], ***Sculptisporis*** Döring et Schulz [S], ***Sphagnites*** Cookson [S], ***Sphagnumsporites*** Raatz ex Potonié, ***Stereisporites*** Pflug [S], and ***Tripunctisporis*** Krutzsch [S].

Remarks: The perispore may not be or only poorly preserved in fossil state, which is common for all spores. The perispore often sloughs off partially or entirely in acetolysis preparations and can be presumed to do the same during fossilization (Traverse, 2007). ***Distancoraesporis*** (Krutzsch) Srivastava, ***Distverrusporis*** Krutzsch, and ***Sphagnumsporites*** Raatz ex Potonié are comparable to spores of extant ***Sphagnum*** Linnaeus (Potonié, 1956; Worobiec, 2009). ***Coralloseratisporis*** Timmermann, ***Duplozonosporis*** Döring et Krutzsch, ***Sculptisporis*** Döring et Schulz, ***Sphagnites*** Cookson, ***Stereisporites*** Pflug, and ***Tripunctisporis*** Krutzsch are synonyms of ***Sphagnumsporites*** Raatz ex Potonié (Potonié, 1956, 1966, 1970).

3.3.2 Pteridophytes

3.3.2.1 Order: CYATHEALES Frank

The extant order CYATHEALES Frank consists of 8 families (Schuettpelz et al., 2016). Fossils with *in situ* spores found in the Mesozoic are ***Sergioa*** Césari (2006) and ***Alsophilites*** Hirmer (Shuklina and Polevova, 2007). Extant species are tree ferns concentrated in the tropics where they are most common within the montane to alpine vegetation. Many species occur in the undergrowth of moist forests, often in ravines, but others prefer more open habitats, even swamps, and some grow preferentially in open areas (Kramer and Green, 1990). They are generally hygrophytes and megathermic plants.

Cibotium barometz **type isospore**

Extant spore: ***Cibotium*** *barometz* (Linnaeus) Smith (Tryon and Lugardon, 1991; p. 223, Pl. 77, Figs. 3-4)
Extant spore: ***Cibotium*** *barometz* (Linnaeus) Smith (Gastony, 1982; p.967, Figs 46-48 ; p. 969-971, Figs. 49-65)

Key characters: This type of isospore is trilete, triangular or subtriangular, with a thick equatorial flange (cingulum), kyrtomes on the proximal face, and coarse ridges forming a triangular area on the distal face, generally 45-80 µm in size. The exospore has two layers.

Dispersed spores: The seven dispersed isospore genera related to this type are ***Cibotiidites*** Ross, ***Cibotiumidites*** (Malyavkina) Potonié, ***Cibotiumspora*** Chang, ***Cibotiumsporites*** Rouse, ***Crassitudisporites*** Hiltmann [?], ***Distaltriangulisporites*** Singh [?], and ***Duplexisporites*** (Deák) Playford et Dettmann.

Remarks: ***Cibotiidites*** Ross, ***Cibotiumidites*** (Malyavkina) Potonié, ***Cibotiumspora*** Chang, ***Cibotiumsporites*** Rouse, and ***Duplexisporites*** (Deák) Playford et Dettmann are comparable to spores of extant ***Cibotium*** Kaulfuss (Cranwell and Srivastava, 2009; Kremp et al., 1957a; Kremp et al., 1958; Kremp et al., 1967, 1968; Song et al., 2000; Srivastava, 1987).

Sergioa austrina **type isospore**

Extant spore: ***Lophosoria*** *quadripinnata* (Gmelin) Christensen (Césari, 2006; p. 235, Pl. IV, Figs. 8, 10 ,11)
Extant spore: ***Lophosoria*** *quadripinnata* (Gmelin) Christensen (Tryon and Lugardon, 1991; p. 241, Pl. 83, Figs. 1-5)
In situ **spore:** ***Sergioa*** *austrina* Césari (Césari, 2006; p. 235, Pl. IV, Figs. 3-7, 9, 12)

Key characters: This type of isospore is trilete, triangular or subtriangular, with a thick equatorial flange (cingulum), perforate or reticulate on the distal face, tuberculate on the proximal face, generally 30-100 µm in size. The exospore has two layers.

Dispersed spores: The dispersed isospore genus related to this type is ***Cyatheacidites*** Cookson ex R. Potonié.

Remarks: ***Cyatheacidites*** Cookson ex R. Potonié is comparable to *in situ* spores of ***Sergioa*** Césari (Césari, 2006).

Alsophilites nipponensis type isospore

Extant spore: ***Alsophila*** *bryophila* Tryon (Tryon and Lugardon, 1991; p. 255, Pl. 85, Fig. 5, 10-11;)
In situ **spore:** ***Alsophilites*** *nipponensis* (Oishi) Krassilov (Shuklina and Polevova, 2007; p. 315, Pl. 10, Figs. 2-3)
In situ **spore:** ***Coniopteris*** *hymenophylloides* (Brongniart) Seward (van Konijnenburg-van Cittert, 1989; p. 276, Pl. II, Figs. 3, 5)
Extant spore: ***Cyathea*** *arborea* (Linnaeus) Smith (Tryon and Lugardon, 1991; p. 263, Pl. 88, Fig. 7)
Extant spore: ***Dicksonia*** *sellowiana* (Presl) Hooker (van Konijnenburg-van Cittert, 1989; p. 292, Pl. VIII, Figs. 5-7)
In situ **spore:** ***Eboracia*** *lobifolia* (Phillips) Thomas (van Konijnenburg-van Cittert, 1989; p. 286, Pl. V, Fig. 4; p. 288, Pl. VI, Figs. 1-3)
Extant spore: ***Hemitelia*** *sp.* (Hofmann, 2002; p. 207, Pl. II, Fig. 12)

Key characters: This type of isospore is trilete, triangular usually with prominent angles and a smooth exospore, generally 20-50 µm in size. The length of the laesura is nearly equal to the radius of the equator. The exospore has two layers. The perispore can be simple or complex.

Dispersed spores: The twelve dispersed isospore genera related to this type are ***Alsophilidites*** Cookson ex Potonié*,* ***Camursporis*** Chlonova, ***Cornutisporites*** Schulz*,* ***Cyathidites*** Couper*,* ***Divisisporites*** Pflug [?], ***Hemitelites*** Romanovskaja*,* ***Kuylisporites*** Potonié*,* ***Maculatisporites*** Döring [S], ***Porisporites*** Pacltová et Simoncsics, ***Synasesporites*** Zhang [?]*,* ***Thuringiasporites*** Schulz*,* and ***Zebrasporites*** Klaus [S].

Remarks: ***Alsophilidites*** Cookson ex Potonié is comparable to spores of extant ***Alsophila*** Brown (Potonié, 1967b). ***Cyathidites*** Couper is comparable to *in situ* spores of ***Alsophilites*** Hirmer (Shuklina and Polevova, 2007), ***Coniopteris*** Brongniart, and ***Eboracia*** Thomas and spores of extant ***Dicksonia*** L'Héritier (Dettmann, 1963). ***Camursporis*** Chlonova, ***Cornutisporites*** Schulz, ***Hemitelites*** Romanovskaja, ***Kuylisporites*** Potonié, ***Porisporites*** Pacltová et Simoncsics, and ***Thuringiasporites*** Schulz are comparable to spores of extant ***Hemitelia*** Brown (Ames and Spackman, 1981, 1985; Traverse and Ames, 1968). ***Maculatisporites*** Döring is a synonym of ***Cyathidites*** Couper (Potonié, 1970), ***Thuringiasporites*** Schulz of ***Zebrasporites*** Klaus (Potonié, 1966).

3.3.2.2 Order: EQUISETALES de Candolle ex Berchtold & Presl

The extant order EQUISETALES de Candolle ex Berchtold & Presl (Schuettpelz et al., 2016) consists of one family EQUISETACEAE Michaux ex de Candolle with a single genus ***Equisetum*** Linnaeus, which is a herbaceous perennial plant. Species of Mesozoic EQUISETALES de Candolle ex Berchtold & Presl are more or less comparable to extant ***Equisetum*** Linnaeus (Taylor et al., 2009). The mode of fossil ***Neocalamites*** *tubulatus* Naugolnykh preservation indicates that the parent plants resembled recent ***Equisetum*** Linnaeus communities and had therefore grown along lake shores inhabited by a near-water hygrophilous plant community of helophytes (Naugolnykh, 2009). Extensive fossil ***Equisetites*** *arenaceus* (Jaeger) Schenk populations occurred in marginal strips along an anastomosing river system. Dense ***Equisetites*** *arenaceus* (Jaeger) Schenk reeds also invaded the levee belt as well as hygromorphic environments surrounding standing waterbodies in a flood plain (Kelber and van Konijnenburg-van Cittert, 1998). ***Equisetum*** Linnaeus has been reported from numerous localities worldwide, where they are primarily plants of open, sunny sand banks along river and lake margins, in marshes, and in other wet places (Taylor et al., 2009). Although the greatest concentrations of extant species are found between 40° and 60° northern latitude, ***Equisetum*** Linnaeus is found worldwide from the southern parts of South America and Africa to north of the Arctic Circle (Kramer and Green, 1990). Therefore, they are generally hygrophytes and eurythermic plants.

Equisetostachys verticillata type isospore

In situ* spore: *Echinostachys *oblonga* (Brongniart) Grauvogel-Stramm (Grauvogel-Stamm and Lugardon, 2009; p.118, Pl. I, Fig. 3)
In situ* spore: *Equisetostachys *verticillata* Grauvogel-Stamm (Grauvogel-Stamm and Lugardon, 2009; p.118, Pl. I, Fig. 5-11)
Extant spore: *Equisetum* *bogotense* Kunth (Tryon and Lugardon, 1991; p. 585, Pl. 226, Figs. 1-2)

Key characters: This type of isospore is trilete or alete, spherical, with a smooth exospore, generally 30-70 µm in size. The laesurae are sometimes invisible or faint. The isospore is with or without elaters that are coiled around the spore. The exospore has two layers.

Dispersed spores: The seven dispersed isospore genera related to this type are ***Aulisporites*** Leschik [?], ***Calamisporites*** Danzé-Corsin et Laveine [S], ***Calamospora*** Schopf, Wilson et Bentall, ***Cuneisporites*** Zhang [?], ***Equisetitriletes*** Zhang [?], ***Pilasporites*** Balme et Hennelly, and ***Scabratisporites*** Visscher [S].

Remarks: During the Mesozoic ***Equisetites*** Sternberg produced both trilete spores of ***Calamospora*** Schopf, Wilson et Bentall and alete spores of ***Pilasporites*** Balme et Hennelly (Kelber and van Konijnenburg-van Cittert, 1998). ***Calamisporites*** Zhang and ***Scabratisporites*** Visscher are synonyms of ***Calamospora*** Schopf, Wilson et Bentall (Potonié, 1970; Shu and Norris, 1988).

3.3.2.3 Order: GLEICHENIALES Schimper

The extant order GLEICHENIALES Schimper consists of three families (Schuettpelz et al., 2016). Fossils can be traced back to the Carboniferous (Taylor et al., 2009). Extant species are terrestrial ferns of rather small to very large sizes (Smith et al., 2006). Fossils with *in situ* spores of ***Aninopteris*** Givulescu et Popa, ***Clathropteris*** Brongniart, ***Dictyophyllum*** Lindley and Hutton, ***Phlebopteris*** Brongniart, and ***Szea*** Yao and Taylor are found in Mesozoic records (Guignard et al., 2009; Litwin, 1985; Wang et al., 2009; Yang et al., 1997). All of the extant species are heliophilous terrestrial ferns in tropical to subtropical regions and most species occur in open, often strongly disturbed and/or pioneer habitats on damp soils (Kramer and Green, 1990; Qian and Chen, 2006). Some plants, such as ***Gleichenites*** Seward, ***Piazopteris*** Lorch, and ***Weichselia*** Stiehler were adapted to semiarid or arid climates during the Mesozoic (van Konijnenburg-van Cittert, 2002). Of course, this does not imply that all plants of GLEICHENIALES Schimper are characterized by the same ecological adaptations. Therefore, they are generally mesophytes and megathermic plants.

Gleichenia dicarpa type isospore

In situ* spore: *Clathropteris *walkeri* (Daugherty) Ash (Litwin, 1985; p. 129, Pl. XII, Figs. 1-6; p. 130, Pl. XIII, Figs. 1-3)
Extant spore: *Dicranopteris* *dichotoma* (Thunberg) Bernhardi (Tryon and Lugardon, 1991; p. 67, Pl. 14, Figs. 1-2)
In situ* spore: *Dictyophyllum *nilssonii* (Brongniart) Goeppert (Guignard et al., 2009; p. 109, Pl. III, Figs. 1-6)
Extant spore: *Gleichenia* *dicarpa* Brown (Tryon and Lugardon, 1991; p. 61, Pl. 13, Fig. 12)
In situ* spore: *Phlebopteris *smithii* (Daugherty) Arnold emend. Ash et al. (Litwin, 1985; p. 122, Pl. IX, Figs. 1-5)

Key characters: This type of isospore is trilete, triangular, generally 20-50 µm in size. It usually has kyrtomes (the arcuate folds) on the proximal or distal face. The exospore has three layers.

Dispersed spores: The sixteen dispersed isospore genera related to this type are ***Auritulinasporites*** Nilsson, ***Canalizonospora*** Li [?], ***Clathroidites*** Bai, ***Clathropterisospora*** Zhang, ***Clavifera*** Bolkhovitina,

Crassulina Maljavkina, ***Dictyophyllidites*** Couper, ***Foveogleicheniidites*** Norvick et Burger [?], ***Gleicheniaceaeauritulina*** (Malyavkina) Potonié, ***Gleicheniidites*** Ross, ***Iraqispora*** Singh [?], ***Kyrtomisporis*** Mädler [?], ***Matonisporites*** Couper, ***Ornamentifera*** Bolchovitina, ***Plicifera*** Bolchovitina, and ***Psilatriletes*** van der Hammen ex Potonié [?].

Remarks: ***Clavifera*** Bolkhovitina, ***Gleicheniidites*** Ross, ***Ornamentifera*** Bolchovitina, and ***Plicifera*** Bolchovitina are comparable to spores of extant ***Gleichenia*** Smith (Bolchovitina, 1967), ***Crassulina*** Maljavkina with spores of extant ***Matonia*** Brown ex Wallich (Ames et al., 1976), ***Dictyophyllidites*** Couper with the *in situ* spores of ***Dictyophyllum*** Lindley et Hutton and ***Phlebopteris*** Brongniart (Cranwell and Srivastava, 2009; Dettmann, 1963). ***Clathroidites*** Bai, ***Clathropterisospora*** Zhang, and ***Gleicheniaceaeauritulina*** (Malyavkina) Potonié are comparable to the *in situ* spores of ***Clathropteris*** Brongniart (Ames et al., 1976; Potonié, 1967; Song et al., 2000), ***Auritulinasporites*** Nilsson and ***Matonisporites*** Couper with the *in situ* spores of ***Phlebopteris*** Brongniart (Kremp and Ames, 1962a, 1965b; Potonié, 1956) and ***Psilatriletes*** van der Hammen ex Potonié with spores of extant ***Gleichenia*** Smith (Kremp and Ames, 1965a).

Szea henanense type isospore

In situ* spore: *Szea *henanense* Yang, Sheng et Wang (Yang et al., 1997; p. 1025, Pl. 2, Figs. j-l)
In situ* spore: *Szea *henanensis* Yang, Sheng et Wang (Wang et al., 2009; p. 151, Pl. VI, Fig. 6)

Key characters: This type of isospore is trilete, triangular, with a granular or verrucate exospore, generally 50-70 µm in size. There are radial thickenings (auriculae or valvae) in the areas beyond the ends of the laesurae.

Dispersed spore: The dispersed isospore genus related to this type is ***Triquitrites*** (Wilson et Coe) Potonié et Kremp.

Remarks: ***Triquitrites*** (Wilson et Coe) Potonié et Kremp is comparable to the *in situ* spore of ***Szea*** Yao and Taylor (Wang et al., 2009; Yao and Taylor, 1988).

Dipteris conjugata type isospore

Extant spore: *Dipteris* *chinensis* Christ (Wang and Dai, 2010; p. 240, Pl .CII, Figs. 4-6)
Extant spore: *Dipteris* *conjugata* Reinwardt (Tryon and Lugardon, 1991; p. 82, Pl. 19, Figs. 1-5)
Extant spore: *Stromatopteris* *moniliformis* Mettenius (Tryon and Lugardon, 1991; p. 69 -70, Pl 15, Figs. 1-6)

Key characters: This type of isospore is monolete, with a smooth exospore, generally 15-40 µm in size. The exospore has three layers.

3.3.2.4 Order: HYMENOPHYLLALES Frank

The extant order HYMENOPHYLLALES Frank consists of one family HYMENOPHYLLACEAE Martius (Schuettpelz et al., 2016). Most species are epiphytes and grow on moss-covered tree trunks. Many terrestrial species are also concentrated in mossy forests. The filmy habit is apparently closely related to the moist air in which these ferns grow (Kramer and Green, 1990). Fossils such as ***Hopetedia*** Axsmith et al. (2001) and ***Eogonocormus*** Deng (2002) are discovered from the Mesozoic. The plants are generally hygrophytes and eurythermic plants.

Hymenophyllum tunbrigense type isospore

Extant spore: *Hymenoglossum* *cruentum* (Cavanilles) Presl (Tryon and Lugardon, 1991; p. 86, Pl. 20, Figs. 1-3)
Extant spore: *Hymenophyllum* *dilatatum* (Forster) Swartz (Tryon and Lugardon, 1991; p. 91, Pl. 22, Figs. 12-13)
Extant spore: *Hymenophyllum* *tunbrigense* (Linnaeus) Smith (Tryon and Lugardon, 1991; p. 89, Pl. 22, Figs. 1-3)
Extant spore: *Mecodium badium* (Hooker et Greville) Copeland (Wang and Dai, 2010; p. 19 Pl. VII, Fig. 8)

Key characters: This type of isospore is trilete, triangular, with a papillate or echinate exospore, generally 30-80 µm in size. The surface is often irregularly convex. The length of laesura is nearly equal to the radius of the equator. The exospore has three layers. For some spores, there is a thin perispore.

Dispersed spores: The two dispersed isospore genera related to this type are ***Biretisporites*** Delcourt et Sprumont [S] and ***Hymenophyllumsporites*** Rouse.

Remarks: ***Hymenophyllumsporites*** Rouse is comparable to spores of extant ***Hymenophyllum*** Smith (Kremp et al., 1966) and ***Mecodium*** Presl ex Copel (Song et al., 1999). ***Biretisporites*** Delcourt et Sprumont is a synonym of ***Hymenophyllumsporites*** Rouse (Potonié, 1966).

3.3.2.5 Order: ISOËTALES Prantl

The order ISOËTALES Prantl (Schuettpelz et al., 2016) consists of the Paleozoic family CHALONERIACEAE Pigg et Rothwell, the Mesozoic family PLEUROMEIACEAE Potonié, and the extant family ISOËTACEAE Dumortier originated from the Mesozoic (Grauvogel-Stamm, 1993; Pigg and Rothwell, 1983). Extant ISOËTACEAE Dumortier consists of a single genus ***Isoetes*** Linnaeus (Schuettpelz et al., 2016). Species of ISOËTALES Prantl are mostly herbaceous in habit (Taylor et al., 2009). Species of ***Pleuromeia*** Corda indicate that they are growing in extensive monodominant thickets perhaps partly submerged in the bays and lakes of a delta system debouching into coastal lakes, lagoons, or even partly in desert oases (Retallack, 1975; Wang and Wang, 1982). They are widely distributed from low to high palaeolatitudes and are therefore not sensitive to temperature variations (Vakhrameev, 1991). Species of extant ISOËTACEAE Dumortier are cosmopolitan and widespread from cold-temperate to subtropical areas usually as plants of damper habitats such as springs and seepage channels, seasonal pools, flowing water and permanent lakes (Kramer and Green, 1990). The Mesozoic fossil species of ***Isoetites*** Münster which show a remarkable similarity to extant ***Isoetes*** Linnaeus, have internal air channels and lack stomata or only have non-functional stomata. These features are regarded as an adaptation to semi-aquatic and aquatic environments (Moisan and Voigt, 2013). Therefore, they are generally hydrophytes and eurythermic plants.

Isoetes tuckermanii **type megaspore**

Extant megaspore: *Isoetes* *andina* Hooker (Tryon and Lugardon, 1991; p. 629, Pl. 232, Fig. 37)
Extant megaspore: *Isoetes* *echinospora* Durieu (Tryon and Lugardon, 1991; p. 629, Pl. 232, Figs. 38-40; p. 631. Pl. 232, Fig. 48)
Extant megaspore: *Isoetes* *macrospora* Durieu (Kramer and Green, 1990; p. 23, Pl. 2, Fig. B)
Extant megaspore: *Isoetes* *tuckermanii* Engelmann (Tryon and Lugardon, 1991; p. 628, Pl. 232, Fig. 22)

Key characters: This type of megaspore is trilete, generally 300-800 µm in size. It has an equatorial flange that is usually characterized by a compact and low girdle below the flange. Laesurae are conspicuously high and wide and always extend to the equator. The exospore is two-layered. Under SEM, the outer layer is lacunose, thicker, with differentiated zones, while the inner layer is stratified, thinner, and less complicate.

Dispersed spores: The three dispersed megaspore genera related to this type are ***Auriculozonospora*** Singh, Srivastava et Roy [S], ***Minerisporites*** Potonié, and ***Pavlovisporites*** Kozur [S].

Remarks: Without SEM, it is difficult to distinguish this megaspore type from some selaginellalean megaspores also with pronounced equatorial zona and long and high laesurae. However, the selaginellalean plant has not been reported with monolete microspores. ***Minerisporites*** Potonié was first recorded as ***Selaginellites*** Zeiller reflecting their supposed affinity to plant macrofossils resembling ***Selaginella*** Beauv (Potonié, 1956). Later, megaspores of ***Minerisporites*** Potonié and related monolete microspores were found adhering to fragments of cuticles showing closer affinities with ***Isoëtes*** Linnaeus and supporting their isoetalean affinity (Batten and Collinson, 2001; Collinson et al., 1985). The ultrastructure of ***Minerisporites*** Potonié is comparable to megaspore of extant ***Isoëtes*** Linnaeus (Wilde and Hemsley, 2000). ***Auriculozonospora*** Singh, Srivastava et Roy and ***Pavlovisporites*** Kozur are synonyms of ***Minerisporites*** Potonié (Batten and Koppelhus, 1993; Potonié, 1970).

***Annalepis zeilleri* type megaspore**

In situ* megaspore: *Annalepis *zeilleri* Fliche (Grauvogel-Stamm and Duringer, 1983; p. 35, Pl. 5, Figs. 3-10)

In situ* megaspore: *Lycostrobus *scotti* Nathorst (Potonié, 1956; p. 123, Pl. 10, Fig. 96)

Key characters: This type of megaspore is trilete, generally 300-700 µm in size. There are echinae on and around the laesurae.

Dispersed spores: The ten dispersed megaspore genera related to this type are ***Capillisporites*** Kozur [?], ***Dijkstraisporites*** Potonié, ***Henrisporites*** Potonié [?], ***Herbosisporites*** Li et Batten [?], ***Membranisporites*** Delcourt et Sprumont [S], ***Nathorstisporites*** Jung, ***Paxillitriletes*** Hall et Nicolson, ***Sepisporites*** Li et Batten [?], ***Tenellisporites*** Potonié, and ***Thomsonia*** Mädler [S].

Remarks: The wall ultrastructural similarity to extant megaspore of ***Isoetes*** Linnaeus, together with adherent monolete microspores strongly suggest the isoetalean affinity of ***Dijkstraisporites*** Potonié and ***Paxillitriletes*** Hall et Nicolson (Wilde and Hemsley, 2000). ***Tenellisporites*** Potonié is comparable to the *in situ* megaspores of ***Annalepis*** Fliche (Grauvogel-Stamm and Duringer, 1983). ***Membranisporites*** Delcourt et Sprumont and ***Thomsonia*** Mädler are synonyms of ***Paxillitriletes*** Hall et Nicolson (Batten and Koppelhus, 1993). ***Nathorstisporites*** Jung is comparable to the *in situ* megaspores of ***Lycostrobus*** Nathorst (Potonié, 1960, 1966).

***Pleuromeia rossica* type megaspore**

In situ* megaspore: *Pleuromeia *obrutschewii* Elias (Krassilov and Zakharov, 1975; p. 228 Pl. IV, Figs. 1-2)

In situ* megaspore: *Pleuromeia *olenekensis* Krassilov (Krassilov and Zakharov, 1975; p. 227, Pl. III, Figs. 4-5; p. 228 Pl. IV, Figs. 3-5)

In situ* megaspore: *Pleuromeia *rossica* Neuburg (Lugardon et al., 2000; p. 504, Figs. 1-10)

In situ* megaspore: *Pleuromeia *rossica* Neuburg (Naugolnykh, 2013a; p. 12, Pl. 8, Figs. 2-4)

Key characters: This type of megaspore is trilete, generally 300-1000 µm in size. The thick exospore consists of numerous lamellae. It is divided distally and marginally into a thick, loose outer part and a thin, dense inner part. Both parts (layers) are often divided by an empty space that forms a cavity.

Dispersed spores: The three dispersed megaspore genera related to this morphotype are ***Banksisporites*** Dettmann, ***Bowenispora*** Scott & Playford, and ***Maiturisporites*** Maheshwari et Banerji.

Remarks: ***Bowenispora*** Scott & Playford is a megaspore restricted to the Triassic and found in ***Aratrisporites*** Leschik dominated miospore palynofloras (Scott and Playford, 1985). ***Maiturisporites*** Maheshwari et Banerji has been recovered from the pleuromeiacean cone of ***Skilliostrobus*** Ash (Balme, 1995; Glasspool, 2000). ***Banksisporites*** Dettmann has been recovered from the pleuromeiacean cone of ***Cylostrobus*** Helby et Martin which also produced the microspores of ***Aratrisporites*** Leschik and ***Lundbladispora*** Balme (Cantrill and Webb, 1998).

***Isoetes andicola* type microspore**

Extant megaspore: *Isoetes* *andicola* (Amstutz) Gomez (Tryon and Lugardon, 1991; p. 623, Pl. 232, Fig. 3)

Extant megaspore: *Isoetes* *andina* Hooker (Tryon and Lugardon, 1991; p. 624, Pl. 232, Figs. 10-11)

Key characters: This type of microspore is monolete, with a laesura as long as or slightly shorter than the spore, generally 20-55 µm in size. The exospore has two layers and the perispore is intricate.

Dispersed spore: The dispersed microspore genus related to this type is ***Perinomonoletes*** Krutzsch.

Remarks: ***Perinomonoletes*** Krutzsch is identical to microspores produced by living ***Isoëtes*** Linnaeus and it has been suggested that the spore type is adherent to the megaspores of ***Paxillitriletes*** Hall et Nicolson (Wilde and Hemsley, 2000).

Annalepis zeilleri type microspore

In situ* spore:** ***Annalepis *zeilleri* Fliche (Grauvogel-Stamm and Duringer, 1983; p. 37, Pl. 6, Figs. 1-16)

Key characters: This type of microspore is monolete, with a laesura as long as or slightly shorter than the spore, generally 25-40 µm in size. The exospore has two layers which detach from each other and form a cavity in the distal face and at the equator. The two layers only connect to each other in the center of the proximal face.

Dispersed spores: The two dispersed microspore genera related to this type are ***Aratrisporites*** Leschik and ***Saturnisporites*** Klaus [S].

Remarks: ***Aratrisporites*** Leschik is comparable to the *in situ* microspores of ***Annalepis*** *zeilleri* Fliche (Grauvogel-Stamm and Duringer, 1983). ***Saturnisporites*** Klaus is a synonym of ***Aratrisporites*** Leschik (Potonié, 1970).

Pleuromeia rossica type microspore

In situ* spore:** ***Pleuromeia *rossica* Neuburg (Lugardon et al., 1999; p. 437, Figs. 1-9)
In situ* spore:** ***Pleuromeia *rossica* Neuburg (Naugolnykh, 2013a; p. 12, Pl. 8, Fig 1)

Key characters: This type of microspore is trilete, with a laesura as long as or slightly shorter than the spore, generally 40 µm in size. The exospore has two layers which detach from each other and form a cavity. The inner layer forms the so-called corpus (= central body) of the microspore. The outer layer consists of lamellae, which can be separated or, in contrast, conjoined into complex systems of lamellae.

Dispersed spores: The three disperse microspore genera related to this type are ***Centrifugisporites*** Huang [?], ***Densoisporites*** Weyland et Krieger, and ***Lundbladispora*** Balme.

Remarks: ***Densoisporites*** Weyland et Krieger is comparable to the *in situ* spore of ***Pleuromeia*** Corda (Naugolnykh, 2013a). ***Lundbladispora*** Balme is comparable to the *in situ* spore of ***Cylostrobus*** Helby & Martin (Cantrill and Webb, 1998).

3.3.2.6 Order: LYCOPODIALES de Candolle ex Berchtold & Presl

The order LYCOPODIALES de Candolle ex Berchtold & Presl (Schuettpelz et al., 2016) consists of homosporous, eligulate, usually dichotomously branched herbaceous plants, whose fossils have been described from records ranging from Devonian to Pleistocene (Taylor et al., 2009). Extant species are almost cosmopolitan, being absent only from arid areas. The greatest species concentration is in humid, tropical, montane forests and in humid, tropical, alpine vegetation (Kramer and Green, 1990). Therefore, they are generally hygrophytes and eurythermic plants.

Lycopodium clavatum type isospore

Extant spore: ***Huperzia*** *selago* (Linnaeus) Schrank & Martius (Tryon and Lugardon, 1991; p. 591, Pl. 227, Figs. 1-2)
Extant spore: ***Lycopodium*** *clavatum* Linnaeus (Tryon and Lugardon, 1991; p. 597, Pl. 229, Figs. 1-3)
Extant spore: ***Phylloglossum*** *drummondii* Kunze (Tryon and Lugardon, 1991; p. 595, Pl. 228, Figs. 1-5)

Key characters: This type of isospore is trilete, subtriangular, with a reticulate or foveolate exospore, generally 20-60 µm in size. The proximal face can be partially or completely smooth. The exospore is two-layered.

Dispersed spores: The nine dispersed isospore genera related to this type are ***Alveolaspora*** Zhang [?], ***Foveasporis*** Krutzsch [S], ***Foveolatitriletes*** Mädler [?], ***Foveosporites*** Balme, ***Lycopodiumsporites*** (Thiergart)

Delcourt et Sprumont, ***Microfoveolatisporites*** Krutzsch [?], ***Reticulitriletes*** Mädler [?], ***Retitriletes*** Pierce [S], and ***Selagosporis*** Krutzsch.

Remarks: ***Lycopodiumsporites*** (Thiergart) Delcourt et Sprumont, ***Foveosporites*** Mädler, and ***Selagosporis*** Krutzsch are comparable to spores of extant ***Lycopodium*** Linnaeus (Kremp and Ames, 1962b; Potonié, 1956, 1960; Song et al., 1999). ***Foveasporis*** Krutzsch is a synonym of ***Foveosporites*** Balme (Dettmann, 1963). ***Retitriletes*** Pierce is a synonym of ***Lycopodiumsporites*** (Thiergart) Delcourt et Sprumont (Potonié, 1966).

Phlegmariurus mandiocanus type isospore

Extant spore: ***Lycopodium*** *inundatum* Linnaeus (Breckon and Falk, 1974; p 483, Figs. 9-10)

Extant spore: ***Palhinhaea*** *cernua* (Linnaeus) Vasconcellos & Franco (Giacosa et al., 2016; p. 87, Pl. II, Figs. 6-10)

Extant spore: ***Phlegmariurus*** *mandiocanus* (Raddi) Øllgaard (Giacosa et al., 2016; p. 88, Pl. III, Figs. 1-5)

Key characters: This type of isospore is trilete, subtriangular, with a rugulate exospore, generally 24-45 µm in size. The proximal face is partially or completely smooth. The spore may have a thin and narrow equatorial flange (zona). The exospore is two-layered.

Dispersed spores: The six dispersed isospore genera related to this type are ***Hamulatisporis*** Krutzsch, ***Ityospora*** Zhang [?], ***Labrorugaspora*** Zhang [?], ***Latrobosporites*** Harris, ***Rugutetraspora*** Yu & Zhang [?], and ***Tripartina*** (Maljavkina) Potonié [?].

Remarks: ***Hamulatisporis*** Krutzsch and ***Latrobosporites*** Harris are comparable to spores of extant ***Lycopodium*** Linnaeus (Hill, 2017; Traverse and Ames, 1979).

Lycopodiella contexta type isospore

Extant spore: ***Huperzia*** *phlegmaria* (Linnaeus) Rothmaler (Tryon and Lugardon, 1991; p. 591, Pl. 227, Fig. 7)

Extant spore: ***Huperzia*** *quasipolytrichoides* (Hayata) Ching (Tryon and Lugardon, 1991; p. 591, Pl. 227, Fig. 3)

Extant spore: ***Lycopodiella*** *contexta* (Martius) Holub (Tryon and Lugardon, 1991; p. 603, Pl. 230, Fig. 7)

Extant spore: ***Lycopodium*** *volubile* Forster (Tryon and Lugardon, 1991; p. 597, Pl. 229, Fig. 11)

Key characters: This type of isospore is trilete, subtriangular, generally 20-60 µm in size. The spore has a thin equatorial flange (zona) which is remarkably narrow or differentially thickened. The exospore is two-layered.

Dispersed spores: The four dispersed isospore genera related to this type are ***Camarazonosporites*** Pant ex Potonié [?], ***Parajunggarsporites*** (Yu) Song [?], ***Sestrosporites*** Dettmann, and ***Semiretisporis*** Reinhardt [?].

Remarks: ***Sestrosporites*** Dettmann is comparable to isospores of extant ***Lycopodium*** Linnaeus (Dettmann, 1963).

3.3.2.7 Order: MARATTIALES Link

Species of extant MARATTIALES Link (Schuettpelz et al., 2016) are terrestrial ferns distributed exclusively in tropical and subtropical regions under primary and secondary wet forests or along the bank of streams (Kramer and Green, 1990). Fossils of MARATTIALES with *in situ* spores such as ***Dunmites*** (Göppert) Stur (Liu et al., 2001) and ***Pectinangium*** Li et al. (Wan and Basinger, 1992) can be found in the Permian, whereas ***Danaeopsis*** Heer ex Schimper (Kustatscher et al., 2012) and ***Marattia*** Swartz (Wang, 1999a) are known from the Mesozoic. The Mesozoic species lived under rather warm, moist circumstances often probably as understory in forests (van Konijnenburg-van Cittert, 2002). Therefore, they are generally hygrophytes and megathermic plants.

Marattia asiatica type isospore

In situ* spore:** ***Marattia *asiatica* (Kawasaki) Harris (Wang, 1999a; p. 134, Pl. IV, Figs. 3-8)
Extant spore: ***Marattia*** *cicutifolia* Kaulfuss (Tryon and Lugardon, 1991; p. 45, Pl. 8, Figs. 2-3)
Extant spore: ***Marattia*** *weimanniifolia* Liebmann (Tryon and Lugardon, 1991; p. 46, Pl. 8, Figs. 9-11)

Key characters: This type of isospore is monolete, with a faint laesura and a rugate to coarsely echinate exospore, generally 15-40 µm in size. The contours largely formed by the exospore. The perispore conforms to exospore and is usually detached from the three-layered exospore.

Dispersed spores: The dispersed isospore genus related to this type is ***Marattisporites*** Couper.

Remarks: ***Marattisporites*** Couper is comparable to the spores of extant ***Marattia*** Swartz and *in situ* spores of ***Marattiopsis*** Schimper (Kremp and Ames, 1962a).

Pectinangium lanceolatum type isospore

Extant spore: ***Angiopteris*** *tonkinensis* (Hayata) Camus (Kramer and Green, 1990; p. 175, Pl. 88, Fig. b)
Extant spore: ***Angiopteris*** *yunnanensis* Hieronymus (Tryon and Lugardon, 1991; p. 39, Pl. 4, Figs. 1-2)
In situ* spore:** ***Danaeites *rigida* Gu and Zhi (Liu et al., 2001; p. 110, Figs. 10; p. 112, Figs. 16-20)
In situ* spore:** ***Danaeopsis *fecunda* Halle (Kustatscher et al., 2012; p. 37, Figs. 2.1, 2.4)
In situ* spore:** ***Pectinangium *lanceolatum* Li et al (Wan and Basinger, 1992; p. 225, Pl. III, Figs. 1, 3)

Key characters: This type of isospore is trilete, circular, with faint laesurae and a tuberculate to rugate exospore, generally 20-40 µm in size. The exospore is three-layered.

Dispersed spores: The dispersed isospore genus related to this type is ***Angiopteridaspora*** Chang.

Remarks: ***Angiopteridaspora*** Chang is comparable to spores of extant ***Angiopteris*** Hoffmann (Kremp et al., 1967).

3.3.2.8 Order: OPHIOGLOSSALES Link

The order OPHIOGLOSSALES Link (Schuettpelz et al., 2016) consists of one extant family OPHIOGLOSSACEAE Martinov including also the former families of BOTRYCHIACEAE Horaninow and HELMINTHOSTACHYACEAE Ching (Smith et al., 2006). Fossils with *in situ* spores of ***Lugardonia*** Kustatscher et al., which possibly belong to this family, can be found in the Mesozoic (Kustatscher et al., 2009). Extant species are mainly terrestrial herbs, small and fleshy, nearly worldwide in distribution and can be found in tropical, temperate or even polar regions. Most of them are associated with habitat disturbances and are genera especially of an early to middle succession. In extreme drought the leaf may remain dormant and not appear until normal moisture returns. The best habitats for them are open pastures, young second-growth woods, and grassy slopes (Kramer and Green, 1990). They are mesophytes and eurythermic plants.

Ophioglossum engelmannii type isospore

Extant spore: ***Botrychium*** *schaffneri* Underwear (Tryon and Lugardon, 1991; p. 29, Pl. 1, Fig. 1)
In situ* spore:** ***Lugardonia *paradoxa* Kustatscher et al. (Kustatscher et al., 2009; p. 95, Pl. III, Figs. 1-11)
Extant spore: ***Ophioglossum*** *engelmannii* Prantl (Tryon and Lugardon, 1991; p. 35, Pl. 3, Figs. 3-4)

Key characters: This type of isospore is trilete, with laesurae ranging from 1/2 - 2/3 of the spore's radius and a rugulate to finely reticulate exospore, generally 20-55 µm in size. The exospore is three-layered.

Dispersed spores: The two dispersed isospore genera related to this type are ***Lycopodiacidites*** (Couper) Potonié and ***Reticulisporites*** Potonié et Kremp.

Remarks: ***Lycopodiacidites*** (Couper) Potonié and ***Reticulisporites*** Potonié et Kremp are comparable to the spores of ***Botrychium*** Swartz, ***Lycopodium*** Linnaeus and ***Ophioglossum*** Linnaeus (Dettmann, 1963; Potonié, 1956; Potonié, 1967). The descriptions for the holotypes of ***Lycopodiacidites*** (Couper) Potonié and ***Reticulisporites*** Potonié et Kremp did not mentioned by how many layers the exospores are characterized. The exospore of ***Lycopodium*** Linnaeus has two layers (Tryon and Lugardon, 1991), but, however, in this paper, only ***Lycopodiacidites*** (Couper) Potonié and ***Reticulisporites*** Potonié et Kremp with exospores that have three layers are linked to OPHIOGLOSSACEAE Martinov.

3.3.2.9 Order: OSMUNDALES Link

Species of extant OSMUNDALES Link (Schuettpelz et al., 2016) are terrestrial ferns distributed throughout most temperate and tropical regions in sites with either high edaphic or high atmospheric moisture (or both) (Kramer and Green, 1990; Tryon and Lugardon, 1991). Fossils with *in situ* spores of ***Bromsgrovia*** Seyfullah et al., ***Osmundopsis*** Harris, and ***Todites*** Seward are found in the Mesozoic (Litwin, 1985; Seyfullah et al., 2013; van Konijnenburg-van Cittert, 1978). The Mesozoic species probably grew under warm, humid circumstances, either along riverbanks or in freshwater marshes where they often formed peat resulting in coal (van Konijnenburg-van Cittert, 2002). However, the extant species, such as ***Osmunda*** *claytoniana* Linnaeus, can also distribute in the cooler montane regions of the Himalayas and Far East of Russia (Ching and Shing, 1990; Ching, 2006). Therefore, they are generally hygrophytes and eurythermic plants.

Osmunda regalis **type isospore**

In situ **spore: *Bromsgrovia*** *willsii* Seyfullah et al. (Seyfullah et al., 2013; p. 21, Pl. IV, Figs. 1-4; Pl. V, Figs. 1-3)

In situ **spore: *Osmundopsis*** *plectrophora* Harris (van Konijnenburg-van Cittert, 1978; p. 133, Pl. IV, Fig. 4)

Extant spore: *Osmunda* *regalis* Linnaeus (Tryon and Lugardon, 1991; p. 53, Pl. 10, Figs. 6, 8, 11; p.54, Pl.10, Figs. 12-18)

Extant spore: *Todea* *barbara* (Linnaeus) Moore (Tryon and Lugardon, 1991; p. 56, Pl. 11, Figs. 1-5)

In situ **spore: *Todites*** *fragilis* (Daugherty) Ash (Litwin, 1985; p. 106, Pl. II, Figs. 1-6)

Key characters: This type of isospore is trilete, spheroidal, with a baculate, echinate or tuberculate exospore, generally 40-80 μm in size. The exospore has three layers.

Dispersed spores: The seven dispersed isospore genera related to this type are ***Baculatisporites*** Pflug et Thomson, ***Bracteolinasporites*** Nilsson [?], ***Conosmundasporites*** Klaus [?], ***Osmundacidites*** Couper, ***Rubinella*** Maljavkina, ***Rugulatisporites*** Pflug, and ***Todisporites*** Couper.

Remarks: *Baculatisporites* Pflug et Thomson, ***Osmundacidites*** Couper, ***Rubinella*** Maljavkina, ***Rugulatisporites*** Pflug are comparable to spores of extant ***Todea*** Willdenow ex Bernhardi and ***Osmunda*** Linnaeus (Dettmann, 1963; Potonié, 1956, 1966; Traverse et al., 1975). ***Todisporites*** Couper is comparable to the *in situ* spores of ***Todites*** Seward (Litwin, 1985; Potonié, 1960).

3.3.2.10 Order: POLYPODIALES Link

Family: POLYPODIACEAE Presl et Presl

The species of extant POLYPODIACEAE Presl et Presl (Schuettpelz et al., 2016) are mostly pantropical, but a few are temperate (Smith et al., 2006). Extant species are usually terrestrial or epiphytic, sometimes epilithic, usually small to medium-sized, sometimes large ferns occupying a variety of habitats. With epiphytism prevailing, there are still a few representatives that occur regularly, either terrestrially or on rocks. Many species prefer ever-wet forests at low to middle elevation, but some are also found in monsoon seasonal vegetation and drier habitats. Some species occur up to an altitude of about 4000 m (Kramer and Green, 1990). Fossils of ***Polypodites*** Göppert have been found in the Cretaceous of China (Sun et al., 2010). POLYPODIACEAE Presl et Presl are generally hygrophytes and megathermic plants.

Polypodium aureum **type isospore**

Extant spore: *Campyloneurum* *phyllitidis* (Linnaeus) Presl (Tryon and Lugardon, 1991; p. 335, Pl. 123, Fig. 11)

Extant spore: *Polypodium* *aureum* Linnaeus (Tryon and Lugardon, 1991; p. 344, Pl. 131, Fig. 1)

Extant spore: ***Pyrrosia*** *adnascens* (Swartz) Ching (Wang and Dai, 2010; p. 241, Pl. CIII, Figs. 11-12)

Key characters: This type of isospore is monolete, with a verrucate, tuberculate, or rugate exospore, generally 30-100 µm in size. Usually, it has a thin perispore. The exospore has two layers.

Dispersed spores: The eleven dispersed isospore genera related to this type are ***Cyclophorusisporites*** Sung et Lee ex Zhang, ***Gemmamonoletes*** Pierce [S], ***Gemmatosporis*** Krutzsch [S], ***Polypodiaceaesporites*** Thiergart ex Potonié, ***Polypodiidites*** Ross, ***Polypodiisporites*** Potonié [S], ***Polypodiumsporites*** Raatz [S], ***Polypodites*** Bolchovitina, ***Radiomonolites*** Song et Zhong [?], ***Verrucatosporites*** Pflug et Thomson [S], and ***Verrumonoletes*** van der Hammen [S].

Remarks: ***Cyclophorusisporites*** Sung et Lee ex Zhang is comparable to spores of extant ***Pyrrosia*** Mirbel (Song et al., 1999), ***Polypodiidites*** Ross and ***Polypodites*** Bolchovitina with spores of extant ***Polypodium*** Linnaeus (Kremp and Ames, 1962b; Kremp et al., 1957a). Potonié (1956) stated that ***Polypodiaceaesporites*** Thiergart ex Potonié was a dispersed spore of POLYPODIACEAE Presl et Presl, but he did not compare it to any *in situ* nor extant spores. ***Gemmamonoletes*** Pierce, ***Gemmatosporis*** Krutzsch, ***Polypodiisporites*** Potonié, ***Verrucatosporites*** Pflug et Thomson, and ***Verrumonoletes*** van der Hammen are synonyms of ***Polypodiidites*** Ross (Potonié, 1956, 1966). ***Polypodiumsporites*** Raatz is a synonym of ***Polypodiaceaesporites*** Thiergart ex Potonié (Potonié, 1956).

Family: PTERIDACEAE Kirchner

Fossils of PTERIDACEAE Kirchner such as ***Arctopeteris*** Samylina and ***Palibiniopteris*** Prynada can be found in the Cretaceous from China (Sun et al., 2010). Extant species are essentially worldwide in distribution centred in the tropics. Most species grow in rather open, often rocky, habitats. Some, such as ***Adiantum*** Linnaeus and ***Pteris*** Linnaeus, are common in forests. There is an unusual ecological diversity, with, e.g., ***Ceratopteris*** Brongniart as an aquatic genus and ***Acrostichum*** Linnaeus as often associated with mangroves. Some genera, such as ***Cheilanthes*** Swartz and ***Notholaena*** Brown, are often important elements within the flora of xeric habitats, with leaves that are often dormant when desiccated but revive with rainfall (Kramer and Green, 1990). ***Pteris*** *stenophylla* Wallich ex Hooker et Wu is distributed in the cooler and xeric montane region of the Himalaya at altitudes of 2500-3000 m (Ching and Shing, 1990). Therefore, they are euryphytes and eurythermic plants.

Pteris cretica type isospore

Extant spore: ***Eriosorus*** *cheilanthoides* Tryon (Tryon and Lugardon, 1991; p. 134, Pl. 36, Figs. 3, 4)
Extant spore: ***Jamesonia*** *goudotii* (Hieronymus) Christensen (Tryon and Lugardon, 1991; p. 136, Pl. 37, Figs. 3, 4)
Extant spore: ***Onychium*** *contiguum* Hope (Tryon and Lugardon, 1991; p. 143, Pl. 42, Figs. 1-3)
Extant spore: ***Pteris*** *cretica* Linnaeus (Tryon and Lugardon, 1991; p. 191, Pl. 62, Figs. 14, 15)

Key characters: This type of isospore is trilete, with a rugate or tuberculate exospore, generally 30-80 µm in size. It has a thick equatorial flange (cingulum), with or without kyrtomes in proximal face. There can be ridges adjacent to the equatorial flange forming a triangular or circular area in proximal face, or distal face, or both faces. It has a thin perispore. The exospore has two layers.

Dispersed spores: The eleven dispersed isospore genera related to this type are ***Asseretospora*** Schuurman, ***Contignisporites*** Dettmann [?], ***Coronasporites*** Zhang [?], ***Muricingulisporis*** Krutzsch, ***Onychiumsporites*** Hu, ***Pteridaceoisporis*** Sun et He, ***Pterisisporites*** Sun et Zheng [?], ***Polypodiaceoisporites*** Potonié [?], ***Sotasporites*** Archangelsky & Archangelsky, ***Tigrinispora*** Chang [?], and ***Verrutetraspora*** Song et Zheng.

Remarks: ***Asseretospora*** Schuurman, ***Onychiumsporites*** Hu, ***Pteridaceoisporis*** Sun et He, and ***Verrutetraspora*** Song et Zheng are comparable to spores of extant ***Pteris*** Linnaeus and ***Onychium*** Kaulfuss (Hill, 2017; Song et al., 1999). ***Muricingulisporis*** Krutzsch and ***Sotasporites*** Archangelsky & Archangelsky are comparable to spores of extant ***Pteris*** Linnaeus (Archangelsky and Archangelsky, 2006).

***Hemionitis arifolia* type isospore**

Extant spore: *Gymnopteris* *bipinnata* Christ (Wang and Dai, 2010; p. 172 Pl. XXXIV, Fig. 1)
Extant spore: *Hemionitis* *arifolia* (Burman) Moore (Wang and Dai, 2010; p. 173, Pl. XXXV, Figs. 1, 2)

Key characters: This type of isospore is trilete, with weak laesurae, generally 25-80 µm in size. Its perispore forms the dominant reticulate contour. The exospore has two layers.

Dispersed spores: The dispersed isospore genus related to this type is ***Dictyotosporites*** Cookson et Dettmann.

Remarks: *Dictyotosporites* Cookson et Dettmann is closely related to spores of extant ***Hemionitis*** *arifolia* (Burman) Moore (Dettmann, 1963).

***Ceratopteris cornuta* type isospore**

Extant spore: *Ceratopteris* *cornuta* (de Beauvois) Leprieur (Tryon and Lugardon, 1991; p. 126, Pl. 33, Figs. 1, 2; p. 128, Pl. 33, Figs. 10-12)
Extant spore: *Ceratopteris* *pteridoides* (Hooker) Hieronymus (Wang and Dai, 2010; p.171, Pl. XXXIII, Figs. 4-6)

Key characters: This type of isospore is trilete, with a striate exospore, generally 70-160 µm in size. The striae (ridges) originate from the angles of the proximal pole, leave a triangular blank on the proximal center and extend to and cover the entire distal pole. The exospore has one layer.

Dispersed spores: The two dispersed isospore genera related to this type are ***Hammenisporis*** Saxena & Trivedi and ***Magnastriatites*** Germeraad, Hopping et Muller.

Remarks: *Hammenisporis* Saxena & Trivedi and ***Magnastriatites*** Germeraad, Hopping et Muller are comparable to spores of extant ***Ceratopteris*** Brongniart (Saxena and Trivedi, 2009; Song et al., 1999).

3.3.2.11 Order: SALVINIALES Link

The species of the extant order SALVINIALES Link are water ferns, including the families MARSILEACEAE Mirbel, SALVINIACEAE Martinov and the former AZOLLACEAE Wettstein (Smith et al., 2006). Fossils with *in situ* spores of ***Paleoazolla*** Archangelsky et al. and ***Regnellidium*** Lindman are found in Mesozoic records (Archangelsky et al., 1999; Lupia et al., 2000). Extant species are distributed all over the world as free-floating plants that occur on the surface of ponds or in sloughs of rivers. Most species live in tropical and subtropical regions (Kramer and Green, 1990). They are generally hydrophytes and megathermic plants.

***Marsilea strigosa* type megaspore**

Extant megaspore: *Azolla* *filiculoides* Lamarck (Tryon and Lugardon, 1991; p. 578, Pl. 225, Fig. 3)
In situ* megaspore: *Hydropteris *pinnata* Rothwell & Stockey (Rothwell and Stockey, 1994; p. 486, Figs, 29-41)
Extant megaspore: *Marsilea* *strigosa* Willdenow (Tryon and Lugardon, 1991; p. 567, Pl. 221, Figs. 7-8)
In situ* megaspore: *Paleoazolla *patagonica* Archangelsky et al. (Archangelsky et al., 1999; p. 1202, Figs. 1-4)
Extant megaspore: *Pilularia* *americana* Braun (Tryon and Lugardon, 1991; p. 573, Pl. 223, Fig. 3)
In situ* megaspore: *Regnellidium *upatoiensis* Lupia et al. (Lupia et al., 2000; p. 980, Pl. 4, Figs. 23-25)

Key characters: This type of megaspore is trilete, with faint laesurae, generally 200-950 µm in size. The ratio of the length of the polar axis to the equatorial diameter (P/E ratio) is bigger than 1 or even 2. The exospore forms different accessory structures such as floats, collars and filaments. The exospore has two layers.

Dispersed spores: The thirteen dispersed megaspore genera related to this type are ***Arcellites*** Miner, ***Ariadnaesporites*** Potonié, ***Balmeisporites*** Cookson et Dettmann, ***Capulisporites*** Potonié [?], ***Clockhousea***

Batten, ***Ghoshispora*** Srivastava, ***Glomerisporites*** Potonié, ***Grapnelispora*** Stover & Partridge, ***Hallisporites*** Nowak et Lupia, ***Molaspora*** Schemel, ***Parazolla*** Hall, ***Pyrobolospora*** Hughes [S], and ***Styx*** Norton & Hall.

Remarks: Because of the fact that for most of the megaspores the P/E ratio is smaller than 1, the high P/E ratio is the remarkable character for this type of megaspore. ***Arcellites*** Miner is comparable to megaspores of extant ***Marsilea*** Linnaeus and has been found associated with the microspores of ***Crybelosporites*** Dettmann which are comparable to the microspores of extant ***Pilularia*** Linnaeus (de Seoane and Archangelsky, 2008; Eklund et al., 2004). ***Molaspora*** Schemel is comparable to the megaspores of extant ***Marsilea*** Linnaeus and ***Regnellidium*** Lindman (Batten et al., 2011; Lupia et al., 2000). ***Ariadnaesporites*** Potonié, ***Balmeisporites*** Cookson et Dettmann, ***Ghoshispora*** Srivastava, ***Glomerisporites*** Potonié, ***Hallisporites*** Nowak et Lupia and ***Styx*** Norton & Hall are comparable to megaspores of extant ***Azolla*** Lamarck (Batten and Collinson, 2001; Batten et al., 2011; Nowak and Lupia, 2005; Srivastava, 1971). ***Parazolla*** Hall has been found as *in situ* spore of the fossil fern ***Hydropteris*** Rothwell & Stockey (Rothwell and Stockey, 1994). ***Clockhousea*** Batten is comparable to megaspores of extant ***Regnellidium*** Lindman (Batten, 2009). ***Grapnelispora*** Stover & Partridge comparable to megaspores of extant ***Azolla*** Lamarck and is found associated with ***Mendozaphyllum*** Puebla et al. and ***Paleoazolla*** Archangelsky et al. (Puebla et al., 2015). ***Pyrobolospora*** Hughes is a synonym of ***Arcellites*** Miner (Potonié, 1966). ***Capulisporites*** Potonié is a synonym of ***Ariadnaesporites*** Potonié (Potonié, 1970) .

Regnellidium diphyllum type microspore

Extant spore: ***Regnellidium*** *diphyllum* Lindman (Tryon and Lugardon, 1991; p. 569, Pl. 222, Fig. 1)
In situ* spore:** ***Regnellidium *upatoiensis* Lupia et al. (Lupia et al., 2000; p. 978, Pl. 2, Figs. 9-11)

Key characters: This type of microspore is trilete, with short and faint laesurae, generally 35 - 55 µm in size. The exospore has two layers. The outer layer of the exospore is spongiose on the distal face and the lateral area.

Dispersed spores: The five dispersed microspore genera related to this type are ***Brevilaesuraspora*** Yu [?], ***Crybelosporites*** Dettmann, ***Gabonisporis*** (Boltenhagen) Srivastava [?], ***Salviniaspora*** Song et Zhang, and ***Thecaspora*** Elsik [?].

Remarks: ***Crybelosporites*** Dettmann has been found associated with the megaspores of ***Arcellites*** Miner and is comparable to the microspores of extant ***Pilularia*** Linnaeus, ***Marsilea*** Linnaeus, and ***Regnellidium*** Lindman (Li and Batten, 1986). ***Salviniaspora*** Song et Zhang is comparable to spores of extant ***Salvinia*** Séguier (Song et al., 1999).

3.2.12 Order: SCHIZAEALES Schimper

Family: ANEMIACEAE Link

The species of the extant family ANEMIACEAE Link (Schuettpelz et al., 2016) are widely distributed in tropical and subtropical regions (Tryon and Lugardon, 1991). The great majority live in the drier parts of America from Texas to Argentina, a few in Africa and also India (Kramer and Green, 1990). Fossils with *in situ* spores that have been found in Mesozoic records are ***Schizaeopsis*** Berry (Kvacek et al., 2006) and ***Ruffordia*** Seward (Mohr et al., 2015). The species of the family prefer mainly mesic, disturbed, grassy habitats and live often on rocky pastures and trail banks at sunny or light shaded places (Mickel, 1982). They are generally mesophytes and megathermic plants.

Anemia lanuginosa type isospore

Extant spore: ***Anemia*** *lanuginosa* (Linnaeus) Swartz (Tryon and Lugardon, 1991; p. 108, Pl. 29, Fig. 2)
Extant spore: ***Anemia*** *collina* Raddi (Labiak et al., 2015; p.1152, Pl. 8, Fig. O)
Extant spore: ***Mohria*** *caffrorum* (Linnaeus) Desvaux (Tryon and Lugardon, 1991; p. 115, Pl. 30, Figs. 1-3, 7-8)
In situ* spore:** ***Ruffordia *goeppertii* (Dunker) Seward (Mohr et al., 2015; p. 23, Pl 4, Figs. d-g)
In situ* spore:** ***Schizaeopsis *ekrtii* Kvacek et al. (Kvacek et al., 2006; p. 54, Pl. II, Figs. 3-10)

Key characters: This type of isospore is trilete, triangular in polar view, striate, generally 40 - 120 µm in size. On each of the facets that are separated by laesurae (interradial area), the striae are parallel to each other and to the equator. On the boundaries of the facets the striae of neighbouring facets can be connected. Some spores have auriculae. The exospore has two layers.

Dispersed spores: The ten dispersed isospore genera related to this type are ***Appendicisporites*** Weyland et Krieger, ***Cicatricosisporites*** Potonié et Gelletich, ***Costatoperforosporites*** Deák, ***Mohrioisporites*** Thiergart [S], ***Nodosisporites*** (Deák) Dettmann & Clifford, ***Palaeomohria*** Archangelsky, ***Plicatella*** Maljavkina, ***Ruffordiaspora*** Dettmann & Clifford, ***Tauresporites*** Zhang [?], and ***Trilaterina*** Maljavkina [S].

Remarks: ***Cicatricosisporites*** Potonié et Gelletich and ***Palaeomohria*** Archangelsky are comparable to spores of extant ***Mohria*** Swartz (Archangelsky, 2009). ***Appendicisporites*** Weyland et Krieger (Traverse et al., 1973a), ***Costatoperforosporites*** Deák (Mendes et al., 2017), and ***Plicatella*** Maljavkina (Potonié, 1966) are comparable to spores of extant ***Anemia*** Swartz. ***Ruffordiaspora*** Dettmann & Clifford is comparable to *in situ* spores of ***Ruffordia*** Seward (Cranwell and Srivastava, 2009). ***Mohrioisporites*** Thiergart and ***Trilaterina*** Maljavkina are synonyms of ***Cicatricosisporites*** Potonié et Gelletich (Potonié, 1956, 1960).

Family: LYGODIACEAE Roemer

The extant family LYGODIACEAE Roemer (Schuettpelz et al., 2016) consists of a single genus ***Lygodium*** Swartz. Fossils with *in situ* spores of ***Stachypteris*** Pomel and ***Klukia*** Raciborski are known from the Mesozoic (van Konijnenburg-van Cittert, 1981). Extant plants are pantropical terrestrial climbing ferns (Smith et al., 2006). As shade-loving plants they prefer thickets and forest edges in the wet regions such as river valleys or near river banks (Kramer and Green, 1990; Qian and Chen, 2006). Therefore, they are generally hygrophytes and megathermic plants.

Lygodium salicifolium type isospore

Extant spore: ***Lygodium*** *salicifolium* Presl (Tryon and Lugardon, 1991; p. 104, Pl. 28, Fig. 1)
Extant spore: ***Lygodium*** *subareolatum* Christ (Wang and Dai, 2010; p. 142, Pl. IV, Figs. 4-5)

Key characters: This type of isospore is trilete, with a gemmate or psilate exospore, generally 50-130 µm in size. The exospore has two layers. It has a complex perispore.

Dispersed spores: The eleven dispersed isospore genera related to this type ***Concavissimisporites*** Delcourt et Sprumont [?], ***Corrugatisporites*** Thomson & Pflug [S], ***Crassoretitriletes*** Germeraad, Hopping et Muller, ***Impardecispora*** Venkatachala, Kar et Raza [?], ***Lygodioisporites*** Potonié, ***Lygodiumsporites*** Potonié, ***Pilosisporites*** Delcourt et Sprumont, ***Tenuangulasporis*** Jia [?], ***Toroisporis*** Krutzsch, ***Trilobosporites*** Pant ex Potonié, and ***Varirugosisporites*** Döring.

Remarks: The size of the spore is diagnostic, since in general isospores are smaller than 50 µm. ***Crassoretitriletes*** Germeraad, Hopping et Muller, ***Lygodioisporites*** Potonié, ***Lygodiumsporites*** Potonié, ***Pilosisporites*** Delcourt et Sprumont, ***Trilobosporites*** Pant ex Potonié, and ***Varirugosisporites*** Döring are comparable to spores of extant ***Lygodium*** Swartz (Dettmann, 1963; Potonié, 1956; Traverse and Ames, 1971; Traverse et al., 1973a). ***Toroisporis*** Krutzsch is morphologically comparable to spores of extant ***Gleichenia*** Smith and ***Matonia*** Brown ex Wallich (Traverse and Ames, 1979; Traverse et al., 1973a). However, both the mature spores of extant ***Gleichenia*** Smith and ***Matonia*** Brown ex Wallich are three-layered, while ***Toroisporis*** Krutzsch is only two-layered. Therefore, ***Toroisporis*** Krutzsch is more comparable to the spores of extant ***Lygodium*** Swartz (Song et al., 1999). ***Corrugatisporites*** Thomson & Pflug is the synonym of ***Lygodioisporites*** Potonié (Potonié, 1970). ***Concavissimisporites*** Delcourt et Sprumont is comparable to the spores of extant ***Cyathea*** Smith, ***Dicksonia*** L'Héritier, and ***Lygodium*** Swartz (Potonié, 1966).

Klukia exilis type isospore

In situ* spore:** ***Klukia *exilis* (Phillips) Raciborski (van Konijnenburg-van Cittert, 1981; p. 170, Pl. I, Figs. 1-6)

In situ* spore: *Klukia* *tyganensis Krassilov (Avramenko and Polevova, 2013; p. 442, Pl. 1, Figs a-h; P. 444, Pl. 2, Figs a-f)
Extant spore: *Lygodium* *reticulatum* Schkuhr (Tryon and Lugardon, 1991; p. 105, Pl. 28, Figs 8-9)
Extant spore: *Lygodium* *scandens* Linnaeus (Wang and Dai, 2010; p. 143, Pl. IV, Figs 1-4)
In situ* spore: *Stachypteris *spicans* Pomel (van Konijnenburg-van Cittert, 1981; p. 172, Pl. II, Figs. 1-5)

Key characters: This type of isospore is trilete, with a coarsely reticulate exospore, generally 50-130 µm in size. The exospore has one or two layers.

Dispersed spores: The three dispersed isospore genera related to this type are ***Crassoretitriletes*** Germeraad, Hopping et Muller, ***Klukisporites*** Couper, and ***Ramanujamiaspora*** Kar et Sah.

Remarks: The exospore of ***Klukia*** *tyganensis* Krassilov consist of only one layer (Avramenko and Polevova, 2013), whereas the exospore of ***Lygodium*** Swartz has two layers (Tryon and Lugardon, 1991). However, Avramenko and Polevova (2013) also reported that the exospores of ***Lygodium*** Swartz and ***Anemia*** Swartz have only one layer. The exospore structure of this type needs study in detail. Anyway, the coarsely reticulate sculpture is the key character that separates this type spore from all others. ***Klukisporites*** Couper, ***Ramanujamiaspora*** Kar et Sah are comparable to the *in situ* spores of ***Klukia*** Raciborski and ***Stachypteris*** Pomel (Dettmann, 1963; Kar and Sah, 1969; Potonié, 1960), whereas ***Crassoretitriletes*** Germeraad, Hopping et Muller is similar to spores of extant ***Lygodium*** Swartz (Germeraad et al., 1968).

Family: SCHIZAEACEAE Kaulfuss

Species of extant SCHIZAEACEAE Kaulfuss (Schuettpelz et al., 2016) are terrestrial or epilithic and small to large ferns with a creeping or erect stem. They are essentially tropical and southern warm-temperate but exceed the Tropic of Cancer considerably in North America and East Asia. The plants often inhabit mineral-poor and/or periodically dry or swampy and open habitats (Kramer and Green, 1990). Several species of schizaeaceous ferns are known from compression-impression remains of Triassic and Jurassic age (Taylor et al., 2009). The plants are generally mesophytes and megathermic plants.

Schizaea laevigata type isospore

Extant spore: *Schizaea* *digitata* (Linnaeus) Swartz (Wang and Dai, 2010; p. 140, Pl. II, Figs. 10-12)
Extant spore: *Schizaea* *laevigata* Mettenius (Tryon and Lugardon, 1991; p. 117, Pl. 31, Figs. 3-4)

Key characters: This type of isospore is monolete, with a striate exospore, generally 35-100 µm in size. The exospore has two layers.

Dispersed spores: The four dispersed isospore genera related to this type are ***Cicatricososporites*** Thomson & Pflug ex Krutzsch [S], ***Schizaeites*** Bolchovitina [S], ***Schizaeoisporites*** Potonié ex Delcourt et Sprumont, and ***Striamonoletes*** Mathur [S].

Remarks: *Schizaeoisporites* Potonié ex Delcourt et Sprumont is comparable to spores of extant ***Schizaea*** Smith (Potonié, 1960). ***Cicatricososporites*** Thomson & Pflug ex Krutzsch, ***Schizaeites*** Bolchovitina, and ***Striamonoletes*** Mathur are synonyms of ***Schizaeoisporites*** Potonié ex Delcourt et Sprumont (Potonié, 1960, 1970).

Schizaea pusilla type isospore

Extant spore: *Schizaea* *pennula* Swartz (Tryon and Lugardon, 1991; p. 119, Pl. 31, Figs. 17-18)
Extant spore: *Schizaea* *pusilla* Pursh (Tryon and Lugardon, 1991; p. 117, Pl. 31, Figs. 1-2)

Key characters: This type of isospore is monolete, with a foveolate exospore, generally 35-100 µm in size. The exospore has two layers.

Dispersed spores: The four dispersed isospores related to this type are ***Foveomonoletes*** van der Hammen ex Mathur [S], ***Microfoveolatosporis*** Krutzsch, ***Reticulosporis*** Krutzsch [S], and ***Retimonoletes*** Pierce [S].

Remarks: ***Microfoveolatosporis*** Krutzsch is comparable to spores of extant ***Schizaea*** Smith (Dettmann, 1963; Potonié, 1966). ***Foveomonoletes*** van der Hammen ex Mathur, ***Reticulosporis*** Krutzsch, and ***Retimonoletes*** Pierce are the synonyms of ***Microfoveolatosporis*** Krutzsch (Potonié, 1966, 1970).

3.3.2.13 Order: SELAGINELLALES Prantl

The extant order SELAGINELLALES Prantl consists of the family SELAGINELLACEAE Willkomm with the single genus ***Selaginella*** de Beauvois (Schuettpelz et al., 2016). Fossils with *in situ* spores of ***Selaginella*** de Beauvois and ***Selaginellites*** Zeiller can already be found in the Carboniferous (Bek et al., 2001; Rossler and Buschmann, 1994). Extant species are adapted to various environments from cold to warm as well as from wet to dry. For example, ***Selaginella*** *vardei* Léveillé is mainly distributed in the cold region of Tibet at altitudes between 2700 and 3800 m, whereas ***Selaginella*** *pseudopaleifera* von Handel-Mazzetti mainly lives in the warm and wet region of North China at altitudes between 200 and 350 m (Zeng and Huo, 2004). ***Selaginella*** *selaginoides* (Linnaeus) Link is a base-rich mire plant with a circumboreal range of habitats. ***Selaginella*** *deflexa* Brackenridge is endemic to bogs in the warm Hawaiian archipelago. The so-called resurrection plant ***Selaginella*** *lepidophylla* (Hooker & Greville) Spring is adapted to seasonal drought by having the ability to inroll both leaves and stems to prevent excessive water loss (Kramer and Green, 1990). Therefore, the plants are generally euryphytes and eurythermic plants.

***Selaginellites gutbierii* type megaspore**

Extant megaspore: ***Selaginella*** *alligans* Hieronymus (Tryon and Lugardon, 1991; p. 617, Pl. 231, Fig. 65)
In situ* megaspore:** ***Selaginella *gutbierii* (Göppert) Thomas (Bek et al., 2001; p. 61, Pl. II, Figs. 3-6)
In situ* megaspore:** ***Selaginellites *gutbieri* (Göppert) Kidston (Rossler and Buschmann, 1994; p. 266, Pl. IV, Fig. 3)

Key characters: This type of megaspore is trilete, circular or slightly subtriangular, generally 200-1040 µm in size. The trilete laesurae are raised and extend to the equator. It has an equatorial flange. The ornament on the distal face is more prominent than on the proximal face and become strongly radial towards and upon the flange.

Dispersed spores: The dispersed megaspore genus related to this type is ***Triangulatisporites*** Potonié et Kremp.

Remarks: ***Triangulatisporites*** Potonié et Kremp has been discovered as *in situ* spores of ***Selaginella*** de Beauvois (Bek et al., 2001) and ***Selaginellites*** Zeiller (Rossler and Buschmann, 1994).

***Selaginella rupestris* type megaspore**

Extant megaspore: ***Selaginella*** *eclipes* Buck (Tryon and Lugardon, 1991; p. 613, Pl. 231, Fig. 42)
Extant megaspore: ***Selaginella*** *rupestris* (Linnaeus) Spring (Tryon and Lugardon, 1991; p. 613, Pl. 231, Figs. 35-36)

Key characters: This type of megaspore is trilete, circular or slightly subtriangular, generally 200-1040 µm in size. Its laesurae normally do not extend to the equator. It has no equatorial flange.

Dispersed spores: The thirteen dispersed megaspore genera related to this type are ***Aneuletes*** Harris, ***Bacutriletes*** van der Hammen ex Potonié, ***Cabochonicus*** Batten and Ferguson, ***Echitriletes*** van der Hammen ex Potonié, ***Erlansonisporites*** Potonié, ***Horstisporites*** Potonié, ***Hughesisporites*** Potonié [?], ***Istisporites*** Potonié, ***Kerhartisporites*** Knobloch, ***Ricinospora*** Bergad, ***Rugotriletes*** van der Hammen ex Potonié, ***Thylakosporites*** Potonié, and ***Verrutriletes*** van der Hammen ex Potonié [?].

Remarks: ***Aneuletes*** Harris, ***Bacutriletes*** van der Hammen ex Potonié, ***Cabochonicus*** Batten and Ferguson, ***Echitriletes*** van der Hammen ex Potonié, ***Erlansonisporites*** Potonié, ***Horstisporites*** Potonié, ***Kerhartisporites*** Knobloch, ***Ricinospora*** Bergad, ***Rugotriletes*** van der Hammen ex Potonié, and ***Thylakosporites*** Potonié are comparable to megaspores of extant ***Selaginella*** de Beauvois (Batten, 2012; Batten and Ferguson, 1987; Cottnam et al., 2000; Morbelli, 1990). The original name of ***Istisporites*** Potonié is ***Selaginellites*** Zeiller. However, since ***Selaginellites*** Zeiller has been used as the name for the fossil plant, the name ***Istisporites*** Potonié was given for the dispersed megaspore (Potonié, 1956).

Selaginella gutbierii type microspore

In situ* spore: *Selaginella *gutbierii* (Göppert) Thomas (Bek et al., 2001; p. 60, Pl. I, Figs. 5-8)
Extant spore: *Selaginella* *leptophylla* Baker (Tryon and Lugardon, 1991; p. 609, Pl. 231, Fig. 19)
Extant spore: *Selaginella* *rossii* (Baker) Warburg (Tryon and Lugardon, 1991; p. 609, Pl. 231, Fig. 11)
Extant spore: *Selaginella* *selaginoides* Michigan (Tryon and Lugardon, 1991; p. 609, Pl. 231, Figs. 1-2)

Key characters: This type of microspore is trilete, with a gemmate, verrucate or echinate exospore, generally 18-60 µm in size. The proximal face can be partially or completely smooth. Some spores have a membranous equatorial flange (zona). The exospore has two layers.

Dispersed spores: The thirty-one dispersed microspore genera related to this type are ***Aequitriradites*** Delcourt et Sprumont [S], ***Anapiculatisporites*** Potonié et Kremp [?], ***Anaplanisporites*** Jansonius [?], ***Anguisporites*** Potonié et Klaus [?], ***Antulsporites*** Archangelsky & Gamerro [S], ***Bayanhuasporites*** Yu [?], ***Cadargasporites*** de Jersey et Paten [?], ***Carnisporites*** Mädler, ***Cepulina*** Maljavkina [S], ***Ceratosporites*** Cookson et Dettmann, ***Cirratriradites*** Wilson et Coe, ***Cirratrisporites*** Leveine [S], ***Clavatisporites*** Kedves et Simoncsics, ***Dentellisporites*** Mädler [S], ***Echinatisporis*** Krutzsch, ***Heliosporites*** Schulz ex Srivastava, ***Herkosporites*** Stover [?], ***Indotriradites*** Tiwari [S], ***Kraeuselisporites*** Leschik, ***Liburnisporis*** Srivastava [?], ***Limbosporites*** Nilsson, ***Lusatisporis*** Krutzsch, ***Multinodisporites*** Chlonova, ***Neoraistrickia*** Potonié, ***Patellisporites*** Ouyang, ***Perotriletes*** Erdtman ex Couper [?], ***Pustechinosporis*** Krutzsch [?], ***Selaginellidites*** Krasnova, ***Tethysispora*** Vijaya et Tiwari [?], ***Tririctus*** Wilson, and ***Uvaesporites*** Döring.

Remarks: ***Anguisporites*** Potonié et Klaus, ***Ceratosporites*** de Jersey et Paten, ***Clavatisporites*** Kedves et Simoncsics, ***Echinatisporis*** Krutzsch, ***Heliosporites*** Schulz ex Srivastava, ***Kraeuselisporites*** Leschik, ***Limbosporites*** Nilsson, ***Lusatisporis*** Krutzsch, ***Multinodisporites*** Chlonova, ***Neoraistrickia*** Potonié, ***Patellasporites*** Ouyang, ***Selaginellidites*** Krasnova, ***Tririctus*** Wilson, and ***Uvaesporites*** Döring are comparable to the spores of modern ***Selaginella*** de Beauvois (Ames and Spackman, 1981; Dettmann, 1963; Kremp and Ames, 1965b; Kremp et al., 1967; Potonié, 1966, 1970; Traverse and Ames, 1971, 1979; Traverse et al., 1973b; Traverse et al., 1969). ***Aequitriradites*** Delcourt et Sprumont is a synonym of ***Selaginellidites*** Krasnova (Potonié, 1966). ***Carnisporites*** Mädler and ***Cirratriradites*** Wilson et Coe are comparable to the *in situ* spores of ***Selaginellites*** Zeiller and ***Selaginella*** de Beauvois (Bek et al., 2001; Potonié, 1958; Rossler and Buschmann, 1994; Traverse and Ames, 1968). ***Cirratrisporites*** Leveine is a synonym of ***Cirratriradites*** Wilson et Coe, ***Cepulina*** Maljavkina of ***Neoraistrickia*** Potonié, ***Dentellisporites*** Mädler of ***Limbosporites*** Nilsson, ***Indotriradites*** Tiwari of ***Kraeuselisporites*** Leschik, ***Antulsporites*** Archangelsky & Gamerro of ***Heliosporites*** Schulz ex Srivastava (Potonié, 1966, 1970).

3.3.3 Gymnospermae

3.3.3.1 Order: ARAUCARIALES Gorozhankin

Family: ARAUCARIACEAE Henkel & Hochstetter

Most species of extant ARAUCARIACEAE Henkel & Hochstetter (Christenhusz et al., 2011) are restricted to subtropical rainforests in the Pacific and the Southeast Asian region and tend to be most common at the margins of complex forest types. Normally they are exposed to the atmosphere above the forest canopy and they are not able to regenerate under a dense canopy in the absence of disturbances such as tectonic and volcanic activity (Kershaw and Wagstaff, 2001). Fossils with *in situ* pollen of ***Alkastrobus*** Del Fueyo & Archangelsky and ***Upatoia*** Leslie, Herendeen, et Crane are known from the Mesozoic (Del Fueyo and Archangelsky, 2005; Leslie et al., 2009). The plants are generally hygrophytes and megathermic plants.

Alkastrobus peltatus type pollen

In situ* pollen: *Alkastrobus* *peltatus Del Fueyo et Archangelsky (Del Fueyo and Archangelsky, 2005; p. 762, Pl. 4, Figs. D-E)
Extant pollen: *Araucaria* *araucana* (Molina) Koch (van Konijnenburg-van Cittert, 1971; p. 92, Pl. XII, Figs. 1-2)
In situ* pollen: *Apterocladus *lanceolatus* Archangelsky (Archangelsky, 1966; p. 313, Pl. 68, Figs. 68-70)

Key characters: This type of pollen is circular, with a smooth or scabrate exine, generally 50-70 µm in size. Its nexine detach from the sexine at the equator and shrunk to some degree forming an "inner body" which appears to be "monosaccate" or "polysaccate". On some grains, there is a tetrad scar.

Dispersed pollen: The seven dispersed pollen genera related to this type are ***Applanopsipollenites*** Levet-Carette [S], ***Applanopsis*** Döring, ***Balmeiopsis*** Archangelsky, ***Callialasporites*** Sukh Dev [S], ***Cyclusphaera*** Elsik, ***Pflugipollenites*** Pocock [S], and ***Singhiapollis*** Kar et Sah [S].

Remarks: ***Cyclusphaera*** Elsik is comparable to the *in situ* pollen of ***Alkastrobus*** Del Fueyo et Archangelsky (Del Fueyo and Archangelsky, 2005). ***Callialasporites*** Sukh Dev is comparable to the *in situ* pollen of ***Apterocladus*** Archangelsky (Balme, 1995). ***Applanopsipollenites*** Levet-Carette, ***Applanopsis*** Döring, ***Pflugipollenites*** Pocock, and ***Singhiapollis*** Kar et Sah are synonyms of ***Callialasporites*** Sukh Dev (Song et al., 2000). But ***Applanopsis*** Döring has priority over ***Callialasporites*** Sukh Dev (van Konijnenburg-van Cittert, 1971). ***Balmeiopsis*** Archangelsky is comparable to ***Cyclusphaera*** Elsik (Archangelsky, 1994).

Araucaria bidwillii type pollen

Extant pollen: *Agathis* *australis* Salisbury (Pocknall, 1981a; p. 271, Pl. 3, Figs. a-d)
Extant pollen: *Araucaria* *bidwillii* Hooker (Li et al., 2011; p. 125, Figs. 1-4)
In situ* pollen: *Upatoia *barnardii* Leslie, Herendeen et Crane (Leslie et al., 2009; p. 130, Pl. 1, Figs. C-D)
Extant pollen: *Wollemia* *nobilis* Jones, Hill et Allen (Chambers et al., 1998; p. 170, Pl. 7, Figs. A-D)

Key characters: This type of pollen is circular, with a smooth or scabrate exine, generally 45-80 µm in size. The exine is often folded and split. A large thinning zone is often preserved on one pole.

Dispersed pollen: The five dispersed pollen genera related to this type are ***Araucariacites*** Cookson ex Couper, ***Dilwynites*** Harris, ***Granulonapites*** Cookson ex Nilsson [S], ***Hunanpollenites*** Qian, Zhao et Wu [?], and ***Xilinipollis*** Liu et Hua [?].

Remarks: ***Araucariacites*** Cookson ex Couper is comparable to the *in situ* pollen of ***Upatoia*** Leslie, Herendeen et Crane (Leslie et al., 2009) and the extant pollen of ***Agathis*** Salisbury and ***Araucaria*** Jussieu (Batten and Dutta, 1997). ***Dilwynites*** Harris is comparable to the to pollen of extant ***Wollemia*** Jones, Hill et Allen (Chambers et al., 1998). ***Granulonapites*** Cookson ex Nilsson is the synonym of ***Araucariacites*** Cookson ex Couper (Potonié, 1960).

Family: PODOCARPACEAE Endlicher

Species of extant PODOCARPACEAE Endlicher (Christenhusz et al., 2011) are shrubs and trees that are mostly restricted to the Southern Hemisphere in tropical-subtropical mountains. Drier climates are tolerated only by a limited number of species. Most of them are in the wet mountain forests of tropical regions, and compete for rocky habits (Kramer and Green, 1990). Fossils with *in situ* pollen of ***Trisacocladus*** Archangelsky are known from the Mesozoic (Baldoni and Taylor, 1982). PODOCARPACEAE Endlicher are generally hygrophytes and megathermic plants.

Dacrydium franklinii type pollen

Extant pollen: *Acmopyle* *pancheri* (Brongniart & Gris) Pilger (Moller et al., 2000; p. 151, Pl. 1, Fig. A)
Extant pollen: *Dacrydium* *franklinii* Hooker (Schwendemann et al., 2007; p. 1373-1374, Figs.1, 4, 7, 10, 13)
Extant pollen: *Nageia* *nagi* Kuntze (Li et al., 2011; p. 77, Figs. 1-6)
Extant pollen: *Phyllocladus* *hypophyllus* Hooker (Moller et al., 2000; p. 151, Pl. 1, Fig. C)

Extant pollen: ***Podocarpus*** *forrestii* Craib et Smith (Li et al., 2011; p. 78, Figs. 1-6)

Key characters: This type of pollen is bisaccate, with a distal sulcus and a proximal cappa, generally 25-120 µm in size. The cappa can be granulate, rugulate, or reticulate. The sacci are typically distally inclined.

Dispersed pollen: The twelve dispersed pollen genera related to this type are ***Dacrydiumites*** Cookson ex Harris, ***Gamerroites*** Archangelsky, ***Indusiisporites*** Leschik, ***Lygistepollenites*** (Cookson ex Pike) Harris, ***Microalatidites*** Mildenhall, ***Parcisporites*** Leschik, ***Parvisaccites*** Couper, ***Phrixipollenites*** Haskell [?], ***Phyllocladidites*** Cookson ex Couper, ***Podocarpidites*** (Cookson ex Couper) Potonié, ***Pristinuspollenites*** Tschudy [?], and ***Rugubivesiculites*** Pierce.

Remarks: ***Dacrydiumites*** Cookson ex Harris, ***Lygistepollenites*** (Cookson ex Pike) Harris, ***Parcisporites*** Leschik, ***Parvisaccites*** Couper, ***Phyllocladidites*** Cookson ex Couper, and ***Rugubivesiculites*** Pierce are comparable to pollen of extant ***Dacrydium*** Lambert (Ames et al., 1976; Kremp and Ames, 1962a, 1965a; Potonié, 1958; Povilauskas, 2012; Traverse et al., 1973a). ***Indusiisporites*** Leschik and ***Phyllocladidites*** Cookson ex Couper are comparable to the pollen of extant ***Phyllocladus*** Richard ex Mirbel (Potonié, 1958, 1960, 1966). ***Gamerroites*** Archangelsky and ***Podocarpidites*** (Cookson ex Couper) Potonié are comparable to the pollen of extant ***Podocarpus*** L'Hér. ex Pers (Archangelsky and Seoane, 2005; Kremp et al., 1958). Potonié (1960) supposed that ***Quadraeculina*** Maljavkina was most close to the pollen of ***Indusiisporites*** Leschik, but did not provided the reason in detail. Based on the study of the ultrastructure of the exine, Batten and Dutta (1997) demonstrated the protosaccate morphology of ***Quadraeculina*** Maljavkina and concluded that the pollen is not comparable to pollen of any modern gymnosperm family.

Dacrycarpus dacrydioides type pollen

Extant pollen: ***Dacrycarpus*** *dacrydioides* (Richard) de Laub (Hesse et al., 2009; p. 99, Figs. 5-6)
Extant pollen: ***Dacrycarpus*** *dacrydioides* (Richard) de Laub (Pocknall, 1981b; p.92, Pl. 16, Figs. a-l)
Extant pollen: ***Microstrobos*** *niphophilus* Garden & Johnson (Hesse et al., 2009; p. 99, Figs. 3-4)
Extant pollen: ***Podocarpus*** *nivalis* Hooker (Pocknall, 1981b; p.88, Pl. 14, Figs. e-f)
In situ **pollen:** ***Trisacocladus*** *trigrensis* Archangelsky (Baldoni and Taylor, 1982; p. 25, Pl. I, Figs. 2-5)

Key characters: This type of pollen is polysaccate, with a distal sulcus and a proximal cappa, generally 65-80 µm in size. The cappa can be granulate, rugulate, or reticulate. The sacci are typically distally inclined.

Dispersed pollen: The four dispersed pollen genera related to this type are ***Dacrycarpites*** Cookson & Pike, ***Microcachryidites*** Cookson ex Couper, ***Podosporites*** Rao, and ***Trisaccites*** Cookson & Pike.

Remarks: ***Dacrycarpites*** Cookson & Pike is comparable to the pollen of extant ***Podocarpus*** L'Hér. ex Pers and ***Dacrycarpus*** de Laubenfels (Kremp and Ames, 1962a). ***Podosporites*** Rao is comparable to the pollen of extant ***Podocarpus*** L'Hér. ex Pers and ***Microstrobos*** Garden & Johnson (Schrank, 2010; Traverse and Ames, 1968). ***Trisaccites*** Cookson & Pike is comparable to the *in situ* pollen of ***Trisacocladus*** Archangelsky (Baldoni and Taylor, 1982). ***Microcachryidites*** Cookson ex Couper has been found *in situ* with the wood of ***Podocarpoxylon*** Gothan (Césari et al., 2015) and it is comparable to the pollen of extant ***Microstrobos*** Garden & Johnson (Specht et al., 1992).

3.3.3.2 Order: BENNETTITALES Engler

The order BENNETTITALES Engler (McLoughlin et al., 2018) is also called CYCADEOIDEALES Berry (Potonié, 1967a). The Mesozoic species were 1- to 3-m-tall shrubs distributed in both the northern and southern hemispheres (Pott and McLoughlin, 2014; Taylor et al., 2009). The order consists of the two families WILLIAMSONIACEAE Carruthers with mainly Late Triassic and Jurassic representatives and BENNETTITACEAE Engler (CYCADEOIDEACEAE Wieland) with mainly Cretaceous representatives (Popa, 2019). ***Nilssoniopteris*** Nathorst (Zhao et al., 2018) and ***Otozamites*** Braun (Wang et al., 2008) have been found mainly in the subtropical-tropical climate zone of the Mesozoic. Leaves of the WILLIAMSONIACEAE Carruthers are commonly associated with coaly facies and the parent plants may have been specialized to colonize the surfaces of mires (Pott and McLoughlin, 2014). Therefore, the BENNETTITALES Engler were generally hygrophytes and megathermic plants.

Cycadeoidea dacotensis type pollen

In situ* pollen: *Cycadeoidea *dacotensis* (McBride) Ward (Osborn and Taylor, 1995; p. 1076-1078, Figs. 1-16)

In situ* pollen: *Cycadeoidea *dacotensis* (McBride) Ward (Taylor, 1973; p. 159, Pl. I, Figs. 1-8)

In situ* pollen: *Weltrichia *sol* Harris (van Konijnenburg-van Cittert, 1971; p. 88, Pl. VIII, Figs. 1-3)

In situ* pollen: *Wielandia *punctata* Nathorst (Potonié, 1958; p. 137, Pl. 11, Fig. 126)

In situ* pollen: *Wielandia *magna* Malyavkina (Kremp et al., 1968; p. 147, Fig. 1)

In situ* pollen: *Williamsonia *gigas* Carruthers (Harris and Museum, 1969; p. 197, Pl. 5, Figs. 3-4)

In situ* pollen: *Williamsoniella *coronata* Thomas (van Konijnenburg-van Cittert, 1971; p. 87, Pl. VII, Figs. 3-4)

In situ* pollen: *Williamsoniella *coronata* Thomas (Zavialova and van Konijnenburg-van Cittert, 2011; p. 18, Pl. VII, Fig. 6)

Key characters: This type of pollen is monosulcate, generally 20-100 µm in size. The sulcus extends along the whole length of the pollen grain. The exine is two-layered with individual layers delimited from one another and often forms different folds.

Dispersed pollen: The five dispersed pollen genera related to this type are ***Bennettitaceaeacuminella*** Maljavkina, ***Bennettitaceaeinvolutella*** Maljavkina [?], ***Bharadwajapollenites*** (***Bharadwajipollenites***) Jain, ***Huabeisporites*** Qu, and ***Ricciisporites*** Lundblad.

Remarks: Technically, a sulcus is a furrow when located on the distal surface, usually with the distal pole as its center, whereas a colpus is a longitudinal furrow on a “meridional line” crossing the equator. However, most palynologists use the terms more loosely (Traverse, 2007). Based on the definition of Traverse (2007), the term colpus used by van Konijnenburg-van Cittert (1971) for the pollen of ***Williamsoniella*** *coronata* Thomas describes actually a sulcus. ***Bennettitaceaeacuminella*** Maljavkina is comparable to the *in situ* pollen of ***Wielandia*** Nathorst, while ***Bennettitaceaeinvolutella*** Maljavkina is close to ***Bennettitaceaeacuminella*** Maljavkina (Ames et al., 1976; Potonié, 1958). ***Bharadwajapollenites*** Jain and ***Ricciisporites*** Lundblad are ultrastructurally comparable to the *in situ* pollen of ***Cycadeoidea*** Buckland ex Lindley & Hutton (Mander et al., 2012; Zhang et al., 2020). ***Huabeisporites*** Qu is comparable to the *in situ* pollen of ***Cycadeoidea*** Buckland ex Lindley & Hutton and ***Weltrichia*** (Braun) Harris (Zhang et al., 2020). ***Bharadwajapollenites*** Jain sometimes is misspelled as ***Bharadwajipollenites*** Jain (e.g., Zavada, 1990).

3.3.3.3 Order: CAYTONIALES Thomas

The order CAYTONIALES Thomas consists of one family CAYTONIACEAE Thomas (Thomas and Seward, 1925). The species were cosmopolitan and rather common small trees in the Mesozoic plant communities though they never attaining a dominant status (Krassilov, 1977; Taylor and Taylor, 2006; Taylor and Taylor, 2009). The *in situ* fossils indicate a deltaic or floodplain environment in which water supply is abundant and where arborescent plants provide shade (Harris, 1964; Rees, 1993; van Konijnenburg-van Cittert, 1971). They were mainly distributed in the subtropical region of both hemispheres (Vakhrameev, 1991). Therefore, the CAYTONIALES Thomas were hygrophytes and megathermic plants.

Caytonanthus arberi type pollen

In situ* pollen: *Caytonanthus *arberi* (Thomas) Harris (Osborn, 1994; p. 1522, Figs. 4-11; p. 1523, Figs. 12-18; p. 1524, Figs. 19-24)

In situ* pollen: *Caytonanthus *arberi* (Thomas) Harris (van Konijnenburg-van Cittert, 1971; p. 81, Pl. I, Figs. 1, 2, 4)

In situ* pollen: *Caytonanthus *arberi* (Thomas) Harris (Zavada and Crepet, 1986; p. 261, Figs. 2-5)

In situ* pollen: *Caytonanthus *tyrmensis* Krassilov (Krassilov, 1977; p. 173, Pl. IX, Figs. 4-12; p. 174, Pl. X, Figs. 1-4; p. 175, Pl. XI, Figs. 1-4; p. 176, Pl. XII, Figs. 1-5; p. 177, Pl. XIII, Figs. 1-4;)

In situ* pollen: *Hydropterangium* *roesleri van Konijnenburg-van Cittert et al. (van Konijnenburg-van Cittert et al., 2017; p. 143, Pl. 3, Figs. D-K)

In situ* pollen: *Sagenopteris* *nilsoniana (Brongniart) Ward (Potonié, 1958; p. 129, Pl. 7, Fig. 66)

Key characters: This pollen of type is protobisaccate, with a distal sulcus and a proximal cappa, generally 20-40 µm in size. The sacci typically show lateral attachment, although in several grains the sacci are distally inclined. The cappa is generally psilate or finely ornamented.

Dispersed pollen: The four dispersed pollen genera related to this type are ***Caytodipterella*** Maljavkina, ***Caytonialespollenites*** Plausch [S], ***Caytonipollenites*** Couper [S], and ***Vitreisporites*** (Leschik) Jansonius.

Remarks: *Vitreisporites* (Leschik) Jansonius is comparable to the *in situ* pollen of ***Hydropterangium*** Halle and ***Caytonanthus*** Harris (van Konijnenburg-van Cittert, 1971; van Konijnenburg-van Cittert et al., 2017). ***Caytodipterella*** Maljavkina, ***Caytonialespollenites*** Plausch, and ***Caytonipollenites*** Couper are synonyms of ***Vitreisporites*** (Leschik) Jansonius (Potonié, 1958, 1960, 1970).

3.3.3.4 Order: CHEIROLEPIDIALES Anderson et Anderson

The order CHEIROLEPIDIALES Anderson et Anderson (Krassilov, 2009) consists of one family of Mesozoic conifers, the CHEIROLEPIDIACEAE Takhtajan. The species were large trees, woody shrubs, and possibly herbs (Steart et al., 2014). Evidence from sediments and cuticle morphology, most notably the sunken papillate stomata, indicate that the plants were adapted to xeric habitats and grew in brackish coastal mires as well as on the margin of freshwater rivers and lakes (Alvin, 1982; Steart et al., 2014). Generally, they are drought resistant, thermophilous shrubs and trees with a preference for subtropical to tropical climates, and were never dominant in cool regions (Francis, 1983; Vakhrameev, 1991). They were also adapted to semi-arid and arid low-lying water-margin environments that produce mud flats (Taylor et al., 2009; Vakhrameev, 1991). Therefore, they can be described as xerophytes and megathermic plants.

***Classostrobus crossii* type pollen**

In situ* pollen: *Classostrobus* *crossii Rothwell et al. (Rothwell et al., 2007; p. 66, Pl. 9, Figs. a-j)

In situ* pollen: *Classostrobus* *dalatzensis Yang (Yang, 2008; p. 693, Pl. 4, Figs. a-f)

In situ* pollen: *Classostrobus* *elliotii Hieger et al. (Hieger et al., 2015; p. 83, Pl. II, Figs. 1-12)

In situ* pollen: *Frenelopsis* *sp (Barale et al., 1988; p. 199, Pl. 3, Figs. 6-10)

In situ* pollen: *Hirmeriella* *muensteri (Schenk) Jung (Clement-Westerhof and van Konijnenburg-van Cittert, 1991; p. 174, Pl. XI, Figs. 3-5)

In situ* pollen: *Tomaxellia* *biforme Archangelsky (Archangelsky and Gamerro, 1967; p. 181, Pl. I, Figs. B-G)

Key characters: This type of pollen is circular, with a big ring furrow (operculum) near the equator, generally 15-60 µm in size. Some pollen grains show a pore (cryptopore) on the same side of the furrow, whereas other pollen grains have a trilete mark on the opposite side of the furrow. Furthermore, some pollen grains have also striations on the equatorial region.

Dispersed pollen: The twenty dispersed pollen genera related to this type are ***Camerosporites*** (Leschik) Clarke [?], ***Canalopollis*** Pflug [S], ***Circulina*** Maljavkina [S], ***Circumpollis*** Pflug [S], ***Classites*** González-Guzmán [?], ***Classoidites*** van Amerom, ***Classopollis*** Pflug, ***Corollina*** Maljavkina [S], ***Dicheiropollis*** Trevisan, ***Discisporites*** Leschik [?], ***Duplicisporites*** Leschik, ***Geopollis*** Zavialova, Buratti et Roghi, ***Gliscopollis*** Venkatachala [S], ***Granuloperculatipollis*** Venkatachala et Góczán [S], ***Monilapollis*** Chang [S], ***Pagiophyllumpollenites*** Chang [S], ***Paracirculina*** Klaus, ***Partitisporites*** Leschik, ***Praecirculina*** Klaus, and ***Rhaetipollis*** Schulz [?].

Remarks: *Classopollis* Pflug is comparable to the *in situ* pollen of ***Classostrobus*** Alvin, Spicer & Watson, ***Hirmeriella*** Hörhammer and ***Tomaxellia*** Archangelsky (Archangelsky and Gamerro, 1967; Clement-Westerhof and van Konijnenburg-van Cittert, 1991; Hieger et al., 2015; Rothwell et al., 2007). The ultrastructural characters of ***Classoidites*** van Amerom, ***Dicheiropollis*** Trevisan, ***Duplicisporites*** Leschik, ***Geopollis*** Zavialova, Buratti et Roghi, and ***Partitisporites*** Leschik are comparable to that of ***Classopollis*** Pflug (Pocock et al., 1990; Schrank, 2017; Srivastava, 1994; Zavialova et al., 2010; Zavialova and Roghi, 2005). It was proposed that ***Classopollis*** Pflug possibly originated from ***Discisporites*** Leschik and ***Grebespora*** Jansonius (Alvin, 1982; Zavialova et al., 2010), but this has been repeatedly criticized (Zavialova et al., 2010). The operculum, which has never been found on spores, is the most remarkable character for the pollen of CHEIROLEPIDIACEAE Takhtajan (Zhang et al., 2020). ***Canalopollis*** Pflug, ***Circulina*** Maljavkina, ***Circumpollis*** Pflug, ***Corollina*** Maljavkina, ***Gliscopollis*** Venkatachala, ***Monilapollis*** Chang, and ***Pagiophyllumpollenites*** Chang are synonyms of ***Classopollis*** Pflug (Potonié, 1960; Song et al., 2000). ***Granuloperculatipollis*** Venkatachala et Góczán is a synonym of ***Classoidites*** van Amerom (Potonié, 1970). ***Discisporites*** Leschik is comparable to ***Circulina*** Maljavkina (Norris, 1965). ***Paracirculina*** Klaus and ***Praecirculina*** Klaus are comparable to ***Duplicisporites*** Leschik (Potonié, 1966).

3.3.3.5 Order: CORYSTOSPERMALES Petriella

The CORYSTOSPERMALES Petriella (Decombeix et al., 2014) were probably small to large woody shrubs and trees that originated in the late Paleozoic and spread worldwide in the Mesozoic during the climate warming of the Late Permian/Early Triassic (Taylor et al., 2006; Taylor et al., 2009). ***Dicroidium*** Gothan apparently originated in the palaeotropics during the late Palaeozoic and subsequently migrated southwards, eventually colonizing the entire extra-tropical region of Gondwana during the Middle and Late Triassic (Kerp et al., 2006). This geographic expansion was accompanied by a remarkable diversification, enhanced by adaptations to different environmental conditions (Bomfleur and Kerp, 2010). The earliest representatives of ***Dicroidium*** Gothan flourished in the palaeotropics under a hot, humid climate with high annual rainfall and short dry seasons (Abu Hamad et al., 2008; Uhl et al., 2007). The stem anatomy of ***Cuneumxylon*** Artabe & Brea from Argentina indicates that the plants were well adapted to tolerate prolonged periods of water stress in seasons of drought (Artabe and Brea, 2003). The environment of the fossil ***Cuneumxylon*** Artabe & Brea correlates with that of an extant subtropical seasonal forest (dry monsoonal forests) (Brea et al., 2008). Although the leaf fossil of ***Pachypteris*** *papillosa* (Thomas & Bose) Harris from Yorkshire is thought to be a large mangrove shrub forming a thicket beside the river, it should also be noted that the leaf of ***Pachypteris*** *lanceolata* Brongn from Yorkshire shows no link to marine horizons (Harris, 1983). Therefore, the CORYSTOSPERMALES Petriella were mesophytes and megathermic plants.

Pteruchus dubius **type pollen**

In situ **pollen:** ***Pteroma*** *thomasi* Harris (van Konijnenburg-van Cittert, 1971; p. 82, Pl. II, Figs. 1, 3, 4, 6)
In situ **pollen:** ***Pteruchus*** *africanus* Thomas (Townrow, 1962; p. 29, Pl. 5, Figs. b, c, e, f)
In situ **pollen:** ***Pteruchus*** *dubius* (Thomas) Townrow (Townrow, 1962; p. 29, Pl. 5, Figs. a, d)
In situ **pollen:** ***Pteruchus*** *dubius* (Thomas) Townrow (Taylor et al., 1984; p. 321, Pl. I, Figs. 3, 4)
In situ **pollen:** ***Pteruchus*** *sp.* (Osborn and Taylor, 1993; p. 210, Pl. II, Figs. 1-6)

Key characters: This type of pollen is bisaccate (protobisaccate?), with a distal sulcus and a proximal cappa, generally 60-115 µm in size. The sacci are slightly distally inclined. The ornamentation of the sacci as well as the boundary between sacci and corpus are often obscure.

Dispersed pollen: The four dispersed pollen genera related to this type are ***Alisporites*** (Daugherty) Jansonius, ***Falcisporites*** (Leschik) Klaus, ***Pteruchipollenites*** Couper, and ***Scopulisporites*** Leschik.

Remarks: ***Alisporites*** (Daugherty) Jansonius [?], ***Falcisporites*** (Leschik) Klaus [?], ***Pteruchipollenites*** Couper and ***Scopulisporites*** Leschik are comparable to the *in situ* pollen of ***Pteruchus*** Thomas (Balme, 1995; Kremp et al., 1960a; Osborn and Taylor, 1993; Taylor et al., 1984). Some grains of ***Pteruchus*** *sp* are protosaccate (Osborn and Taylor, 1993), but detail studies especially under TEM are needed.

3.3.3.6 Order: CUPRESSALES Link

Family: CUPRESSACEAE Gray

The extant family CUPRESSACEAE Gray (Christenhusz et al., 2011) includes the former family of

TAXODIACEAE Saporta (Christenhusz et al., 2011). The species are small to large sized trees that distributed worldwide during the Mesozoic (Taylor et al., 2009). Ecologically, many extant species are strictly mesic, occurring mostly in regions of high rainfall and generally high humidity, largely on mountain flanks but also sometimes spreading to riverside and more boggy valley bottom sites. Four genera have species tolerant to wet boggy or swampy sites. Seven genera contain mostly species tolerant to strong illumination, dry air, and considerable summer desiccation in generally Mediterranean environments (Kramer and Green, 1990). They are generally euryphytes and eurythermic plants.

Elatides williamsonii **type pollen**

In situ **pollen:** ***Drumhellera*** *kurrnanniae* Serbet and Stockey (Serbet and Stockey, 1991; p. 74, Pl. IV, Figs. 1-6)

In situ **pollen:** ***Elatides*** *williamsonii* (Bourguignat) Seward (Kurmann, 1991; p. 295, Pl. II, Figs. 1-3, 5-6)

In situ **pollen:** ***Elatides*** *williamsonii* (Bourguignat) Seward (van Konijnenburg-van Cittert, 1971; p. 93, Pl. XIII, Figs. 3, 4)

Key characters: This type of pollen is circular, monoporoid, with a scabrate exine, generally 10-60 µm in size. The sexine is separated from the nexine forming a "perine" structure loosely fitting, normally wrinkled or torn.

Dispersed pollen: The four dispersed pollen genera related to this type are ***Admolia*** Batten [?], ***Exesipollenites*** Balme, ***Perinopollenites*** Couper, and ***Spheripollenites*** Couper.

Remarks: ***Exesipollenites*** Balme and ***Perinopollenites*** Couper are comparable to the *in situ* pollen of ***Elatides*** Heer (Kremp and Ames, 1962a; Potonié, 1960; Srivastava, 1987). ***Elatides*** *williamsonii* (Bourguignat) Seward is comparable to ***Perinopollenites*** Couper, but when its sexine is lost, it is comparable to ***Exesipollenites*** Balme and ***Spheripollenites*** Couper (van Konijnenburg-van Cittert, 1971).

Cryptomeria japonica **type pollen**

Extant pollen: ***Cryptomeria*** *japonica* Don (Hesse et al., 2009; p. 154, Figs. 1, 3)
Extant pollen: ***Cunninghamia*** *lanceolata* (Lamb) Hooker (Hesse et al., 2009; p. 154, Fig. 6)
Extant pollen: ***Metasequoia*** *glyptostroboides* Hu et Cheng (Hesse et al., 2009; p. 154, Figs. 4, 5)
Extant pollen: ***Sequoia*** *sempervirens* (Don) Endlicher (Hui Ho and Sziklai, 1973; p. 20, Pl. II, Figs. 7, 8)
Extant pollen: ***Taxodium*** *ascendens* Brongniart (Li et al., 2011; p. 89, Figs. 1-4)

Key characters: This type of pollen is circular, scabrate, with a leptoma and a papilla on the distal pole, generally 25-50 µm in size. Sometimes, it collapses or splits.

Dispersed pollen: The four dispersed pollen genera related to this type are ***Cryptomeriapollenites*** Kremp ex Potonié, ***Sequoiapollenites*** Thiergart, ***Taxodiaceaepollenites*** Kremp ex Potonié, and ***Taxodiacites*** Botscharnikova [?].

Remarks: ***Cryptomeriapollenites*** Kremp ex Potonié is comparable to extant pollen of ***Cryptomeria*** Don (Potonié, 1960). ***Sequoiapollenites*** Thiergart is comparable to extant pollen of ***Sequoia*** Endlicher (Potonié, 1966). ***Taxodiaceaepollenites*** Kremp ex Potonié is comparable to extant pollen of ***Taxodium*** Richard (Zetter et al., 2011).

Cupressus funebris **type pollen**

Extant pollen: ***Chamaecyparis*** *nootkatensis* (Don) Spach (Li et al., 2011; p. 93, Figs. 1-4)
Extant pollen: ***Cupressus*** *funebris* Endlicher (Li et al., 2011; p. 99, Figs. 1-4)
Extant pollen: ***Juniperus*** *formosana* Hayata (Li et al., 2011; p. 104, Figs. 1-2)
Extant pollen: ***Sabina*** *vulgaris* Antoine (Li et al., 2011; p. 108, Figs. 1-4)

Key characters: This type of pollen is circular, scabrate, with a leptoma, generally 20-30 µm in size. Sometimes, it collapses or splits.

Dispersed pollen: The dispersed pollen genera related to this type is ***Cupressacites*** Bolchovitina.

Remarks: ***Cupressacites*** Bolchovitina is comparable to extant pollen of ***Cupressus*** Linnaeus and ***Juniperus*** Linnaeus (Cavagnetto and Anadon, 1996).

Family: SCIADOPITYACEAE Luerssen

The extant family SCIADOPITYACEAE Luerssen (Christenhusz et al., 2011) consists of on genus with one species, but fossil genera such as ***Sciadopitophyllum*** Christophel, ***Sciadopityostrobus*** Saiki and ***Oswaldheeria*** Bose & Manum can be found in Cretaceous records (Taylor et al., 2009). The only extant species has a thinly scattered distribution through the mountains of southern Japan, at moderate altitudes. Here, it is confined to sites of rather rich moist soils on damp, cloud-wrapped mountain flanks within cool-temperate, mixed evergreen-deciduous, forest vegetation (Kramer and Green, 1990). Fossil ***Sciadopitys*** Siebold & Zuccarini stems found in the Miocene of Germany are reported from an *in situ* peat/swamp forest and thus indicating that the plants of this family were at least in the geological past an important component of the wetland vegetation (Figueiral et al., 1999). Therefore, they are hygrophytes and microthermic plants.

Sciadopitys verticillata **type pollen**

Extant pollen: ***Sciadopitys*** *sp.* (Grimsson and Zetter, 2011; p. 303, Pl. 28, Figs. A-H)

Extant pollen: ***Sciadopitys*** *verticillata* (Thunberg) Siebold et Zuccarini (Hui Ho and Sziklai, 1973; p. 19, Pl. I, Figs. 5-6)

Key characters: This type of pollen is circular, gemmate or verrucate, with a leptoma, generally 35-45 µm in size.

Dispersed pollen: The two dispersed pollen genera related to this type are ***Sciadopitipollenites*** Takahashi and ***Sciadopityspollenites*** Raatz ex Potonié.

Remarks: ***Sciadopitipollenites*** Takahashi and ***Sciadopityspollenites*** Raatz ex Potonié are comparable to pollen of extant ***Sciadopitys*** Siebold & Zuccarini (Potonié, 1966; Zetter et al., 2011).

3.3.3.7 Order: CYCADALES Persoon ex Berchtold et Presl

The extant order CYCADALES Persoon ex Berchtold et Presl consists of two families, the CYCADACEAE Persoon and the ZAMIACEAE Horaninow, with species distributing mainly in tropical and subtropical regions (Christenhusz et al., 2011). Fossils with *in situ* pollen of ***Androstrobus*** Schimper and ***Encephalartos*** Lehmann can be found in Mesozoic records (Hill, 1990; van Konijnenburg-van Cittert, 1971; Zavialova and van Konijnenburg-van Cittert, 2016). Extant cycads can occur in habitats ranging from dense tropical rainforest to open woodland (Kramer and Green, 1990). They are generally mesophytes and megathermic plants.

Androstrobus balmei **type pollen**

In situ **pollen:** ***Androstrobus*** *balmei* Hill (Hill, 1990; p. 167, Figs. 5-7; p. 169, Figs. 9-13)

In situ **pollen:** ***Androstrobus*** *manis* Harris (Zavialova and van Konijnenburg-van Cittert, 2016; p. 36, Pl. II, Figs. 1-14)

Extant pollen: ***Cycas*** *siamensis* Miquel (Li et al., 2011; p. 17, Figs. 1-5)

Extant pollen: ***Cycas*** *micholitzii* Dyer (Tekleva et al., 2007; p. 1168, Pl. 18, Figs. 1-4)

Extant pollen: ***Encephalartos*** *barteri* Carruthers (van Konijnenburg-van Cittert, 1971; p. 86, Pl. VI, Fig. 1)

Extant pollen: ***Stangeria*** *paradoxa* Moore (van Konijnenburg-van Cittert, 1971; p. 85, Pl. V, Figs. 5-7)

Extant pollen: ***Zamia*** *loddigesii* Miquel (van Konijnenburg-van Cittert, 1971; p. 86, Pl. VI, Figs. 3, 5)

Key characters: This type of pollen is ellipsoidal, monosulcate, foveolate or rugulate, generally 20-40 µm in size. The sulcus almost reaches the equator. For some pollen, the sculpture can only be seen under SEM. The exine is two-layered, with a more electron-dense endexine. The infratectum is alveolate.

Dispersed pollen: The three dispersed pollen genera related to this type are ***Brevimonosulcites*** Zhang, ***Cycadaceaelagella*** Malawkina [S], and ***Cycadaceaelagenella*** Maljavkina.

Remarks: ***Brevimonosulcites*** Zhang is comparable to pollen of extant ***Encephalartos*** Lehmann (Song et al., 2000). ***Cycadaceaelagella*** Malawkina and ***Cycadaceaelagenella*** Maljavkina are comparable to the pollen of extant ***Zamia*** Linnaeus (Ames et al., 1976; Potonié, 1958). ***Cycadaceaelagella*** Malawkina is the misspelling of ***Cycadaceaelagenella*** Maljavkina (Ames et al., 1976). ***Cycadopites*** Wodehouse was originally described from the Green River oil shales of Colorado, but Wodehouse did not attempt to separate the numerous forms which he observed (Kremp and Ames, 1961b) and no holotype was mentioned by the author (Potonié, 1958). ***Cycadopites*** (Wodehouse) Wilson & Webster (Kremp and Ames, 1961b) is a pure morphological genus with a broad definition. It has been found *in situ* in cycadalean, bennettitalean, and ginkgoalean plants (Balme, 1995). Therefore, the affinity for either ***Cycadopites*** Wodehouse or ***Cycadopites*** (Wodehouse) Wilson & Webster is obscure.

Androstrobus prisma type pollen

In situ* pollen: *Androstrobus *prisma* Thomas et Harris (Zavialova and van Konijnenburg-van Cittert, 2012; p. 16, Pl. I, Figs. 1-4, 6 ; p. 18, Pl. II, Figs. 1-7 ; p. 19, Pl. III, Figs. 1-11)

In situ* pollen: *Androstrobus *prisma* Thomas et Harris (van Konijnenburg-van Cittert, 1971; p. 84, Pl. IV, Figs. 6,7 ; p. 85, Pl. V, Figs. 1, 2)

In situ* pollen: *Androstrobus *prisma* Thomas et Harris (Hill, 1990; p. 169, Fig. 16)

In situ* pollen: *Cycandra *profusa* Krassilov et Delle (Tekleva et al., 2007; p. 1164, Pl. 16, Figs. 16-18; p. 1174, Pl. 21, Figs. 1-9)

Key characters: This type of pollen is inaperturate or leptomate, generally 25-35 µm in size. It has a indistinct and very thin nexine as well as a sexine with columellae and capita layer and grana, which are in surface view circular. The pollen grains are often folded, giving the impression that there is a colpus (sulcus), but grains that are not folded, do not show such a colpus (sulcus) and only sometimes a thin area.

Dispersed pollen: The dispersed pollen genus related to this type is ***Chasmatosporites*** (Nilsson) Pocock et Jansonius.

Remarks: ***Chasmatosporites*** Nilsson was thought to be comparable to the microspore of ***Lycostrobus*** *scotti* Nathorst (Kremp and Ames, 1965b). ***Chasmatosporites*** (Nilsson) Pocock et Jansonius is comparable to *in situ* pollen of ***Androstrobus prisma*** Thomas et Harris (van Konijnenburg-van Cittert, 1971). ***Chasmatosporites*** (Nilsson) Pocock et Jansonius may sometimes look superficially similar to ***Araucariacites*** Cookson ex Couper and ***Ginkgo*** Linnaeus, but there is no basis for a comparison of their wall structures (Batten and Dutta, 1997).

3.3.3.8 Order: CZEKANOWSKIALES Pant

The species of the order CZEKANOWSKIALES Pant (Huang et al., 2017) were deciduous trees extending from the Late Triassic into the Cretaceous. Based on the association of highly dissected foliage it was intended that they are closely related to the GINKGOALES Gorozhankin (Taylor et al., 2009). Nearly everywhere, where the representatives have been found, they occur in strata which appear to have been deposited under a humid temperate to tropical climate (Ash, 1994). Their leaves are densely distributed on the bedding planes of coal beds indicating that they were seasonally deciduous (Vakhrameev, 1991). Their distribution boundary retreated rapidly under the influence of increasing aridity and they predominated together with ancient GINKGOALES Gorozhankin (Vakhrameev, 1987). It can be therefore inferred that their living condition were similar. Therefore, the CZEKANOWSKIALES Pant were generally mesophytes and mesothermic plants.

Ixostrobus schmidtianus type pollen

In situ* pollen: *Ixostrobus schmidtianus (Heer) Krassilov (Krassilov, 1972; p. 92, Pl. 13, Figs. c, h, n, p)

Key characters: This type of pollen is ellipsoidal, psilate, monosulcate, about 30 µm in size.

Remarks: Krassilov (1972) only provided the sketches of the pollen. No detail is provided to compare it to any dispersed monosulcate pollen.

Leptostrobus cancer **type pollen**

In situ **pollen:** ***Leptostrobus*** *cancer* Harris (van Konijnenburg-van Cittert, 1971; p. 90, Pl. X, Figs. 1, 3)

Key characters: This type of pollen is monosaccate, circular, generally 55-60 µm in size. The corpus is only a little bit smaller than the saccus. The saccus wall is rather thin and scabrate.

Remarks: van Konijnenburg-van Cittert (1971) compared the *in situ* pollen ***Leptostrobus*** *cancer* Harris to ***Tsugaepollenites*** Potonié et Venitz ex Potonié*,* but the *in situ* pollen was described under LM and the description is too rough to be comparable to any dispersed pollen in detail. Even the pollen has been described in detail, it is still questionable, because van Konijnenburg-van Cittert (1971) mentioned that the pollen is not uniform at all, although one type seems to dominate. However, the possibility of contamination by alien pollen cannot be excluded.

3.3.3.9 Order: EPHEDRALES Dumortier

The extant order EPHEDRALES Dumortier consists of one family EPHEDRACEAE Dumortier with a single genus (Christenhusz et al., 2011). Fossils with *in situ* pollen of ***Piroconites*** Gothan have been found in Mesozoic strata (van Konijnenburg-van Cittert, 1992). Extant species are xerophytic, heliophilous, and in part also cold-resistant. Their Eurasian distribution forms a broad belt from the Canary Islands and the Mediterranean through the arid subtropical regions of Inner Asia as far as the Amur and Lena Rivers, with outliers on the Arabian Gulf and in the Tibesti Mountains (Kramer and Green, 1990). They are generally xerophytes and eurythermic plants.

Ephedra gerardiana **type pollen**

Extant pollen: ***Ephedra*** *americana* Humboldt & Bonpland ex Willdenow (El-Ghazaly et al., 1998; p. 226, Pl. 5, Figs. a-d)

Extant pollen: ***Ephedra*** *gerardiana* Wallich (Li et al., 2011; p. 21, Figs. 1-4)

Extant pollen: ***Ephedra*** *sinica* Stapf (Li et al., 2011; p. 24, Figs. 1-4)

In situ **pollen:** ***Piroconites*** *kuespertii* Gothan (van Konijnenburg-van Cittert, 1992; p. 298, Pl. III, Figs. 2-4)

Key characters: This type of pollen is ellipsoidal, inaperturate, bearing vertical ridges (plicate) extending almost from end to end, generally 25-60 µm in size. The exine is two layered. The ectexine curls up forming the ridges.

Dispersed pollen: The six dispersed pollen genera related to this type are ***Ephedracites*** Malyavkina [S], ***Ephedripites*** (Bolchovitina ex Potonié) Krutzsch, ***Ephedrites*** Zaklinskaja [S], ***Gnetaceaepollenites*** Thiergart*,* ***Singhia*** Srivastava [?]*,* and ***Steevesipollenites*** Stover.

Remarks: ***Ephedripites*** (Bolchovitina ex Potonié) Krutzsch is comparable to the *in situ* pollen of ***Piroconites*** Gothan (van Konijnenburg-van Cittert, 1992) and pollen of extant ***Ephedra*** Linnaeus (Song et al., 1999; Traverse et al., 1973a). ***Gnetaceaepollenites*** Thiergart and ***Steevesipollenites*** Stover are comparable to pollen of extant ***Ephedra*** Linnaeus (Potonié, 1958; Schrank, 2010). ***Ephedracites*** Malyavkina is a synonym of ***Ephedripites*** (Bolchovitina ex Potonié) Krutzsch (Potonié, 1960) and ***Ephedrites*** Zaklinskaja of ***Gnetaceaepollenites*** Thiergart (Potonié, 1966).

3.3.3.10 Order: ERDTMANITHECALES Friis & Pedersen

The Mesozoic fossil family ERDTMANITHECACEAE Friis & Pedersen is established for ***Eucommiidites***-producing plants and the order ERDTMANITHECALES Friis & Pedersen to accommodate this family (Friis and Pedersen, 1996). It proliferated during the Jurassic and Early Cretaceous and became extinct during the early part of the Late Cretaceous (Mendes et al., 2008). Their seeds are organized in the same way as

BENNETTITALES Engler and EPHEDRACEAE Dumortier, and may reflect similar ecological preferences. The *in situ* fossils are normally from sedimentary sequences where ephedroid seeds are also common (Friis et al., 2009; Mendes et al., 2010). This indicates that their living environment was maybe similar to that of the plants of the EPHEDRACEAE Dumortier. They were generally xerophytes and eurythermic plants.

Erdtmanitheca texensis **type pollen**

In situ **pollen:** ***Bayeritheca*** *hughesii* Kvacek and Pacltova (Kvacek and Pacltova, 2001; p. 702, Pl. 6, Figs. A-E)

In situ **pollen:** ***Bayeritheca*** *hughesii* Kvacek and Pacltova (Tekleva and Krassilov, 2009; p. 134, Pl. II, Fig. 7)

In situ **pollen:** ***Erdtmanispermum*** *balticum* Pedersen et al. (Pedersen et al., 1989; p. 289, Pl. 5, Figs. F-G; p. 291, Pl. 6, Figs. A-B)

In situ **pollen:** ***Erdtmanitheca*** *portucalensis* Mendes et al. (Mendes et al., 2010; p. 30, Pl. 4, Figs. A-L; p. 31, Pl. 5, Figs. A-D)

In situ **pollen:** ***Erdtmanitheca*** *texensis* Pedersen et al. (Pedersen et al., 1989; p. 283, Pl. 2, Figs. A-F)

In situ **pollen:** ***Eucommiitheca*** *hirsuta* Friis and Pedersen (Friis and Pedersen, 1996; p. 354, Pl. 3, Figs. B-D)

Key characters: This type of pollen is tricolpate, foveolate, with one well developed and two less developed colpi, generally 15-40 µm in size. The exine is two-layered. The ectexine is homogenous for inner and outer layers, granular for middle layer.

Dispersed pollen: The seven dispersed pollen genera related to this type are ***Decussosporites*** Brenner [?], ***Eucommiidites*** Erdtman ex Potonié*,* ***Hadrotricolpites*** Song et Qian [?]*,* ***Pretricolpipollenites*** Danzé-Corsin et Laveine [S]*,* ***Protoquercus*** Bolchovitina [?]*,* ***Pseudotricolpites*** Stanley [?]*,* and ***Trifossapollenites*** Rouse [S].

Remarks: Based on the definition of Traverse (2007) and Punt et al. (2007), the colpi on this type of pollen grain are actually sulci. The well developed colpus is a sulcus at the distal pole and the two less developed colpi are sulci at the proximal pole. But some authors (e.g., Pedersen et al., 1989) take all the three as colpi. ***Eucommiidites*** Erdtman ex Potonié is comparable to *in situ* pollen of ***Bayeritheca*** Kvacek & Pacltová*,* ***Erdtmanispermum*** Pedersen, Crane et Friis*,* ***Erdtmanitheca*** Pedersen, Crane et Friis*,* and ***Eucommiitheca*** Friis et Pedersen (Friis and Pedersen, 1996; Kvacek and Pacltova, 2001; Mendes et al., 2010; Pedersen et al., 1989). ***Decussosporites*** Brenner is comparable to ***Eucommiidites*** Erdtman ex Potonié (Brenner, 1963), but has only one proximal sulcus. The ultrastructure of ***Decussosporites*** Brenner is also comparable to some pollen grains of the Cycadophytes (Brenner, 1963), but the latter do not have a proximal sulcus. ***Decussosporites*** Brenner has also similarities with the *in situ* pollen of ***Brenneria*** Pedersen et al. with uncertain botanical affinity (Pedersen et al., 1993). ***Pretricolpipollenites*** Danzé-Corsin et Laveine and ***Trifossapollenites*** Rouse are synonyms of ***Eucommiidites*** Erdtman ex Potonié (Potonié, 1966).

3.3.3.11 Order: GINKGOALES Gorozhankin

Ginkgo *biloba* Linnaeus, the only extant species of the GINKGOALES Gorozhankin (Christenhusz et al., 2011), is a deciduous tree that can be 30 m in height and 9 m in trunk circumference (Kramer and Green, 1990). Mesozoic ginkgoalean plant fossils are found world-wide, except for equatorial regions and in Antarctica. After the Cretaceous, ginkgoalean plants began to decline rapidly. Their abundance was reduced and their distribution narrowed to only temperate forests (Wang et al., 2017). In spite of their broad adaptability, however, it appears that ginkgoaleans were more abundant and diverse in mesic, warm temperate to temperate climates similar to the climate in the relictual area of their living representative ***Ginkgo*** *biloba* Linnaeus (Zhou, 2009). Therefore, they are mesophytes and mesothermic plants.

Ginkgo biloba **type pollen**

In situ **pollen:** ***Allicospermum*** *sp.* (Zavialova et al., 2014; p. 1998, Pl. 3, Figs. b-c, e-i)

Extant pollen: ***Ginkgo*** *biloba* Linnaeus (Zavialova et al., 2014; p. 2006, Pl. 8, Figs. a-h)

Extant pollen: ***Ginkgo*** *biloba* Linnaeus (Zavialova et al., 2011; p. 195, Pl. 9, Figs. A-H; p. 197, Pl.10, Figs. A-K)

Key characters: This type of pollen is ellipsoidal, psilate or scabrate, monosulcate, generally 30-50 µm in size. Some pollen grains are rugulate under SEM. The exine is two-layered, with a more electron-dense endexine. The infratectum is variable in architecture resembling stalactites and stalagmites of irregular outlines.

Dispersed pollen: The two dispersed pollen genera related to this type are ***Ginkgocycadophytus*** Samoilovitch and ***Ginkgoretectina*** Maljavkina.

Remarks: ***Ginkgocycadophytus*** Samoilovitch is comparable to the *in situ* pollen of ***Allicospermum*** Harris (Zavialova et al., 2014), whereas ***Ginkgoretectina*** Maljavkina is comparable to the pollen of extant ***Ginkgo*** Linnaeus (Potonié, 1960).

3.3.3.12 Order: PALISSYALES Doweld

The Mesozoic fossil order PALISSYALES Doweld (Pattemore and Rozefelds, 2019) consists of the single family PALISSYACEAE Florin (Van Konijnenburg-van Cittert et al., 2021). The species are believed to be woody plants that were only distributed in the northern hemisphere. Associated coal seams, marine fauna, and wetland fossil plants suggest that the ***Palissya*** type conifers were small bushes that grew in tropical-subtropical swampy peat (coal) environments in scattered, terrestrial-marine wetland habitats (Wang, 2012). Therefore, they were generally hygrophytes and megathermic plants.

Stachyotaxus lipoldi type pollen

In situ* pollen: *Stachyotaxus *lipoldi* Stur (Potonié, 1967; p. 239, Pl. A, Figs. 27-29)

Key characters: This type of pollen is ellipsoidal, monosulcate, with transverse striae (costae) on the proximal face, generally 35-40 µm in size.

Dispersed pollen: The seven dispersed pollen genera related to this type are ***Decussatisporites*** Leschik, ***Lagenella*** Leschik, ***Marsupipollenites*** (Balme & Hennelly) Pocock et Jansonius [?], ***Paravittatina*** Balme [S], and ***Weylandites*** Bharadwaj et Srivastava [S].

Remarks: ***Lagenella*** Leschik and ***Decussatisporites*** Leschik are comparable to the *in situ* pollen of ***Stachyotaxus*** Nathorst (Balme, 1995; Potonié, 1967b; Tekleva and Roghi, 2018). ***Paravittatina*** Balme and ***Weylandites*** Bharadwaj et Srivastava are synonyms of ***Decussatisporites*** Leschik (Bharadwaj and Dwivedi, 1981). Whereas a striate ornamentation on ***Marsupipollenites*** *triradiatus* Balme & Hennelly is unclear, the ornamentation is obvious on ***Marsupipollenites*** *triradiatus* Balme & Hennelly forma *striatus* Balme & Hennelly. Such an ornamentation is remarkable also for ***Marsupipollenites*** *fasciolatus* Balme & Hennelly and ***Marsupipollenites*** *scutatus* Balme & Hennelly (Kremp and Ames, 1961a). Therefore, probably not all pollen of the genus ***Marsupipollenites*** (Balme & Hennelly) Pocock et Jansonius can be related to the PALISSYACEAE Florin, but at lest the species with remarkable striate ornamentation. To get its affinity, ultrastructural studies for both ***Marsupipollenites*** (Balme & Hennelly) Pocock et Jansonius and ***Stachyotaxus*** Nathorst are needed.

3.3.3.13 Order: PELTASPERMALES Taylor

The seed ferns of the PELTASPERMALES Taylor (Naugolnykh, 2012) are probably originated in tropical areas during the Late Pennsylvanian and became extinct during the Mesozoic with globally distributed fossils (Taylor et al., 2009; Wan et al., 2016). They might have been shrub-like plants (He et al., 2017). Epidermal features of ***Glenopteris*** *splendens* Sellards are consistent with those extant plants adapted to (seasonal) moisture limitation and elevated soil and ground water salinity (Krings et al., 2005). Furthermore, epidermal features indicate that ***Peltaspermum*** *martinsii* (Germar) Poort lived in drier or saline influenced biotopes (Poort and Kerp, 1990) and that ***Peltaspermum*** *retensorium* (Zalessky) Naugolnykh et Kerp lived in a relatively dry habitat (Naugolnykh and Kerp, 1996). Plants from the Sobernheim population with ***Autunia*** *conferta* (Sternberg) Kerp grew in a mineral soil under relatively dry conditions (elevated sandy lake margins, sand and river banks) (Kerp, 1988). Although the sedimentary analysis indicates that the climate was more humid with dry seasons, the thick cuticle, sunken stomata and the papillae surrounding the stomatal aperture indicate that ***Scytophyllum*** *karamayense* He et al. may have suffered from water stress, with the cuticle being adapted to reducing water loss (He et al., 2017). Therefore, the plants were xerophytes and megathermic plants.

Permotheca disparis **type pollen**

In situ* pollen: *Permotheca *colovratica* Naugolnykh (Naugolnykh, 2013b; p. 121, Pl. 15, Figs 1-2, 5-6, 8)

In situ* pollen: *Permotheca *disparis* (Zalessky) Naugolnykh (Krassilov et al., 1999; p. 22, Fig. 1; p.23, Pl. 2, Figs. 1-12)

Key characters: This type of pollen is protomonosaccate or protobisaccate, with cappa and sulcus, generally 50-85 µm in size.

Remarks: This type of pollen is difficult to be separated from the ***Pteruchus*** *dubius* type pollen. For example, dispersed pollen genera such as ***Alisporites*** (Daugherty) Jansonius and ***Falcisporites*** (Leschik) Klaus are reported to be comparable to the *in situ* pollen of ***Permotheca*** (Zalessky) Naugolnykh (Krassilov et al., 1999; Naugolnykh, 2013b) and ***Pteruchus*** Thomas (Osborn and Taylor, 1993; Taylor et al., 1984). Those dispersed pollen genera are deemed as the ***Pteruchus*** *dubius* type pollen in this paper because the *in situ* pollen species of ***Pteruchus*** *dubius* type are mostly be found in Mesozoic (Balme, 1995) while the ***Permotheca*** *disparis* type are mostly be found in Paleozoic (Krassilov et al., 1999; Naugolnykh, 2013b).

Permotheca striatifera **type pollen**

In situ* pollen: *Permotheca *sp.* (Meyen, 1984; p. 60, Pl. 19, Figs. D-E)

In situ* pollen: *Permotheca *striatifera* Meyen et Gomankov (Zavialova and Karasev, 2015; p. 33, Pl. III, Figs. 1-6; p. 34, Pl. IV, Figs. 1-3)

Key characters: This type of pollen is protobisaccate, with ribs on the proximal face (cappa), generally 50-70 µm in size.

Dispersed pollen: The thirty-nine dispersed pollen genera related to this type are ***Accinctisporites*** Leschik [S], ***Citrullesaccites*** Zhang [?], ***Conovalipollis*** Zhang [?], ***Costapollenites*** Tschudy et Kosanke [?], ***Crustaesporites*** Leschik [?], ***Distriatites*** Bharadwaj [S], ***Distriomonosaccites*** Bharadwaj [?], ***Faunipollenites*** Bharadwaj [S], ***Guttulapollenites*** Goubin [?], ***Hamiapollenites*** Wilson [S], ***Hindipollenites*** Bharadwaj [S], ***Lahirites*** Bharadwaj [S], ***Lunatisporites*** Leschik [S], ***Mesostriatites*** Mädler [?], ***Mucrosaccus*** Wilson [?], ***Parataeniaesporites*** Liu [?], ***Pemphygaletes*** Luber [S], ***Protocedrus*** Bolchovitina [S], ***Protodiploxypinus*** Samoilovitch [S], ***Protohaploxypinus*** (Samoilovitch) Hart, ***Protosacculina*** Maljavkina [S], ***Rhizomaspora*** Wilson [S], ***Striapollenites*** Bharadwaj [S], ***Striatisaccus*** Mädler [S], ***Striatites*** Pant [S], ***Striatoabieites*** (Sedova) Hart, ***Striatoabietites*** (Sedova) Hart [?], ***Striatopiceites*** Sedova [S], ***Striatopinites*** Sedova [S], ***Striatopodocarpites*** (Sedova) Hart [S], ***Striatosaccites*** Jizba [?], ***Striomonosaccites*** Bharadwaj [?], ***Strotersporites*** Wilson [S], ***Taeniaepollenites*** Visscher [S], ***Taeniaesporites*** Leschik [S], ***Thuringisaccus*** Mädler [S], ***Tubantiapollenites*** Visscher [?], ***Verticipollenites*** Bharadwaj [S], and ***Vittatina*** (Luber) Jansonius.

Remarks: *Protohaploxypinus* (Samoilovitch) Hart (Zavialova and Karasev, 2015) and ***Vittatina*** (Luber) Jansonius (Zavialova and van Konijnenburg-van Cittert, 2011) are comparable to the *in situ* pollen of ***Permotheca*** (Zalessky) Naugolnykh. ***Faunipollenites*** Bharadwaj, ***Lunatisporites*** Leschik, ***Pemphygaletes*** Luber, ***Protosacculina*** Maljavkina, ***Striatites*** Pant, ***Striatopiceites*** Sedova, ***Striatopinites*** Sedova, and ***Taeniaesporites*** Leschik are synonyms of ***Protohaploxypinus*** (Samoilovitch) Hart (Potonié, 1966). ***Accinctisporites*** Leschik is a synonym of ***Lunatisporites*** Leschik (Scheuring, 1974). ***Hamiapollenites*** Wilson, ***Protocedrus*** Bolchovitina and ***Protodiploxypinus*** Samoilovitch are synonyms of ***Protohaploxypinus*** (Samoilovitch) Hart (Traverse et al., 1973b). ***Hindipollenites*** Bharadwaj, ***Lahirites*** Bharadwaj, ***Striatites*** Pant, ***Striatopodocarpites*** (Sedova) Hart, ***Strotersporites*** Wilson, ***Rhizomaspora*** Wilson, ***Verticipollenites*** Bharadwaj and ***Taeniaepollenites*** Visscher are synonyms of ***Taeniaesporites*** Leschik (Traverse and Ames, 1972). ***Distriatites*** Bharadwaj and ***Striapollenites*** Bharadwaj are synonyms of ***Hamiapollenites*** Wilson (Potonié, 1966).***Thuringisaccus*** Mädler is a synonym of ***Striatopinites*** Sedova (Traverse and Ames, 1968). In the Palaeozoic, ***Permotheca*** (Zalessky) Naugolnykh also produced ***Vesicaspora***-like pollen without a taeniate sculpture (Meyen, 1984), but whether such kind of pollen were also produced in the Mesozoic is questionable.

3.3.3.14 Order: PINALES Gorozhankin

The extant order PINALES Gorozhankin consists of the single family PINACEAE Sprengel ex Rudolphi (Christenhusz et al., 2011). Originated at least in the Late Triassic, the extant species are common in temperate regions of the Northern Hemisphere and mainly shrubs and trees with up to 100 m height (Taylor et al., 2009). Most of the PINACEAE Sprengel ex Rudolphi are trees of generally poor, acidic and either wet or rocky habitats, sometimes forming mixed evergreen or evergreen broad-leaved forests, but more often forming extensive monotypic stands over large, north-temperate areas. There are concentrations of species in both, North America and in the east of Asia, with a considerable number of endemic species with more restricted range in the Sino-Himalayan region. The limited number of species which spread southward in Central America or in SE Asia are essentially montane (Kramer and Green, 1990). They are generally mesophytes and microthermic plants.

Larix kaempferi **type pollen**

Extant pollen: ***Larix*** *kaempferi* (Lehmann) Carrière (Li et al., 2011; p. 73, Figs. 1-4)
Extant pollen: ***Larix*** *gmelini* (Ruprecht) Ruprecht (Li et al., 2011; p. 71, Figs. 1-4)
Extant pollen: ***Pseudotsuga*** *sinensis* Dode (Li et al., 2011; p. 74, Figs. 1-2)

Key characters: This type of pollen is inaperturate, circular, normally with irregular depressions on the surface, generally 25-85 µm in size. Under LM the pollen is smooth, but under SEM small round particles inside the depression are often recognizable.

Dispersed pollen: The four dispersed pollen genera related to this type are ***Laricispollenites*** Nagy, ***Laricoidites*** Potonié, Thomson et Thiergart ex Potonié, ***Laricoipollenites*** Potonié [S], and ***Larixidites*** Maljavkina [S].

Remarks: ***Laricispollenites*** Nagy and ***Laricoidites*** Potonié, Thomson et Thiergart ex Potonié are comparable to pollen of extant ***Larix*** Miller (Ames and Spackman, 1981; Worobiec, 2009). ***Laricoipollenites*** Potonié and ***Larixidites*** Maljavkina are the synonyms of ***Laricoidites*** Potonié, Thomson et Thiergart ex Potonié (Potonié, 1960; Song et al., 1999).

Tsuga canadensis **type pollen**

Extant pollen: ***Tsuga*** *canadensis* Carriere (Hesse et al., 2009; p. 97, Fig. 3)
Extant pollen: ***Tsuga*** sp. (Hesse et al., 2009; p. 97, Figs. 1-2)

Key characters: This type of pollen is circular, monosaccate, generally 60-110 µm in size. Proximal thickening extends over to distal surface and margined by the monosaccus. The ornamentation of the body is finely verrucate or gemmate. There is a leptoma on the distal surface.

Dispersed pollen: The nine dispersed pollen genera related to this type are ***Abietipites*** Wodehouse, ***Anizonosaccites*** (Sun et He) Zhang [?], ***Cerebropollenites*** Nilsson, ***Jiaohepollis*** Li [?], ***Protocerebropollenites*** Huang [?], ***Tsugaepollenites*** Potonié et Venitz ex Potonié, ***Tsugapollenites*** Raatz [S], ***Tsugella*** Maljavkina [S], and ***Zonalapollenites*** Pflug [S].

Remarks: ***Cerebropollenites*** Nilsson and ***Tsugaepollenites*** Potonié et Venitz ex Potonié are comparable to the pollen of extant ***Tsuga*** (Endlicher) Carrière (Srivastava, 1987). ***Tsugapollenites*** Raatz, ***Tsugella*** Maljavkina, and ***Zonalapollenites*** Pflug are the synonyms of ***Tsugaepollenites*** Potonié et Venitz ex Potonié (Potonié, 1958, 1960, 1966), whereas ***Jiaohepollis*** Li, ***Anizonosaccites*** (Sun et He) Zhang and ***Protocerebropollenites*** Huang are only used by Chinese authors. The resemblance of ***Abietipites*** Wodehouse to winged pollen of the PINACEAE Sprengel ex Rudolphi is obvious, but the resemblance to the ***Tsuga*** type is stronger than to any of the two-winged types (Kremp et al., 1966).

Pinus armandi **type pollen**

Extant pollen: ***Abies*** *nephrolepis* Maximovich (Li et al., 2011; p. 29, Figs. 1-6)
Extant pollen: ***Cathaya*** *argyrophylla* Chun et Kuang (Li et al., 2011; p. 41, Figs. 1-6)

Extant pollen: ***Cedrus*** *deodara* (Roxburgh) Don (Li et al., 2011; p. 42, Figs. 1-6)
Extant pollen: ***Keteleeria*** *evelyniana* Masters (Li et al., 2011; p. 43, Figs. 1-6)
Extant pollen: ***Picea*** *asperata* Masters (Li et al., 2011; p. 36, Figs. 1-6)
Extant pollen: ***Pinus*** *armandi* Franchet (Li et al., 2011; p. 46, Figs. 1-6)

Key characters: This type of pollen is bisaccate, with a proximal cappa and a distal leptoma, generally 40-110 µm in size. The sacci are often distally attached. The sacci are generally smaller than the corpus; but in polar view the widths of the sacci are more or less the same as the width of the corpus. Under SEM the sacci are generally smooth but under LM reticulate.

Dispersed pollen: The thirteen dispersed pollen genera related to this type are ***Abiespollenites*** Thiergart ex Raatz, ***Abietineaepollenites*** Potonié (Delcourt & Sprumont), ***Cathayapollis*** Ziembińska-Tworzydło, ***Cedridites*** Maljavkina [?], ***Cedripites*** Wodehouse, ***Erlianpollis*** Zhao [?], ***Granatrivesiculites*** Pierce, ***Keteleeriaepollenites*** Nagy, ***Piceaepollenites*** (Potonié) Potonié, ***Piceapollenites*** Thiergart [S], ***Piceapollis*** Krutzsch, ***Pinuspollenites*** Raatz ex Potonié, and ***Taedaepollenites*** Nilsson.

Remarks: ***Abiespollenites*** Thiergart ex Raatz is comparable to the pollen of extant ***Abies*** Miller and ***Abietineaepollenites*** Potonié (Delcourt & Sprumont), ***Pinuspollenites*** Raatz ex Potonié and ***Granatrivesiculites*** Pierce to the pollen of extant ***Pinus*** Linnaeus (Ames et al., 1976; Kremp and Ames, 1965a, b; Potonié, 1958). ***Piceaepollenites*** (Potonié) Potonié and ***Piceapollis*** Krutzsch are similar to the pollen of extant ***Picea*** Dietrich (Kremp and Ames, 1961b; Kremp et al., 1960a; Song et al., 1999). ***Cedripites*** Wodehouse is comparable to the pollen of extant ***Cedrus*** Trew (Traverse et al., 1969), ***Keteleeriaepollenites*** Nagy to the pollen of extant ***Keteleeria*** Carrière (Song et al., 1999) and ***Taedaepollenites*** Thiergart is comparable to the pollen of extant ***Pinuspollenites*** Raatz ex Potonié (Potonié, 1960). ***Piceapollenites*** Thiergart is a synonym of ***Piceaepollenites*** (Potonié) Potonié (Potonié, 1958).

3.3.3.15 Order: VOLTZIALES Andreanszky

Species of the order VOLTZIALES Andreanszky (Naugolnykh, 2014) were conifers extended from the Late Paleozoic into the Mesozoic. There were a number of Paleozoic and Mesozoic voltzialean conifers not known in sufficient detail to be included within well-defined families (Taylor et al., 2009). Fossils with *in situ* pollen of ***Darneya*** Schaarschmidt et Maubeuge, ***Leastrobus*** Hermsen, Taylor et Taylor, ***Patokaea*** Pacyna, Barbacka et Zdebska, ***Sertostrobus*** Grauvogel-Stamm, and ***Willsiostrobus*** Grauvogel-Stamm et Schaarschmidt have been found in Mesozoic records (Hermsen et al., 2007; Pacyna et al., 2017; Taylor and Grauvogel-Stamm, 1995). The Mesozoic species were distributed in tropical, arid to semi-arid oasis (Vakhrameev, 1991). Therefore, they were generally xerophytes and megathermic plants.

Leastrobus fallae type pollen

In situ **pollen:** ***Darneya*** *dentata* Grauvogel-Stamm (Taylor and Grauvogel-Stamm, 1995; p. 292, Pl. VI, Fig. 5; p. 294, Pl. VII, Figs. 1-7; p. 295, Pl. VIII, Figs. 2-6)
In situ **pollen:** ***Leastrobus*** *fallae* Hermsen et al. (Hermsen et al., 2007; p. 116, Pl. II, Figs. 1-4)
In situ **pollen:** ***Sertostrobus*** *laxus* Grauvogel-Stamm (Taylor and Grauvogel-Stamm, 1995; p. 294, Pl. IX, Figs. 2-7)
In situ **pollen:** ***Willsiostrobus*** *willsii* (Townrow) Grauvogel-Stamm et Schaarschmidt (Taylor and Grauvogel-Stamm, 1995; p. 282, Pl. I, Figs. 1-7)

Key characters: This type of pollen is protobisaccate, with well-defined distal aperture between the sacci, generally 35-100 µm in size.

Dispersed pollen: The six dispersed pollen genera related to this type are ***Complexisporites*** Jizba [S], ***Illinites*** Kosanke, ***Sahnisporites*** Bhardwaj [S], ***Succinctisporites*** Leschik [S], ***Triadispora*** Klaus, and ***Voltziaceaesporites*** Klaus.

Remarks: ***Illinites*** Kosanke and ***Voltziaceaesporites*** Klaus are comparable to the *in situ* pollen of ***Willsiostrobus*** Grauvogel-Stamm et Schaarschmidt (Balme, 1995; Taylor and Grauvogel-Stamm, 1995).

Triadispora Klaus is comparable to the *in situ* pollen of ***Sertostrobus*** Grauvogel-Stamm and ***Darneya*** Schaarschmidt & Maubeuge (Taylor and Grauvogel-Stamm, 1995). ***Complexisporites*** Jizba, ***Sahnisporites*** Bhardwaj, and ***Succinctisporites*** Leschik of ***Illinites*** Kosanke (Potonié, 1970; Traverse and Ames, 1968).

***Majonica alpina* type pollen**

In situ* pollen: *Majonica *alpina* Clement-Westerhof (Clement-Westerhof, 1987; p. 390, Pl. VI, Figs. 3-4)
In situ* pollen: *Sashinia *sp* (Meyen, 1984; p. 82, Pl. 26, Fig. H)

Key characters: This type of pollen is bisaccate, bitaeniate, with proximal dilete mark, generally 50-70 µm in size.

Dispersed pollen: The ten pollen genera related to this type are ***Chordasporites*** Klaus [?], ***Colpectopollis*** Pflug [?], ***Infernopollenites*** Scheuring [?], ***Iunctella*** Kara-Mursa [?], ***Lueckisporites*** (Potonié et Klaus) Klaus, ***Ovalipollis*** (Krutzsch) Klaus [?], ***Scutasporites*** Klaus, ***Staurosaccites*** Dolby [?], ***Unatextisporites*** Leschik [?], and ***Weiyuanpollenites*** Zhang [?].

Remarks: *Lueckisporites* (Potonié et Klaus) Klaus and ***Scutasporites*** Klaus are comparable to the *in situ* pollen of ***Sashinia*** Meyen (Gomankov, 2009; Meyen, 1997). Different authors use different definitions for ***Lueckisporites*** based on the leasura and the numbers of ribs on the proximal face. Potonié (1958) stated that ***Lueckisporites*** (Potonié et Klaus) Potonié has no leasura on the proximal face and that there can be more than two ribs on the face. Based on this definition, he believed that ***Lueckisporites*** (Potonié et Klaus) Potonié is a synonym of ***Protohaploxypinus*** (Samoilovitch) Hart (Potonié, 1966). In contrast, Klaus (1963) stated that ***Lueckisporites*** (Potonié et Klaus) Klaus has a leasura on the proximal face and that there are always two ribs on the face.

***Ortiseia jonkeri* type pollen**

In situ* pollen: *Ortiseia *jonkeri* Clement-Westerhof (Clement-Westerhof, 1984; p. 159, Pl. XXX, Fig. 4)
In situ* pollen: *Ortiseia *leonardii* Florin (Clement-Westerhof, 1984; p. 134, Pl. X, Fig. 5)
In situ* pollen: *Ortiseia *visscheri* Clement-Westerhof (Clement-Westerhof, 1984; p. 144, Pl. XVIII, Fig. 4)
In situ* pollen: *Ortiseia sp. (Clement-Westerhof, 1984; p. 161, Pl. XXXII, Figs. 1-2)

Key characters: This type of pollen is monosaccate, with proximal trilete mark, generally 150-300 µm in size.

Dispersed pollen: The seven dispersed pollen genera related to this type are ***Cannanoropollis*** Potonié et Sah, ***Crucisaccites*** Lele et Maithy [S], ***Dyupetalum*** Jansonius et Hills [?], ***Gigantosporites*** Klaus [?], ***Nuskoisporites*** Potonié et Klaus, ***Potonieisporites*** Bhardwaj, and ***Vestigisporites*** Balme et Hennelly [S].

Remarks: *Nuskoisporites* Potonié et Klaus and ***Potonieisporites*** Bhardwaj are comparable to the *in situ* pollen of ***Otovicia*** Florin (Clement-Westerhof, 1984; Kerp et al., 1990). ***Cannanoropollis*** Potonié et Sah is suggested to be produced by ***Ferugliocladus*** Archangelsky & Cúneo (Archangelsky and Cuneo, 1987). ***Crucisaccites*** Lele et Maithy and ***Vestigisporites*** Balme et Hennelly are synonyms of ***Potonieisporites*** Bhardwaj (Potonié, 1970).

***Ullmannia bronni* type pollen**

In situ* pollen: *Ullmannia *bronni* (Schlotheim) Göppert (Townrow, 1962; p. 32, Pl. 6, Figs. c, e, g)
In situ* pollen: *Ullmannia *bronni* (Schlotheim) Göppert (Potonié and Schweitzer, 1960; p. 33, Pl. 5, Figs, a-d)
In situ* pollen: *Ullmannia *frumentaria* (Schlotheim) Göppert (Potonié and Schweitzer, 1960; p. 29, Pl. 1, Figs. 1-13; p. 33, Pl. 5, Figs, e-f)

Key characters: This type of pollen is protosaccate, mono- or bisaccate, with cappa, generally 35-80 µm in size. The roots of sacci not offset distally. Some grains are monolete or trilete.

Dispersed pollen: The eleven dispersed pollen genera related to this type are ***Cuneatisporites*** Leschik,

Gardenasporites Klaus, ***Jugasporites*** Leschik, ***Limitisporites*** Leschik, ***Platysaccus*** (Naumova ex Ishchenko) Potonié et Klaus, ***Protoconiferus*** Bolchovitina [?], ***Protopinus*** Bolchovitina [?], ***Protopodocarpus*** Bolchovitina [?], ***Pseudowalchia*** Bolchovitina [?], ***Triadispora*** Klaus, and ***Tumoripollenites*** Bharadwaj.

Remarks: ***Jugasporites*** Leschik, ***Limitisporites*** Leschik, and ***Platysaccus*** (Naumova ex Ishchenko) Potonié et Klaus are comparable to the *in situ* pollen of ***Ullmannia*** Göppert (Balme, 1995; Potonié, 1966; Traverse and Ames, 1972). ***Gardenasporites*** Klaus is comparable to ***Limitisporites*** Leschik (Potonié, 1966). ***Cuneatisporites*** Leschik and ***Tumoripollenites*** Bharadwaj are comparable to ***Platysaccus*** (Naumova ex Ishchenko) Potonié et Klaus (Potonié, 1958; Traverse and Ames, 1972). ***Protopodocarpus*** Bolchovitina is comparable to ***Platysaccus*** (Naumova ex Ishchenko) Potonié et Klaus (Shu and Norris, 1999).

Patokaea silesiaca **type pollen**

In situ **pollen:** ***Patokaea*** *silesiaca* Pacyna, Barbacka et Zdebska (Pacyna et al., 2017; p. 47, Pl. XI, Figs. 3-7; p. 48, Pl. XII, Figs. 1-8)

Key characters: This type of pollen is circular, inaperturate, with a rugate sculpture on the whole pollen grain, generally 25-40 µm in size.

Dispersed pollen: The five dispersed pollen genera related to this type are ***Ellipsovelatisporites*** Klaus [?], ***Enzonalasporites*** Leschik, ***Patinasporites*** Leschik, ***Pseudoenzonalasporites*** Scheuring, and ***Vallasporites*** Leschik.

Remarks: ***Enzonalasporites*** Leschik, ***Patinasporites*** Leschik, ***Pseudoenzonalasporites*** Scheuring, and ***Vallasporites*** Leschik are comparable to the *in situ* pollen of ***Patokaea*** Pacyna, Barbacka et Zdebska (Pacyna et al., 2017). Some authors describe this type of pollen as monosaccate or monosaccoid pollen (Van der Eem, 1983). As the pollen grains that found in a *Patokaea silesiaca* Pacyna, Barbacka et Zdebska, show no alveolar structure under TEM, they are probably asaccate (Pacyna et al., 2017). However, detailed TEM investigations are also needed for the dispersed pollen grains related to this type of pollen.

3.3.3.16 Order: WELWITSCHIALES Skottsberg ex Reveal

The extant order WELWITSCHIALES Skottsberg ex Reveal consists of one family WELWITSCHIACEAE Caruel with a single species (Christenhusz et al., 2011). Fossils with *in situ* pollen of ***Bicatia*** Friis, Pedersen et Crane are known from the Mesozoic (Friis et al., 2014). The extant genus ***Welwitschia*** Hooker is confined to a narrow coastal strip in the subtropical Namib Desert of South West Africa. The layer of calcium oxalate in the outer cell walls of the leaf epidermis of the plant may contribute to reflecting excessive radiation (Kramer and Green, 1990). The plants are generally xerophytes and megathermic plants.

Bicatia costata **type pollen**

In situ **pollen:** ***Bicatia*** *costata* Friis et al. (Friis et al., 2014; p. 182, Pl. 4, Figs. A-D)
In situ **pollen:** ***Bicatia*** *juncalensis* Friis et al. (Friis et al., 2014; p. 185, Pl. 7, Figs. A-D)
In situ **pollen:** ***Bicatia*** *rugosa* Friis et al. (Friis et al., 2014; p. 190, Pl. 10, Figs. B-G)
Extant pollen: ***Welwitschia*** *mirabilis* Hooker (Rydin and Friis, 2005; p. 140 Pl. 4, Figs. A-E)
Extant pollen: ***Welwitschia*** *mirabilis* Hooker (Tekleva, 2016; p. 298, Figs. e, f, i)
Extant pollen: ***Welwitschia*** *mirabilis* Hooker (Wetschnig and Depisch, 1999; p. 175, Fig. 6)

Key characters: This type of pollen is ellipsoidal, monosulcate, bearing vertical ridges (plicate) extending almost from end to end, generally 15-45 µm in size.

Dispersed pollen: The sixteen dispersed pollen genera related to this type are ***Alaticolpites*** Regali, Uesugui et Santos [?], ***Chomsiipites*** Smirnova, ***Corniculatisporites*** Kuvaeva [S], ***Elaterocolpites*** Jardiné et Magloire [?], ***Elateroplicites*** Herngreen [?], ***Elateropollenites*** Herngreen [?], ***Elaterosporites*** Jardiné [?], ***Galeacornea*** Stover [?], ***Jugella*** Mchedlishvili et Shakhmundes, ***Pentapsis*** Lammons [?], ***Quantonenpollenites*** Yu, Guo et Mao [?], ***Regalipollenites*** de Lima [?], ***Senegalosporites*** Jardiné et Magloire [?], ***Sofrepites*** Jardiné [?], ***Welwitschiapites*** Bolchovitina ex Potonié, and ***Welwitschites*** Zaklinskaja [S].

Remarks: ***Chomsiipites*** Smirnova and ***Jugella*** Mchedlishvili et Shakhmundes are comparable to *in situ* pollen of ***Bicatia*** Friis, Pedersen et Crane (Friis et al., 2014). ***Welwitschiapites*** Bolchovitina ex Potonié is comparable to the pollen of extant ***Welwitschia*** Hooker (Kremp et al., 1959; Potonié, 1967). ***Welwitschites*** Zaklinskaja is a synonym of ***Welwitschiapites*** Bolchovitina ex Potonié (Potonié, 1960). ***Corniculatisporites*** Kuvaeva is comparable to ***Welwitschiapites*** Bolchovitina ex Potonié (Song et al., 2000). ***Alaticolpites*** Regali, Uesugui et Santos, ***Elaterocolpites*** Jardiné et Magloire, ***Elateroplicites*** Herngreen, ***Elateropollenites*** Herngreen, ***Elaterosporites*** Jardiné, ***Galeacornea*** Stover, ***Pentapsis*** Lammons, ***Regalipollenites*** de Lima, ***Senegalosporites*** Jardiné et Magloire, and ***Sofrepites*** Jardiné are also known as the elater-bearing pollen because of their elater-like protuberances (Dino et al., 1999). The protuberances are supposed to evolve from the pollen grains resembling the characteristic ribbed pollen of extant ***Ephedra*** Linnaeus and ***Welwitschia*** Hooker (Crane, 1996). As the pollen of extant ***Ephedra*** Linnaeus does not have any sulcus but most of the elater-bearing pollen genera have a remarkable sulcus, the elater-bearing pollen is more close to the pollen of extant ***Welwitschia*** Hooker.

3.4 Discussions

3.4.1 The problems of the lack of in situ sporomorphs

To identify the parent plants of fossil spores or pollen, the study of *in situ* sporomorphs from sporangia of fossil plants is needed (Traverse, 2007). Only a sufficient number of studied *in situ* sporomorphs and reproducible results will guarantee that observable peculiarities of morphology and ultrastructure are indeed typical of a taxon under study (Zavialova et al., 2018). However, for Mesozoic plants, the number of *in situ* sporomorphs is restricted. A further complication is that the parent plants of dispersed sporomorphs from the Mesozoic can generally only be recovered at the order or family level. For example, during the Mesozoic, the GINKGOALES Gorozhankin were composed of several families including the GINKGOACEAE Engler, the KARKENIACEAE Krassilov, the UMALTOLEPIDIACEAE (Stanislavsky) Zhou, the YIMAIACEAE Zhou, and the SCHMEISSNERIACEAE Zhou (Taylor et al., 2009; Zhou, 2009). However, an assignment of dispersed pollen to one of the latter four families is not possible, because the ultrastructure of *in situ* pollen is unknown. Therefore, the pollen can only be linked to the order GINKGOALES Gorozhankin. Currently, it can only be predicted that all the families included in the GINKGOALES Gorozhankin produce pollen, which are similar to the pollen of GINKGOACEAE Engler. Also, the lack of proper *in situ* sporomorphs can lead to a wrong parent plant affiliation. For example, ***Eucommiidites*** Erdtman ex Potonié was formerly believed to be comparable to the angiosperm of extant ***Eucommia*** Oliver (EUCOMMIACEAE Engler) (Potonié, 1966), since the pollen grains of ***Eucommiidites*** Erdtman ex Potonié and ***Eucommia*** Oliver are morphologically similar. An important difference is that the pollen of ***Eucommiidites*** Erdtman ex Potonié has one well developed and two less developed colpi, while the pollen of ***Eucommia*** Oliver is characterized by three well-developed colpi (Li et al., 2011). However, only with the recent analysis of *in situ* gymnosperm pollen grains of ***Bayeritheca*** Kvacek et Pacltová, ***Erdtmanitheca*** Pedersen, Crane et Friis, and ***Eucommiitheca*** Friis et Pedersen (Kvacek and Pacltova, 2001; Mendes et al., 2010), it became apparent that ***Eucommiidites*** Erdtman ex Potonié is gymnosperm pollen.

3.4.2 The problems of LM

Visible light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM) are the three main methods to study spore and pollen morphology, but the latter two methods can reveal morphological features that are not observable by LM (Hesse et al., 2018). However, LM is still the workhorse method to study spore and pollen morphology and it will remain the case for the immediate future (Traverse, 2007). For the Mesozoic, most of the dispersed sporomorphs have been described under LM. However, if a sporomorph of a specific parent plant is studied only by LM, morphological differences to sporomorphs of other parent plants that are only visible by SEM or TEM are unknown. For example, the protosaccate/eusaccate morphology could be evidently determined only by the application of TEM (Zavialova and Gomankov, 2009). If only the LM method has been used, the risk for a wrong identification of the parent plants is higher, since diagnostic morphological features may only be identified by SEM or TEM. For example, ***Polyphacelus*** Yao, Taylor et Taylor, a fossil plant discovered from the Mesozoic, has been compared to extant ***Dipteris*** Reinwardt (GLEICHENIALES Schimper) and ***Astralopteris*** Tidwell, Rushforth et Reveal to extant ***Drynaria*** Smith (POLYPODIACEAE Presl et Presl) (Taylor et al., 2009). Both extant ***Dipteris*** Reinwardt and

Drynaria Smith can produce monolete isospores with smooth walls. Differences between these two kinds of spores can only be recognized under TEM because the wall of the ***Dipteris*** type spore is three-layered but the wall of the ***Drynaria*** type spore only one-layered (Tryon and Lugardon, 1991). However, dispersed monolete spores with smooth walls such as ***Crassimonoletes*** Singh, Srivastava et Roy*,* ***Intrapunctatosporis*** Krutzsch*,* ***Intrapunctosporis*** Krutzsch*,* and ***Laevigatosporites*** Ibrahim*,* which are known from the Mesozoic and identified mainly under LM, are too roughly described to allow a link to either ***Dipteris*** type or ***Drynaria*** type isospores.

3.4.3 Spore/pollen ratio

Visscher and van der Zwan (1981) regard spores as hygrophytes and pollen as xerophytes so that they use the spore/pollen ratio to reflect trends of the hygrophytes/xerophytes ratio. The concept is still well accepted by other authors (e.g., Hochuli and Vigran, 2010; Mueller et al., 2016). The result of this paper reveals that among the spore-producing plants, ANEMIACEAE Link, GLEICHENIALES Schimper, OPHIOGLOSSACEAE Martinov, POLYPODIACEAE Presl et Presl, and SCHIZAEACEAE Kaulfuss are mesophytes and PTERIDACEAE Kirchner and SELAGINELLACEAE Willkomm euryphytes. Among the pollen-producing plants, ARAUCARIACEAE Henkel & Hochstetter, CAYTONIACEAE Thomas, PALISSYACEAE Florin, PODOCARPACEAE Endlicher, and SCIADOPITYACEAE Luerssen are hygrophytes, whereas the CHEIROLEPIDIACEAE Takhtajan and PELTASPERMALES Taylor are xerophytes. Therefore, both spore-producing plants, as well as pollen-producing plants, are adapted to different kinds of humidity. The concept of using the spore/pollen ratio to reflect the hygrophytes/xerophytes ratio is questionable and need to be refined.

3.5 Conclusions

1) Based on the comparison to *in situ* and extant spores and pollen grains, for almost all of the plant orders or families of Mesozoic bryophytes, pteridophytes, and gymnosperms, dispersed sporomorph genera have been identified and assigned to different Eco-Plant groups with different humidity, salinity, and temperature demands. This allows to better quantify palaeoenvironmental conditions in the depositional record by quantitatively analysed samples of dispersed sporomorphs. The paleoenvironmental analysis of a succession is an important tool for correlation and sequence stratigraphic approaches, which is valuable for research and industry applications such as the prediction of reservoir potential or raw materials.

2) The lack of sufficient Mesozoic *in situ* sporomorphs is the main reason that the parent plants of dispersed sporomorphs can only be recovered at the order or family level. It can also lead to the wrong identification of a parent plant of a dispersed sporomorph. New discoveries of *in situ* sporomorphs can improve the precision of assignments of dispersed sporomorphs to specific parent plants.

3) The limitation to the usage of LM as one of the principal identification methods is one of the main reasons that some dispersed sporomorphs cannot be linked precisely to a parent plant at the moment. Therefore, additional studies under SEM and TEM are recommended for dispersed sporomorphs.

4) During the Mesozoic, both spore-producing plants and pollen-producing plants are adapted to different kinds of humidity. The concept of using the spore/pollen ratio to reflect the hygrophytes/xerophytes ratio is questionable and should be refined.

3.6 Acknowledgements

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4. Database-based Eco-Plant analysis for Mesozoic dispersed sporomorphs

Published article

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Abstract

Patterns of community assemblage for plants are associated with particular climatic elements such as water, heat, light, and air. The classification based on these plant assemblages is referred to here as the ecogroup of plants (Eco-Plant), whereas the method of analysing palaeoenvironmental and palaeoclimate variation by using Eco-Plant is called the Eco-Plant model. The online database ***Sporopollen*** was created to quickly assign eco-climatic traits to quantitative fossil sporomorph data to assess implications for past vegetation patterns and climatic changes. A user-friendly interface has been created, where users can upload their data to the database and in return get immediate results. This database can automatically link all Mesozoic and Cenozoic sporomorphs to their putative parent plants at phylum, order, or family level. It can also automatically link all Triassic and Jurassic sporomorphs to Eco-Plant groups to assess the effect of humidity (EPH) and the effect of temperature (EPT).

- The Eco-Plant model allows to reconstruction of relative Triassic and Jurassic humidity and temperature changes.
- A useful tool for palaeoenvironmental reconstruction.
- A useful tool for (high-resolution) palynological studies.

4.1 Background

The seminal work of Warming (1895) and Schimper (1898) recognised that patterns of community assemblage for plants were associated with particular climatic elements such as water, heat, light, and air. The classification based on these plant assemblages is referred to here as the ecogroup of plants (Eco-Plant), whereas the method of analysing palaeoenvironmental and palaeoclimate variation by using Eco-Plant is called the Eco-Plant model (Zhang et al., 2020). The term is used to distinguish the model from the Sporomorph Ecogroup Model (SEG model) created by Abbink et al. (2004b). The Eco-Plant model has been widely used by palaeobotanists for extant (e.g., Baeza et al., 2010; Godin, 2017; Sheremetov and Sheremetova, 2017; Veisberg, 2017), Cenozoic (e.g., Bozukov et al., 2009; Yang et al., 2013; Yurtsev, 2001), Mesozoic (e.g., Hill, 2017; Vakhrameev, 1991), and Paleozoic (e.g., Bashforth et al., 2014; Wang, 1999b) palaeoenvironmental reconstructions. It is also applied by palynologists for palaeoenvironmental reconstructions using dispersed sporomorphs from the Cenozoic (e.g., Aranbarri et al., 2014; Kern et al., 2012; Popescu et al., 2006; Suc and Fauquette, 2012) and Mesozoic (e.g., Césari and Colombi, 2016; Hochuli and Vigran, 2010; Mueller et al., 2016; Roghi et al., 2010; Visscher and van der Zwan, 1981; Wang et al., 2013; Wang et al., 2005; Zhang et al., 2020; Zhao et al., 2014).

Previously, for most of the Mesozoic dispersed sporomorphs, the application of the Eco-Plant model was limited, because either their assignment to a specific Eco-Plant was uncertain or the botanical affinities to natural plant taxa were unclear. It was thus important to identify the botanical affinities of Mesozoic dispersed sporomorphs, to provide reliable assignment to an Eco-Plant (Zhang et al., 2020).

The online database ***Sporopollen*** (http://www.sporopollen.com) was created to link the dispersed sporomorphs (spores and pollen) to past vegetation patterns and climatic changes. The goal of the database is to analyze sporomorph data, especially of Mesozoic sporomorphs, for identification of parent plants, stratigraphic analysis, and to aid palaeoenvironmental reconstruction. This paper only focuses on the algorithm for palaeoenvironmental reconstruction, which automatically assigns eco-climatic traits to fossil sporomorph taxa that are uploaded by users. This can be used without the need to log in at http://www.sporopollen.com/sporemesozoicsegs.php?opencode=paper1. The sporomorph data published by Zhang et al. (2020) are used as examples to show how the database works. The implementation of the Eco-Plant model connects Mesozoic sporomorphs to their most likely plant taxa and their associated temperature and humidity groups (details below). The output varies depending on the options selected but serves as an aid for the researcher who must still interpret the relative abundances of taxa from different Eco-Plant groups in the samples.

4.2 Database concept

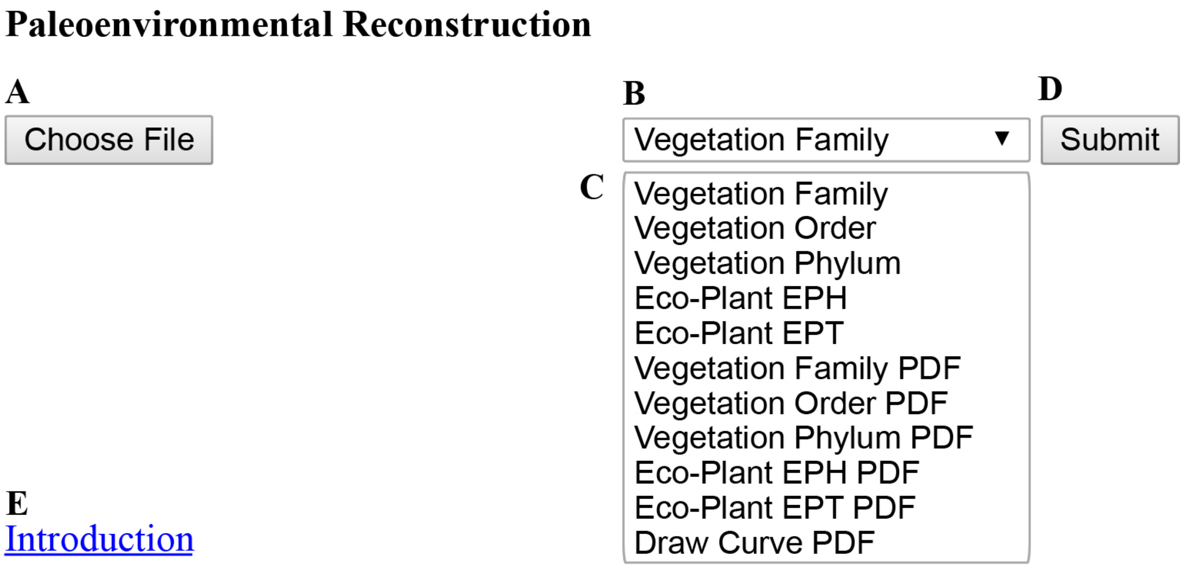

Figure 4-1 User-friendly interface for palaeoenvironmental reconstruction is provided by ***Sporopollen***.

Note: **A.** Choose File button, by click users can upload their data to the database. Currently, only CSV file is accepted; **B.** Drop-down list, by click users can select different modes of palaeoenvironmental reconstruction; **C.** Different modes of palaeoenvironmental reconstruction; **D.** Submit button, by click users can quickly get the result, when a CSV file is uploaded and the palaeoenvironmental reconstruction mode is selected; **E.** Introduction links, by click users can get the detailed manual and example files.
It can be visited at: http://www.sporopollen.com/sporemesozoicsegs.php?opencode=paper1.
Manual and example files can be visited at:
http://www.sporopollen.com/sporeexample.php?opterate=Paleoenvironmental%20Reconstruction.

The database system uses MySQL (Schwartz et al., 2012) for the database server and Hypertext Preprocessor (PHP) (Rochkind and Adams, 2013) for the dynamic website. A user-friendly interface (**Figure 4-1**) has been created, which automatically assigns eco-climatic traits to the uploaded fossil sporomorph data (**Appendix 4-1** for PHP code). In the database, datasets *Taxonomy* (**Table 4-1**) and *Ecogroup* (**Table 4-2**) are created. In dataset *Taxonomy* (**Table 4-1**), six fields *Kingdom, Phylum, Class, Order*, *Family*, and *Genus* are used to store the taxonomic ranks for both plant and sporomorph genera. In dataset *Ecogroup* (**Table 4-2**), three fields *Eph, Ept*, and *Genus* are used to store the Eco-Plant information. As different authors may have slightly different views on the concept of Eco-Plant groups (e.g., Wang et al., 2013; Wang et al., 2005), in this database, the concept that assesses the effects of humidity (EPH) and temperature (EPT) follows Zhang et al. (2020) and (2021b). The Eco-Plant groups separate hydrophytes, hygrophytes, mesophytes, xerophytes, and euryphytes based on their adaptation to different humidities (EPH). Additionally, megathermic, mesothermic, microthermic, and eurythermic plants are distinguished based on their adaptation to different temperatures (EPT).

Table 4-1 Part of the dataset Taxonomy storing data of the taxonomic ranks.

Kingdom	Phylum	Class	Order	Family	Genus
Plantae	Gymnospermae		Bennettitales	Williamsoniaceae	*Bharadwajipollenites*
Plantae	Gymnospermae		Bennettitales	Cycadeoidaceae	*Huabeisporites*
Plantae	Gymnospermae		Corystospermales	Umkomasiaceae	*Pteruchipollenites*
Plantae	Pteridophytes	Polypodiopsida	Cyatheales	Cyatheaceae	*Cyathidites*
Plantae	Pteridophytes	Polypodiopsida	Cyatheales	Cibotiaceae	*Duplexisporites*
Plantae	Pteridophytes	Equisetopsida	Equisetales	Equisetaceae	*Calamospora*
Plantae	Gymnospermae		Ginkgoales	Ginkgoaceae	*Ginkgocycadophytus*
Plantae	Pteridophytes	Polypodiopsida	Gleicheniales	Dipteridaceae	*Dictyophyllidites*
Plantae	Pteridophytes	Lycopodiopsida	Isoetales	Pleuromeiaceae	*Aratrisporites*
Plantae	Pteridophytes	Lycopodiopsida	Lycopodiales	Lycopodiaceae	*Hamulatisporis*
Plantae	Pteridophytes	Lycopodiopsida	Lycopodiales	Lycopodiaceae	*Foveolatitriletes*
Plantae	Pteridophytes	Marattiopsida	Marattiales	Marattiaceae	*Angiopteridaspora*
Plantae	Bryophytes	Anthocerotopsida	Notothyladales	Notothyladaceae	*Annulispora*
Plantae	Pteridophytes	Polypodiopsida	Osmundales	Osmundaceae	*Osmundacidites*
Plantae	Gymnospermae		Peltaspermales	Peltaspermaceae	*Protohaploxypinus*
Plantae	Gymnospermae		Pinales	Pinaceae	*Pinuspollenites*
Plantae	Gymnospermae		Pinales	Cheirolepidiaceae	*Discisporites*

Table 4-2 Part of the dataset Ecogroup storing data of Eco-Plant groups that assess the effect of humidity (EPH) and the effect of temperature (EPT).

Genus	EPH	EPT
Angiopteridaspora	hygrophytes	megathermic
Annulispora	hygrophytes	eurythermic
Aratrisporites	hydrophytes	eurythermic
Calamospora	hygrophytes	eurythermic
Cyathidites	hygrophytes	megathermic
Dictyophyllidites	mesophytes	megathermic
Discisporites	xerophytes	megathermic
Duplexisporites	hygrophytes	megathermic
Foveolatitriletes	hygrophytes	eurythermic
Ginkgocycadophytus	mesophytes	mesothermic
Hamulatisporis	hygrophytes	eurythermic
Huabeisporites	hygrophytes	megathermic
Osmundacidites	hygrophytes	eurythermic
Pinuspollenites	mesophytes	microthermic
Protohaploxypinus	xerophytes	megathermic
Pteruchipollenites	mesophytes	megathermic

In the database, the taxonomic ranks of extant plants mainly follow Christenhusz et al. (2011), Goffinet and Buck (2004), and Smith et al. (2006), the taxonomic ranks of fossil plants mainly Taylor et al. (2009) and the taxonomic ranks of Mesozoic fossil pollen of angiosperms mainly Song et al. (2004) and Muller et al. (1981). By comparing the unique outline and structure/sculpture of the sporomorph wall with that of modern plants and *in situ* fossil plants (plants with spores and pollen grains in situ within a sporangium), 861 dispersed Mesozoic sporomorph genera of Bryophytes, Pteridophytes, and Gymnosperms are reviewed (Zhang et al., 2021b). The illustrations, descriptions, and definitions of dispersed sporomorphs are mainly after Jiang et al. (2016), Huang (2008), Liu (2003), Shang (2011), Song et al. (1999), Song et al. (2000), Shu and Norris (1999), the 6 volumes book series of "*Synopsis der Gattungen der Sporae dispersae*" (Potonié, 1956, 1958, 1960, 1966, 1970; Potonié and Kremp, 1970), and the 26 volumes book series of "*Catalog of fossil spores and pollen*" (Ames and Spackman, 1985; Ames et al., 1976; Kremp and Ames, 1959, 1961b, 1962a, b, 1965a, b; Kremp et al., 1957a, b; Kremp et al., 1958, 1959, 1960a, b; Kremp et al., 1966; Kremp et al., 1967, 1968; Traverse and

Ames, 1968, 1969, 1971, 1979; Traverse et al., 1973a, 1974, 1975; Traverse et al., 1969). Illustrations and descriptions of extant sporomorphs are mainly after Zhang et al. (2006), Wang and Dai (2010), Li et al. (2011), Tryon and Lugardon (1991), Hesse et al. (2009), Boros and Járai-Komlódi (1975), and Kramer and Green (1990). To date, among the 861 dispersed Mesozoic sporomorph genera 484 of them can be linked to their closest parent plants and Eco-Plant groups at family or order level. Because of the lack of detailed ultrastructure descriptions or unclear separation to other genera 387 of 861 dispersed Mesozoic sporomorph genera cannot be linked at the moment to any parent plants and Eco-Plant groups (Zhang et al., 2021b). For each genus that can be linked to its closest parent plant, the most likely plant family is stored in the dataset *Taxonomy*. For 474 of 861 dispersed Mesozoic sporomorph genera, their EPH and EPT are reviewed (Zhang et al., 2021b) and stored in the dataset *Ecogroup* (**Table 4-2**).

Table 4-3 Part of the example uploaded file which can be used for all the analysis modes except Draw Curve PDF.

Depth	Sample	Genus	Abundance
1	HJG 01	*Annulispora*	5.9
1	HJG 01	*Aratrisporites*	7.4
1	HJG 01	*Bharadwajipollenites*	30.9
1	HJG 01	*Cyathidites*	0.7
1	HJG 01	*Dictyophyllidites*	13.2
1	HJG 01	*Discisporites*	1.5
1	HJG 01	*Duplexisporites*	5.9
1	HJG 01	*Ginkgocycadophytus*	4.4
1	HJG 01	*Huabeisporites*	2.9
1	HJG 01	*Osmundacidites*	0.7
1	HJG 01	*Pteruchipollenites*	25
1	HJG 01	*Quadraeculina*	1.5
2	HJG 02	*Angiopteridaspora*	11.3
2	HJG 02	*Annulispora*	0.7
2	HJG 02	*Aratrisporites*	2.4
2	HJG 02	*Bharadwajipollenites*	7.1
2	HJG 02	*Calamospora*	2
2	HJG 02	*Cyathidites*	4
2	HJG 02	*Dictyophyllidites*	7.7
2	HJG 02	*Discisporites*	9.1
2	HJG 02	*Duplexisporites*	0.7
2	HJG 02	*Foveolatitriletes*	5.5
2	HJG 02	*Ginkgocycadophytus*	7.5
2	HJG 02	*Hamulatisporis*	2.9
2	HJG 02	*Huabeisporites*	1.8
2	HJG 02	*Pinuspollenites*	0.7
2	HJG 02	*Protohaploxypinus*	1.3
2	HJG 02	*Pteruchipollenites*	34
2	HJG 02	*Quadraeculina*	1.5

Note: This file must be saved as a CSV file. The field names can be lower case, upper case, and mixed case. The data in the abundance field can be both percentage value and the counted number of the respective grains.
The full file can be downloaded at: http://www.sporopollen.com/sporeexample.php?opterate=Paleoenvironmental%20Reconstruction.

The dataset that will be uploaded by users must include three fields, which are *Sample*, *Genus*, and *Abundance* (**Table 4-3**). The data in field *Abundance* can be either the number of counted grains (raw data) or percentage values of the sporomorphs sorted by sample. Due to the same genus in both the uploaded dataset and the dataset *Taxonomy* (**Table 4-1**), the abundances for Phylum, Order, and Family in each of the samples are calculated. Furthermore, based on the same genus in both the uploaded dataset and the dataset *Ecogroup* (**Table 4-2**), the abundances of EPH and EPT are provided (**Figure 4-2** for dataset relationship).

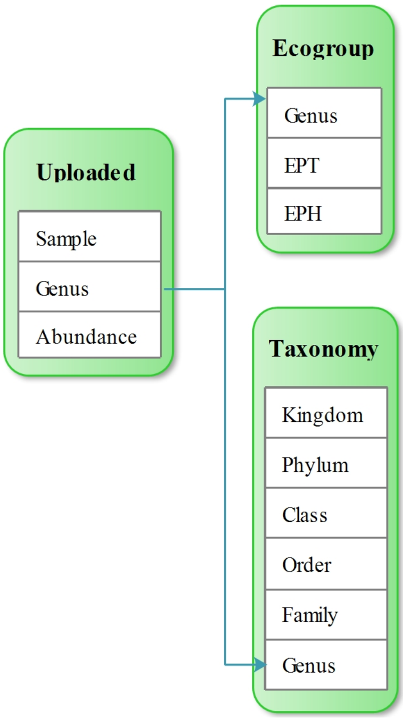

Figure 4-2 The datasets *Taxonomy* (**Table 4-1**) and *Ecogroup* (**Table 4-2**) in the database and the user-uploaded dataset (**Table 4-3**).

Note: All the datasets have the same field of Genus, by the same genera stored in the fields different datasets can be integrated as a single dataset.

Table 4-4 The result for Vegetation Order using the data in **Table 4-3**.

Sample	HJG 01	HJG 02
Bennettitales	33.8	8.9
Corystospermales	25	33.9
Cyatheales	6.6	4.7
Equisetales	0	2
Ginkgoales	4.4	7.5
Gleicheniales	13.2	7.7
Isoetales	7.4	2.4
Lycopodiales	0	8.4
Marattiales	0	11.3
Notothyladales	5.9	0.7
Osmundales	0.7	0
Peltaspermales	0	1.3
Pinales	1.5	9.8
Uncertain	1.5	1.5

Note: This result is based on the combination of the datasets Taxonomy (**Table 4-1**) and the uploaded dataset (**Table 4-3**) by the same genera in the fields of Genus in both datasets. The result abundances are percentages sorted by samples. Genera with uncertain affinities are marked as Uncertain.

The uploaded dataset, strictly following the format of **Table 4-3**, must be saved as a CSV file which is a common way to transfer datasets between different databases. Then the interface at http://www.sporopollen.com/sporemesozoicsegs.php?opencode=paper1 is needed (**Figure 4-1**). Interface manuals and example files can be visited by clicking *Introduction* (**Figure 4-1-E**), which is linked to http://www.sporopollen.com/sporeexample.php?opterate=Paleoenvironmental%20Reconstruction. By clicking the *Choose File* button (**Figure 4-1-A**), a window will pop up for users to select the uploaded dataset stored in the local computer. The name of the button will be different if the user has a non-English system. For example, in the Chinese system, the button will be shown with Chinese characters. When the uploaded dataset is chosen, one of the analysis modes needs to be selected by clicking the *select box* (**Figure 4-1-B**). There are different modes available (**Figure 4-1-C**). The modes of *Vegetation Family*, *Vegetation Order*, and *Vegetation Phylum* will link the sporomorph genera in the uploaded dataset to their parent plant separately at family, order, and phylum level. The modes of *Eco-Plant EPH* and *Eco-Plant EPT* will link the sporomorph genera in the uploaded dataset separately to EPH and EPT. The results of all five modes will be shown in the form of a dataset yielding the abundances, (**Table 4-4**) which are calculated as percentages sorted by samples. If the results mentioned above shall be presented are needed as a graphical diagram (**Figure 4-3**), the modes of *Vegetation Family PDF*, *Vegetation Order PDF*, *Vegetation Phylum PDF*, *Eco-Plant EPH PDF*, or *Eco-Plant EPT PDF* should be selected. Users may want to combine the results of different modes into one diagram or delete some fields from the diagram. Therefore, the mode of *Draw Curve PDF* (**Figure 4-1-C**) should be selected to use this function. In this case, the uploaded dataset must follow the format presented in **Table 4-5** and also be saved as a CSV file. The first column of the uploaded dataset must be named *Sample* and includes the sample names or numbers. The other columns must be used to store the abundances of the palynomorphs in percentages (**Table 4-5**).

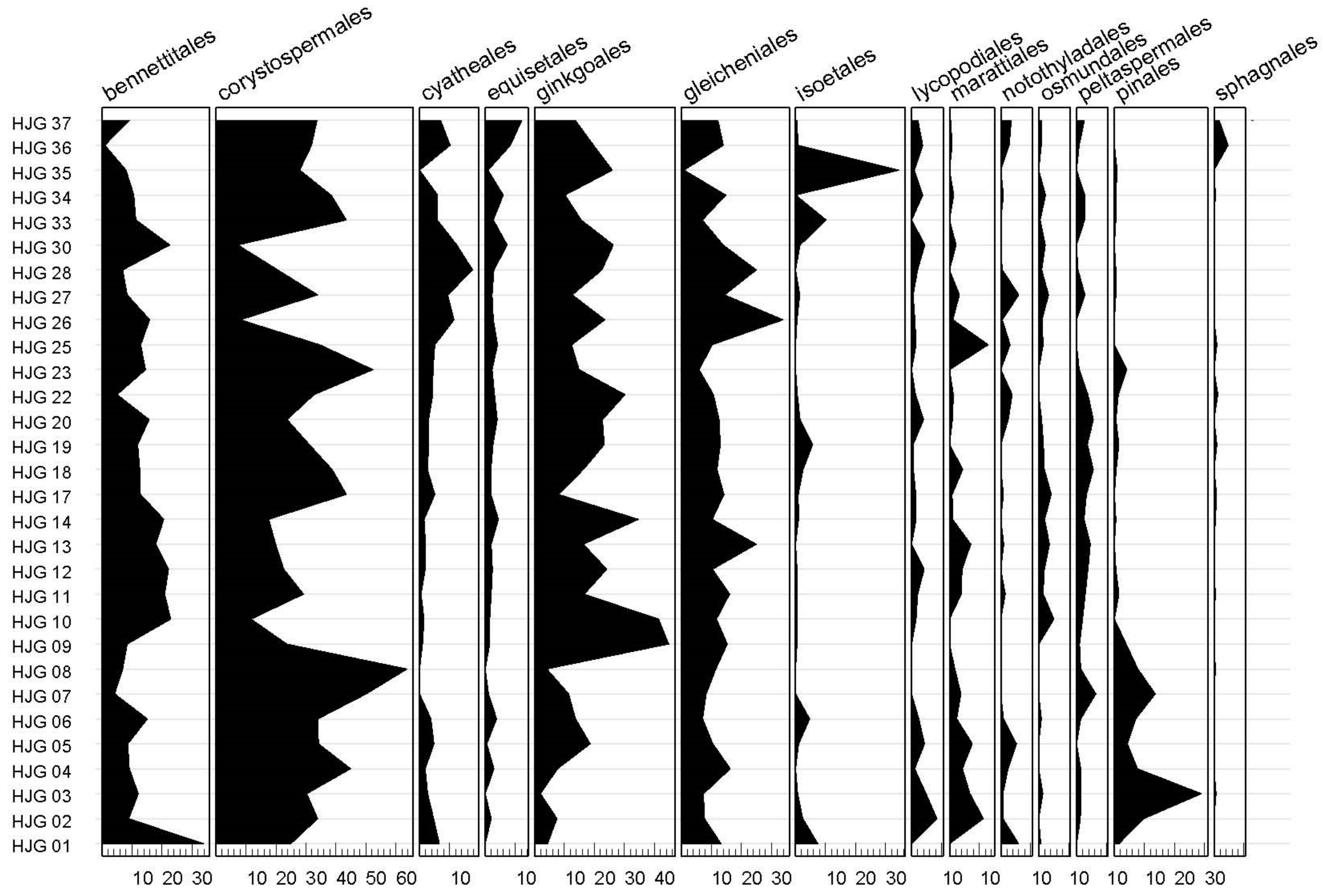

Figure 4-3 The result can be output in the form of a diagram showing the percentages of plant orders.

Note: It is the result of user-uploaded dataset (**Table 4-3**) connected with the dataset Taxonomy (**Table 4-1**) with the analysis mode of Vegetation Order PDF. All of the abundances are in percentages.

Table 4-5 Part of the example file accepted by ***Sporopollen*** which can be used only for Draw Curve PDF.

Sample	Bennettitales	Cheirolepidiaceae	Corystospermales	Cyatheales
HJG 01	33.8	1.5	25	6.6
HJG 02	8.9	9.1	34	4.7
HJG 03	12.1	29.1	30.4	2.7
HJG 04	9.1	7.2	45	1.9
HJG 05	8.6	2.9	34.3	4.8
HJG 06	15.1	5.7	34	3.8
HJG 07	4.2	9.8	50	0
HJG 08	6.9	0.9	63.8	0

Note: This file must be saved as a CSV file. The field names can be lower case, upper case, and mixed case. The first field of the uploaded dataset must be Sample which stores the sample names. The other fields must be used to store the abundances in percentages. The full file can be downloaded at: http://www.sporopollen.com/sporeexample.php?opterate=Paleoenvironmental%20Reconstruction.

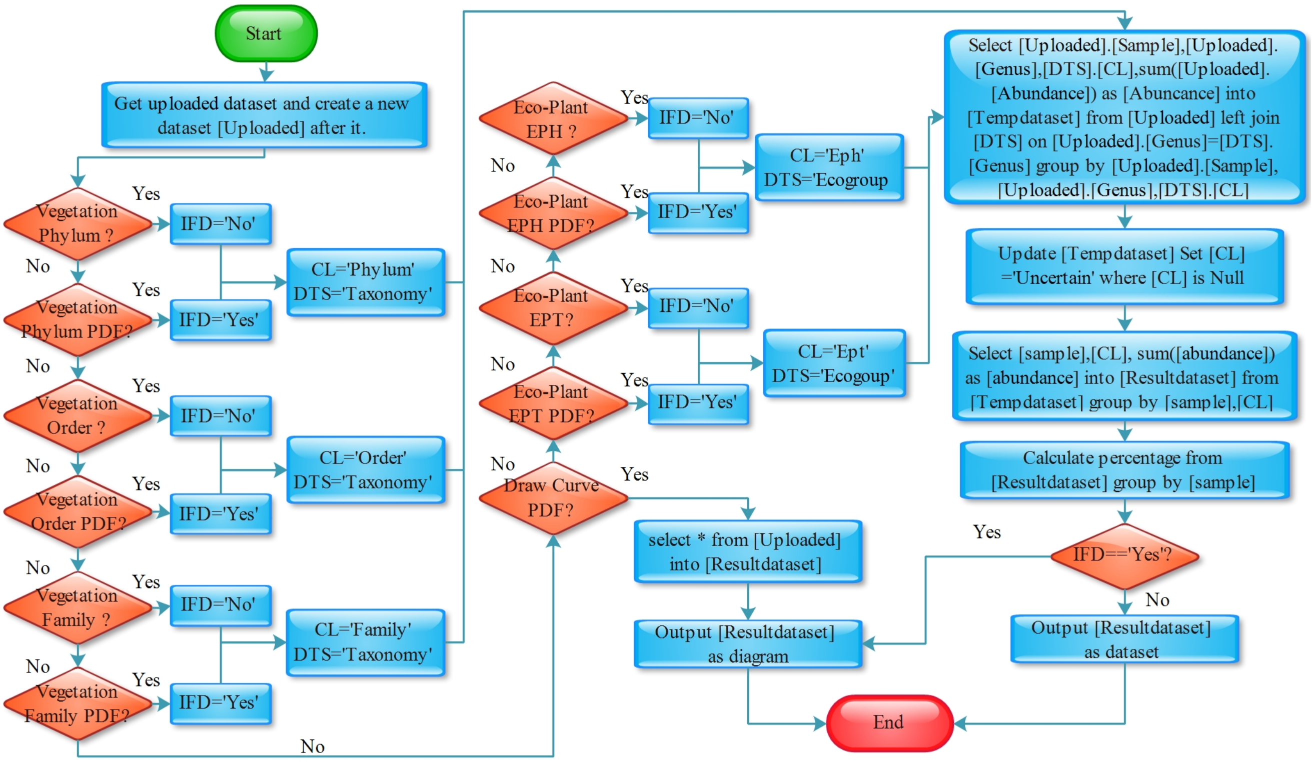

Figure 4-4 Flow chart for palaeoenvironmental reconstruction.

Note: Dataset names and attribute names are in square brackets, e.g., [Sample]. Dataset and field names are in title, e.g., Uploaded and Phylum. Variables are in upper case e.g., CL, DTS, IFD. [Uploaded] is the dataset storing the analysed data uploaded by users; [Tempdataset] is temporary dataset; [Resultdataset] is the result dataset. In this paper [Uploaded] is **Table 4-3** or **5**, [Taxonomy] is **Table 4-1**, and [Ecogroup] is **Table 4-2**.

When the uploaded dataset and analysis mode are chosen, by clicking the *Submit* button (**Figure 4-1-D**) the user immediately gets the result. MySQL combined with PHP codes are used to automatically finish the process (**Figure 4-4** for flowchart; **Appendix 4-2** for PHP and MySQL codes). Based on the codes, the first step of processing the data is to receive the user-uploaded dataset and store it as a new dataset *Uploaded*. Afterwards, based on the chosen process modes, abundances are calculated (**Figure 4-4**).

If the mode *Vegetation Phylum*, *Vegetation Phylum PDF*, *Vegetation Order*, *Vegetation Order PDF*, *Vegetation Family*, or *Vegetation Family PDF* is selected by the user, the user-uploaded dataset will automatically be linked to the dataset *Taxonomy* producing a combined dataset *Tempdataset*. If the mode is *Vegetation Phylum* or *Vegetation Phylum PDF*, abundance values are calculated by grouping the data by the fields *Sample* and *Phylum*. In contrast, if the selected mode is *Vegetation Order* or *Vegetation Order PDF*, abundances are calculated by grouping the data by the fields *Sample* and *Order*. Finally, if the chosen mode is *Vegetation Family* or *Vegetation Family PDF*, abundances are calculated by grouping the data by the fields *Sample* and *Family*. The genera without botanical affinity will be marked as *Uncertain* in all the six modes. For the modes *Vegetation Phylum*, *Vegetation Order*, and *Vegetation Family*, the output is a dataset of abundance data, for the modes *Vegetation Phylum PDF*, *Vegetation Order PDF*, and *Vegetation Family PDF*, the user will get a diagram of abundance data comparable to a pollen diagram.

If the mode *Eco-Plant EPH*, *Eco-Plant EPH PDF*, *Eco-Plant EPT*, or *Eco-Plant EPT PDF* is selected by the user, the uploaded dataset will automatically be linked to the dataset *Ecogroup* producing a combined dataset *Tempdataset*. If the mode is *Eco-Plant EPH* or *Eco-Plant EPH PDF*, abundances are calculated by grouping the data by the fields *Sample* and *Eph*. In contrast, if the chosen mode is *Eco-Plant EPT* or *Eco-Plant EPT PDF*, abundances are calculated by grouping the data by the fields *Sample* and *Ept*. Palynomorph genera without botanic affinity are marked as *Uncertain* in all the modes. For the modes of *Eco-Plant EPH* and *Eco-Plant EPT*, the output is a dataset of abundance data, whereas for the modes of *Eco-Plant EPH PDF* and *Eco-Plant EPT PDF* the user will get a diagram of abundance data comparable to a pollen diagram.

If the user selects *Draw Curve*, the user-uploaded dataset will be directly plotted as a diagram without linking to any database dataset.

4.3 Discussion

The Sporomorph Ecogroup Model (SEG model) of Abbink et al. (2004b) is commonly used for assigning eco-climatic traits to Mesozoic fossil sporomorph taxa of Europe and some parts of China (e.g., Abbink et al., 2001; Abbink et al., 2004a; Abbink et al., 2004b; Heunisch et al., 2010; Li and Wang, 2016; Li et al., 2016). It represents a simplified Eco-Plant model. According to hydrologic and temperature conditions in the Eco-Plant model, plants are classified into different EPH and EPT groups due to their climatic preferences. In contrast, in the SEG model, plants are classified as belonging to a wetter, drier, warmer, or cooler group. Besides, in the SEG model, due to uncertain botanical affinities of some palynomorphs, several plants indicating a different climate and environment are categorized in the same group. For example, in the Eco-Plant model, Ginkgoales are classified as mesophytes and mesothermic plants, but Bennettitales as hygrophytes and megathermic plants (Zhang et al., 2020). In contrast, in the SEG model, Ginkgoales, Cycadales, and Bennettitales are all included in the same group of the “Lowland SEG” and indicate a “drier” and “warmer” climate, since the pollen of Ginkgoales, Cycadales, and Bennettitales can usually only be distinguished under scanning electron microscopy (SEM) or transmission electron microscope (TEM) (Abbink et al., 2004b). Therefore, the Eco-Plant model is chosen in our database since it allows for more detailed and precise statements on palaeoclimate than the SEG model.

Zhang et al. (2020) only linked 19 sporomorph genera to 15 families or orders of Mesozoic plants and Eco-Plant. However, in this database, many more genera are included in dataset *Taxonomy* (**Table 4-1**). Fossil sporomorph taxa from the Mesozoic to extant can be linked to their parent plants at family, order, or phylum level by the database.

The Eco-Plant model is applied by palynologists for palaeoenvironmental reconstructions using dispersed sporomorphs from the Cenozoic (e.g., Aranbarri et al., 2014; Kern et al., 2012; Popescu et al., 2006; Suc and Fauquette, 2012) and Mesozoic (e.g., Césari and Colombi, 2016; Hochuli and Vigran, 2010; Mueller et al., 2016; Roghi et al., 2010; Visscher and van der Zwan, 1981; Wang et al., 2013; Wang et al., 2005; Zhang et al., 2020; Zhao et al., 2014). However, for most of the Mesozoic dispersed sporomorphs, the application of Eco-Plant is limited, because either their assignment to a specific Eco-Plant remains uncertain or the botanical affinities to plant taxa are unclear (Zhang et al., 2020). For the dispersed Mesozoic sporomorph genera of Bryophytes, Pteridophytes, and Gymnosperms (Zhang et al., 2021b), which are included in the database, their EPH and EPT are stored in dataset *Ecogroup* (**Table 4-2**). The dispersed sporomorphs of angiosperms are currently not linked to Eco-Plant. Nevertheless, the first reliable angiosperm is discovered at the top of the

Jurassic (Sun et al., 1998; Sun et al., 2002). Therefore, this database is capable of automatically linking all sporomorph genera from the Triassic and the Jurassic to Eco-Plant to reconstruct relative climate changes. However, the terms used by different authors for Eco-Plant groups are not always the same, making the comparison of results between different authors difficult, e.g., the *Thermophytic form* used by Wang et al. (2005) is more or less the same as the *Megathermic element* used by Suc and Fauquette (2012). The term *Halophytes* is equivocal (Flowers and Colmer, 2008) and it is difficult to distinguish this Eco-Plant group from *Xerophytes*. Therefore, most authors (e.g., Visscher and van der Zwan, 1981; Wang et al., 2005) use the term *Xerophytes* to represent both *Halophytes* and *Xerophytes* in the Mesozoic. In this database, the concept of Eco-Plant groups that assess the effect of humidity (EPH) and the effect of temperature (EPT) follows Zhang et al. (2020) and (2021b), which makes it easier to compare the results between different users using the same concepts. Users can also review published sporomorph data by extracting them from published studies and by uploading these data to the database.

The database provides a tool for linking dispersed sporomorph genera to their parent plants and analysing them for palaeoecological and palaeoclimatic implications. Usually, to get for a user-uploaded dataset the results of the analyses, only several seconds are needed. High-resolution palynomorph studies usually need to process huge amount of sporomorph data. This database can speed up the process and save time for users. The obtained result in the form of a dataset with abundance values (e.g., **Table 4-4**) can be used for, e.g., further statistical analysis by other software, e.g., PAST (Hammer et al., 2001), or for producing diagrams by other programs e.g., PanPlot 11.04 (Sieger and Grobe, 2013). The graphical output in form of a diagram (e.g., **Figure 4-3**) gives the user a quick and vivid overview of the results.

The algorithm that assigns eco-climatic traits to the uploaded fossil sporomorph data (**Figure 4-4**) and the database datasets (**Table 4-1** and **Table 4-2**) are independent, which allows an easy database update. In conclusion, if there are new published studies on botanical affinities of Paleozoic and Mesozoic sporomorph taxa, the related information only needs to be included in the dataset *Taxonomy* (**Table 4-1**). If there are, e.g., new studies on the EPH and EPT of dispersed sporomorphs for angiosperms, only the dataset *Ecogroup* (**Table 4-2**) must be updated. Furthermore, when there are new algorithms needed to process the sporomorph taxa, only the new PHP and MySQL codes must be compiled and linked with the user interface (**Figure 4-1**). In future, any information on the modification of the database will appear below the user interface (**Figure 4-1**). As it is an online database, any new changes in this database will have an immediate benefit for all users.

To produce reliable results, data on botanical affinities of sporomorphs and environmental information for the parent plants stored in the datasets *Taxonomy* (**Table 4-1**) and *Ecogroup* (**Table 4-2**) are based on published studies. However, systematic analysis is needed when there are uncertainties, e.g., on botanical affinities, due to different affinities published in different studies. As an example, *Quadraeculina* Maljavkina, 1949 ex Potonie 1960 is related to the Podocarpaceae (Abbink et al., 2004b) or Caytoniaceae (Gao et al., 1999), etc. However, no reliable *in situ* pollen (pollen grains in situ within a sporangium) has been published. In this case, the affinity of *Quadraeculina* is marked as *Uncertain* in the dataset *Taxonomy*. *Annulispora* De Jersey, 1959 McKellar 1947 was reported to be related to Sphagnaceae (Paterson et al., 2016), but based on scanning electron microscope (SEM) studies, the spore is more comparable with the extant spores of Notothyladaceae (Zhang et al., 2020). In this case, the affinity of *Annulispora* is marked as Notothyladaceae in the dataset *Taxonomy*. Nevertheless, all studies on botanical affinities for the collected sporomorph genera in dataset *Taxonomy* can be viewed by adding a single genus name in the text box combined with clicking the *Search* button at http://www.sporopollen.com/sporeidentify.php?operate=taxonomy&taxonomy=Annulispora or by selecting the genus name at http://www.sporopollen.com/sporefamilygenus.php?language=english. By comparing the unique outline and structure/sculpture of the sporomorph wall with that of pollen/spores of modern plants and *in situ* fossil plants, the botanical affinities, EPH, and EPT of the 861 dispersed Mesozoic sporomorph genera of Bryophytes, Pteridophytes, and Gymnosperms are reviewed by Zhang et al (2021b). In the Mesozoic, the lack of *in situ* sporomorphs is the main reason that the parent plants of dispersed sporomorphs can only be recovered at order or family level. The Eco-Plant model will be improved when more *in situ* sporomorphs are discovered. If the database is updated with data of new studies, the list of new publications will appear below the user interface (**Figure 4-1**). Therefore, the users can verify how botanical affinities, EPH, and EPT for the sporomorph genera are derived.

The quality of sporomorph data in the uploaded dataset can also determine the quality of the result produced by the database. The genera included must be identified precisely by users using the appropriate genus names. All sporomorph names of taxa from different systems, fossil or extant, are governed by *the International Code of Nomenclature for algae, fungi, and plants* (Turland et al., 2018). There are three parallel systems of sporomorph classification (Traverse, 2007): (1) natural, where reference to extant taxa is certain and the modern generic name could be used; (2) half-natural, where reference to an extant taxon is suspected but not proven; (3) artificial, where the relationship is not known at all, and a form-generic name based on morphological features is created. For this reason, different names may be used for the same sporomorph genus. In the Mesozoic, only half-natural and artificial systems are used. However, the differences between the two systems are not clear. Under the present code, "half-natural" names are just morphogenetic names and the same as "artificial" names, providing that they are validly published (Traverse, 2007). Because of the confusing nomenclature systems and the lack of a regulation about which name is the valid one, users should use the genus name with detailed descriptions and certain affinities when different names are available for the same sporomorph taxon. For example, *Cycadopites* Wodehouse 1933 ex Wilson et Webster 1946, has such a broad definition that it includes genera such as *Cycadaceaelagenella* Malyavkina 1953 (Cycadales) and *Ginkgocycadophytus* Samoilovich 1953 (Ginkgoales) (Ames et al., 1976; Huang, 2008; Zavialova et al., 2014). In this case, *Cycadaceaelagenella* and *Ginkgocycadophytus* are advisable to be used rather than *Cycadopites*. For detailed identification of sporomorphs, sometimes SEM or transmission electron microscopy (TEM) are recommended since the specific characters of some pollen and spores can usually only be distinguished under SEM or TEM (Abbink et al., 2004b). However, users can still use the in-advisable names, but they must keep such names as few as possible. In the results produced by the database, the botanical affinities, EPH, and EPT related with the in-advisable names will be marked as *Uncertain* and the sporomorphs have no contribution to the palaeoenvironmental analysis. The use of too many of such elements will make the result produced by the database insignificant. Advisable and in-advisable names for dispersed Mesozoic sporomorph genera of Bryophytes, Pteridophytes, and Gymnosperms are listed at http://www.sporopollen.com/sporefamilygenus.php?language=english.

The lack of *in situ* sporomorphs is also the main reason that the affinities of Paleozoic sporomorph taxa are currently not included in this database. Genera without certain affinities or which have not been included in the database will also be marked as *Uncertain* in the result for the botanical affinities, EPH, and EPT and reduce the quality of the result. Therefore, currently, the database is not suitable for records from the Paleozoic.

The database also provides a platform for possible cooperation. (1) Users are encouraged to contact the first author for including their published data in the datasets *Taxonomy* (**Table 4-1**) and *Ecogroup* (**Table 4-2**). (2) To date, almost all published sporomorph genera since the Early Triassic are included in the dataset *Taxonomy* (**Table 4-1**). However, if users find some genera that are still missing and the related references are available, they can contact the first author to update the database. (3) Suggestions for the improvement of the database by contacting the first author is always appreciated. In any case, the contributions of users to our database will always benefit the other users.

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

5. Palynology and the Eco-Plant model of peat-forming wetlands of the Upper Triassic Haojiagou Formation in the Junggar Basin, Xinjiang, NW China

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Abstract

Terrestrial deposits of the Triassic-Jurassic transition are well developed in the Junggar Basin, located in the Haojiagou Valley of Urumqi, Xinjiang Uygur Autonomous Region of Northwest China. This paper describes the palynology of a 10 m thick lignite bed from the Upper Triassic Haojiagou Formation (Rhaetian) with the aim of reconstructing the palaeovegetation and palaeoenvironment of a peat-forming wetland near the Triassic-Jurassic boundary. The palynoflora contains both Eurasian and Gondwanan elements, and is dominated by the spores and pollen of Bennettitales, Corystospermales, Ginkgoales, and Gleicheniales. At the Triassic/Jurassic boundary (Hettangian), the palynoflora significantly changes as Cyatheales spores become the dominant elements. We analyse assemblages in terms of an Eco-Plant model, which assigns the parent plants of the palynomorphs into five groups based on humidity and four groups based on temperature, and uses multivariate statistical analyses to infer palaeoclimate and palaeoenvironmental conditions. Results suggest that the palaeoclimate of the Rhaetian was generally wet and subtropical with short seasonal drought periods. Our analysis shows that an Eco-Plant model may be a useful tool to reveal past vegetation patterns and climate changes, applicable to other Mesozoic assemblages.

5.1 Introduction

At the Triassic-Jurassic boundary, a mass extinction event resulted in the loss of more than 30% of marine genera, 50% of tetrapod species and a 95% turnover of megafloral species (Benton, 1995; McElwain et al., 1999; Raup and Sepkoski, 1982). In the Junggar Basin, which is located in the Xinjiang Uygur Autonomous Region of Northwest China (**Figure 5-1**), an almost continuous continental sedimentary record has been documented from the Permian to the Cretaceous (Ashraf et al., 2010; Hornung and Hinderer, 2011). In particular, in the Upper Triassic Haojiagou Formation located within the Haojiagou Valley of Urumqi, the terrestrial deposits of the Triassic-Jurassic transition are well developed (Hornung and Hinderer, 2011; Lu and Deng, 2005). They yield a diverse assemblage of non-marine animal and plant fossils (Sun et al., 2010a) as well as fossil spores and pollen (Ashraf et al., 1999; Ashraf et al., 2010; Ashraf et al., 2001; Huang, 2006; Lu and Deng, 2005, 2009). Palynological analysis offers a broad window for unravelling past vegetation patterns and reconstructing climate changes (Li and Wang, 2016; Loinaze et al., 2018); thus, the microflora is crucial for better understanding the terrestrial response of Triassic-Jurassic ecosystems to biotic and geological events in the Junggar Basin.

Several independent studies have used palynological data to determine the general palaeoclimate during parts of the Triassic and/or the Jurassic (e.g., Ashraf et al., 2010; Lu and Deng, 2009). However, most of these studies have their focus on biostratigraphic issues and are based mainly on light microscopy (LM) that limits the accurate identification of parent plant groups within the flora of the uppermost Upper Triassic. Therefore, detailed palynological investigations especially using scanning electron microscopy (SEM) are needed for the assignment of the palynomorphs to their parent plants. These assignments allow Late Triassic plant diversity, and ecosystem-response to climate variations to be revealed across the Triassic-Jurassic boundary. Here, we analyze 37 palynological samples from a 10 m thick lignite bed, from of the stratotype section of the Haojiagou Formation using LM and SEM techniques to reconstruct the palaeovegetation and the palaeoenvironment of a peat-forming wetland. Although significant palynological abundance changes are known from the Triassic-Jurassic boundary, vegetational changes in the Haojiagou Formation are reported as relatively subtle (Ashraf et al., 2010; Lu and Deng, 2009). The generally similar values of $\delta^{13}C_{org}$ for the whole Haojiagou Formation indicate that strong climatic variations can be excluded for the depositional time (Lu and Deng, 2009). Therefore, the studied lignite section should also be representative for the climate change of the whole Haojiagou Formation.

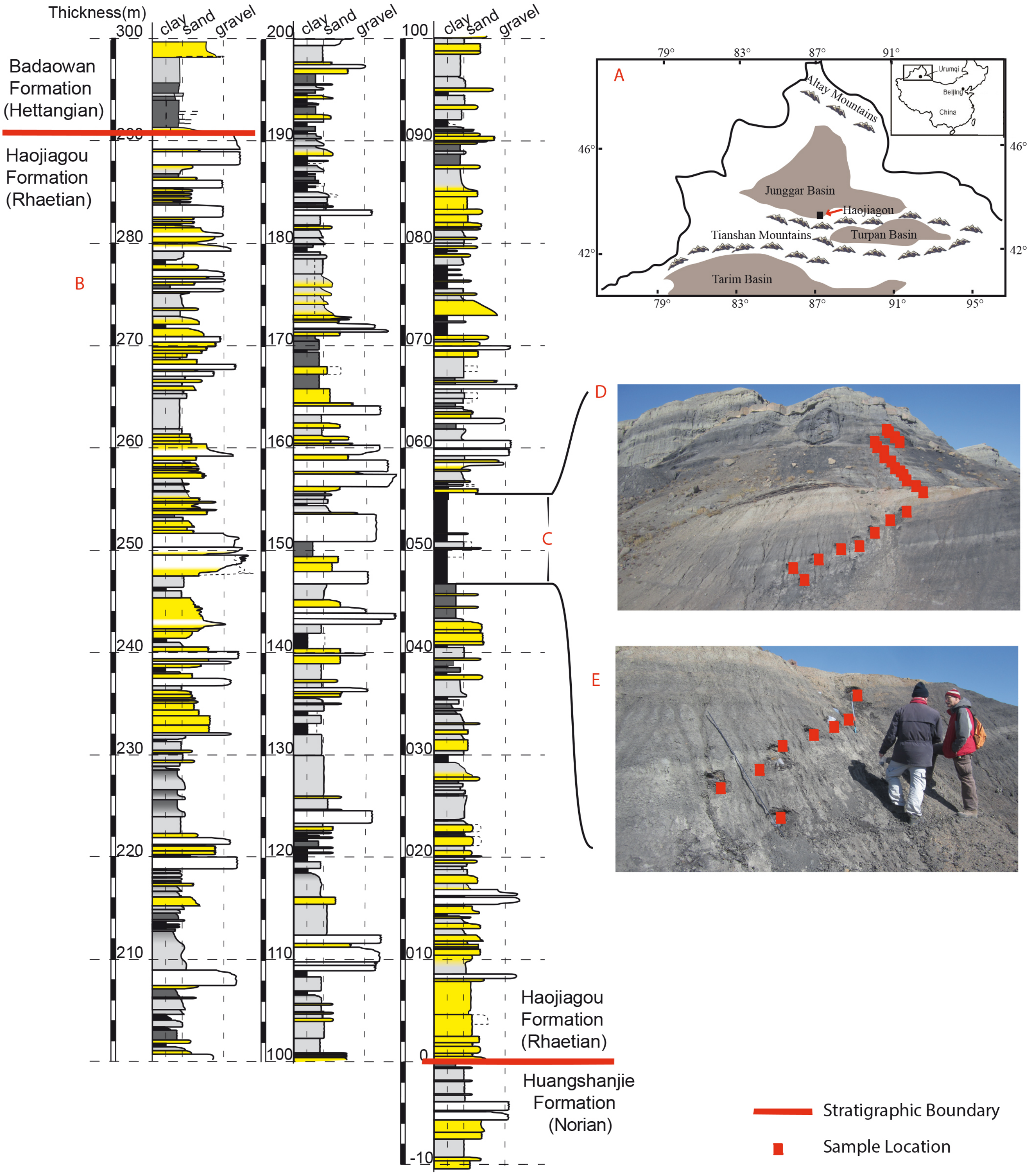


Figure 5-1 The lithological section of the Upper Triassic Haojiagou Formation from the Haojiagou Valley in the Junggar Basin, NW China.

Note: A. The geographic position of Haojiagou Valley located at the southern margin of the Junggar Basin; **B.** Lithological section of the Haojiagou Formation which is conformably overlain by the Lower Jurassic Badaowan Formation and conformably underlain by the Norian Huangshanjie Formation; **C.** The sampled lignite seam is about 10 m thick and represents the thickest lignite bed within the

Haojiagou Formation. There is no lithofacies change for the sampled coal-bearing part; **D.** Overview of the sampled lignite beds. Each of the red square represents a palynological sample; **E.** Detail of the sampled lignite seam with palynological sample locations.

5.2 Geological setting and previous studies

The Junggar Basin is one of three large sedimentary basins located in the Xinjiang Uygur Autonomous Region of Northwest China. It is flanked by the Altay Mountains in the northeast and separated from the Tarim and Turpan Basins by the Tianshan Mountains in the south (**Figure 5-1**-A). Geologically, this area is part of the Central Asian orogenic belt (Chen et al., 2012). The basin was cut off from marine influence during the Carboniferous to Early Permian, when the Tianshan Mountains were folded up through the collision of the cratonic Tarim block and the Eurasian plate (Allen et al., 1993; Sharps et al., 1989; Watson et al., 1987). Since then, non-marine sediments have been deposited in the sedimentary basin, leading to a continuous series of Permian to Late Cretaceous strata, which are unconformably overlain by Cenozoic sediments (Bian et al., 2010). The abundant red beds present in the Lower and Middle Triassic stratigraphic successions demonstrate that this region was subjected to a relatively arid climate during these times. In the Upper Triassic (Rhaetian) Haojiagou Formation charcoal and oriented wood fragments prove that this region was exposed to a relatively humid climate (Hendrix et al., 1992).

The stratotype section of the Haojiagou Formation (43°39'54.47" N, 87°12'40.67" E) is located in the Haojiagou valley, about 40 km southwest of Urumqi, the capital city of the Xinjiang Uygur Autonomous Region. The formation is about 290 m in thickness, mainly composed of grey and greyish-yellow sandstones and conglomerates intercalated with mudstones, sandy mudstones, and lignite beds (**Figure 5-1**-B). It is conformably underlain by the Norian Huangshanjie Formation and conformably overlain by the Lower Jurassic Badaowan Formation.

The Haojiagou Formation is characterized by terrestrial and marginal lacustrine depositional environments and can be subdivided into a lower and an upper part. The Lower Haojiagou Formation is composed of coaly, silty and clayey lithofacies types deposited in a lacustrine delta top with fluvial and back-swamp environments (Hornung and Hinderer, 2011). Fusain (Fiber coal) is particularly common in the lignite deposits, which is formed almost exclusively by forest fires (Ligouis, 2001). A distal alluvial-plain environment with cross-bedded sandstone and conglomeratic units characterizes the Upper Haojiagou Formation (Hornung and Hinderer, 2011). This formation yielded abundant plant macrofossils (Lu and Deng, 2005; Sun et al., 2010a). Among these, *Cycadocarpidium erdmanni*, *Cycadocarpidium swabii,* and *Neocalamites hoerensis* are important elements in the Late Triassic floras of Eurasia. Therefore, the Haojiagou flora is characterized by the *Glossophyllum/Cycadocarpidium* assemblage, which demonstrates a Late Triassic age, probably Norian-Rhaetian (Sun et al., 2010a). Palynologically, the Haojiagou Formation is characterized by the *Concavisporites/Duplexisporites problematicus/Ricciisporites tuberculatus* zone indicating close similarities to other Late Triassic Eurasian microfloras, e.g., of Iran or Germany (Ashraf et al., 2010; Lu and Deng, 2005).

The Triassic-Jurassic boundary occurs at the base of the succeeding Badaowan Formation in this section (Ashraf et al., 1999; Ashraf et al., 2010; Lu and Deng, 2005, 2009; Sun et al., 2010a; Tong et al., 2019). However, the exact position of the Triassic Norian-Rhaetian boundary is under discussion. One view uses the base of the Haojiagou Formation as the boundary (e.g., Ashraf et al., 1999; Ashraf et al., 2010; Ashraf et al., 2001); whereas another view suggests that the Haojiagou formation contains the Upper Norian Stage and the whole Rhaetian Stage (e.g., Tong et al., 2019). Therefore, the boundary between the Norian and Rhaetian Stages is not defined yet and, at present, the global stratotype and boundary markers of Norian-Rhaetian have not yet been decided (Tong et al., 2019).

5.3 Materials and methods

5.3.1 Sampling and sample processing

Most of the lignite beds in the Haojiagou Formation are less than 3 m in thickness. Only one lignite seam with a thickness of about 10 m occurs in the Haojiagou Formation, about 45 m above the top of the Huangshanjie Formation and about 235 m below the base of the Badaowan Formation (**Figures 5-1**-B, C, D, and E). However, it is intercalated with a sandy bed around 1 m thick that is laterally not continuous and most likely represents a channel fill. The lignite bed belongs to the Upper Norian or the Lower Rhaetian Stage. For the lignite seam, a delta-top environment can be assumed characterized by small channels and interbedded crevasse-splay sediments (Hornung and Hinderer, 2011).

The 37 samples that were analyzed were taken from the lignite seam with a sample distance of *c.* 0.3 m., labelled from bottom to top with HJG 01 to HJG 37. Palynological preparation of *c.* 100 g material per sample, including treatment with hydrochloric acid (HCl), hydrofluoric acid (HF) and potassium hydroxide (KOH), followed the standard method as described by Kaiser and Ashraf (1974). After sieving through a 10 µm mesh screen, residues were oxidized using nitric acid (HNO_3) or hydrogen peroxide (H_2O_2) to improve transparency of the palynomorphs. For each sample, the residues were rinsed with 10 litres of distilled water, sieved, and then stored in 3 ml water vials. For each sample, at least one slide was made for LM analysis by mounting 0.025 ml of residue mixed with liquid on the slide using glycerine jelly. For 12 of the samples (HJG 01-12), 0.01 ml of residue was taken and dropped on an aluminium stub with an adhesive carbon pad with an area of approximately 1 cm^2 and dried at approximately 25 °C for 48 h to be used for SEM analysis at the ESEM Lab of the Technische Universität Darmstadt, using a voltage of 12.5-15 kV. To get rid of charging problems, some SEM samples have been coated with gold. All residues, carbon pads, and slides are stored at the Institute of Applied Geosciences, Technische Universität Darmstadt, Germany.

5.3.2 Qualitative and quantitative palynological analysis

SEM can reveal features of palynomorphs at the species level not observable by LM (Hesse et al., 2018). Therefore, SEM was mainly used for the exact identification of palynomorphs while LM was taken for quantitative analysis. For each sample, about 200 palynomorphs were counted using an Olympus light microscope (Olympus BX40) at ×400 magnification. Additionally, for a comprehensible study, each counted grain has been documented by a digital picture. To reconstruct the botanical affinities of the pollen and spores, the systematic scheme of extant plants provided by Goffinet and Buck (2004) and Smith et al. (2006) and the systematic scheme of fossil plants of Taylor et al. (2009) have been used.

The pollen diagrams, produced by our online database ***Sporopollen*** (http://www.sporopollen.com), show the abundance of the palynomorphs related to their parent plants or Eco-Plant groups in percentages.

5.3.3 Eco-Plant model

The Ecogroup classification based on the growth-form of plants (Eco-Plant) was established by the pioneering work of Warming (1895) and Schimper (1898). They analyzed diverse plant associations with relation to principal climatic elements such as water, heat, light, and air. The Eco-Plant model has been widely used for extant (e.g., Baeza et al., 2010; Godin, 2017; Sheremetov and Sheremetova, 2017; Veisberg, 2017), Cenozoic (e.g., Bozukov et al., 2009; Yang et al., 2013; Yurtsev, 2001), Mesozoic (e.g., Hill, 2017; Vakhrameev, 1991), and Paleozoic palaeoenvironmental reconstructions (e.g., Bashforth et al., 2014; Wang, 1999b). It is also applied by palynologists for palaeoenvironmental reconstructions using dispersed sporomorphs from the Cenozoic (e.g., Aranbarri et al., 2014; Kern et al., 2012; Popescu et al., 2006; Suc and Fauquette, 2012) and Mesozoic (e.g., Césari and Colombi, 2016; Hochuli and Vigran, 2010; Mueller et al., 2016; Roghi et al., 2010; Visscher and van der Zwan, 1981; Wang et al., 2013; Wang et al., 2005; Zhao et al., 2014).

For the analysis of palaeoenvironmental and palaeoclimate variations throughout the analyzed record of the Haojiagou Formation, we use an Eco-Plant model that assesses the effect of humidity (EPH) and the effect of temperature (EPT) that has also been used by other authors for Mesozoic records (e.g., Hill, 2017; Vakhrameev, 1991).

EPH separates the palynomorphs and their parent plants into five groups (Runhaar et al., 1997; Sheremetov and Sheremetova, 2017):

a) *Hydrophytes* are aquatic plants that are completely or mostly submerged in water as well as being amphibious plants that grow both in water and in excessively wet habitats along the shorelines of reservoirs, in areas of shallow water, and in swamps.

b) *Hygrophytes* are plants that are living in excessively wet habitats with a high air and soil moisture but usually no water stagnation on the surface, such as the lower tiers of wet forests, or open habitats with constantly wet soils and wet air.

c) *Mesophytes* are plants that have some ability to resist periods of drought or to regulate their water metabolism in moist areas such as dry meadows or pine forests.

d) *Xerophytes* are plants that can resist long periods of drought and are living in stony steppes and dry rock outcrops.

e) *Euryphytes* are plants that are adapted to great variations in humidity.

EPT categorizes the palynomorphs and their parent plants into four groups (Nix, 1982; Prentice et al., 1996; Suc and Fauquette, 2012):

a) *Megathermic* plants inhabiting regions such as tropics and subtropics with a mean annual air temperature (MAT) above 20 °C.

b) *Mesothermic* plants inhabiting regions such as warm temperate zones with a MAT between 14 to 20 °C.

c) *Microthermic* plants inhabiting regions such as the cool temperate zone, the subarctic zone, or elevated areas with a MAT below 14 °C.

d) *Eurythermic* plants that can tolerate a wide range of temperatures.

The Sporomorph Ecogroup Model (SEG model) of Abbink et al. (2004b) is also commonly used for Mesozoic palaeoenvironmental reconstructions of Europe and some parts of China (e.g., Abbink et al., 2001; Abbink et al., 2004a; Abbink et al., 2004b; Heunisch et al., 2010; Li and Wang, 2016; Li et al., 2016). It represents a simplified Eco-Plant model. According to hydrologic and temperature conditions in the Eco-Plant model, plants are classified into different EPH and EPT groups due to their climatic preferences. In contrast, in the SEG model, plants are classified as belonging to a wetter, drier, warmer, or cooler group. Besides, in the SEG model, due to uncertain botanical affinities of some palynomorphs, several plants indicating a different climate and environment are categorized in the same group. For example, in the Eco-Plant model, Ginkgoales are classified as mesophytes and mesothermic plants, but Bennettitales as hygrophytes and megathermic plants (see below). In contrast, in the SEG model, Ginkgoales, Cycadales, and Bennettitales are all included in the same group of the “Lowland SEG” and indicate a “drier” and “warmer” climate, since the pollen of Ginkgoales, Cycadales, and Bennettitales can usually only be distinguished under SEM or TEM (Abbink et al., 2004b). Therefore, we have chosen Eco-Plant since it allows for more detailed and precise statements on palaeoclimate than the SEG model.

However, for most of the Mesozoic dispersed sporomorphs, the application of Eco-Plant is limited, because either their assignment to a specific ecogroup remains uncertain or the botanical affinities to plant taxa are unclear. Therefore, it is first important to identify their botanical affinities, because otherwise their Eco-Plant implications are not reliable. Therefore, we have systematically reviewed the Mesozoic dispersed sporomorphs related with Bryophytes, Gymnosperms, and Pteridophytes and linked them to their possible parent plants as well as Eco-Plant. The primary results are presented in our online database (http://www.sporopollen.com/sporefamilygenus.php).

5.3.4 Statistical analysis

We present complex and multivariate pollen data and use different ordination techniques to show ecological trends. For revealing abundance patterns in the data set, numerical analyses of palynological data were undertaken using plant orders and families as represented in **Table 5-1, 2**. Thereby, some of the sporomorph taxa were lumped together because of similar botanical/ecological affinities such as *Bharadwajipollenites* and *Ricciisporites*, which were treated as Bennettitales. Only one species, *Quadraeculina* with unknown botanical affinity, was used without assignment to a plant family or order in the analyses. For further analyses, we used the different EPH and EPT ecogroups to reveal palaeoecological and palaeoclimate trends in the data set.

Numerical treatment of the palynological data relied on using PAST 3.26 (Hammer et al., 2001). Prior to ordination the raw data values were Wisconsin double standardized. Wisconsin standardization scales the abundance of each taxon to its maximum value and represents the abundance of each taxon by its proportion in the sample (Mander et al., 2010). This equalizes the effects of rare and abundant taxa and removes the influence of sample size on the analysis (Jardine and Harrington, 2008; van Tongeren, 1995).

Constrained cluster analysis using the unweighted pair-group average (UPGMA) method and a Euclidean distance has been applied to the plant order/families data set to identify samples with similar palynomorph contents. We selected constrained analysis for Q-mode defined sample clusters to group only stratigraphically adjacent samples during the clustering procedure and to identify a zonation in the record.

To reveal the underlying pattern as well as ecological gradients, a principal component analysis (PCA) was implemented. PCA was chosen as the appropriate multivariate model, because a gradient analysis (detrended correspondence analysis, DCA; Hill and Gauch (1980)) using CANOCO 4.5 (Leps and Smilauer, 2003) determined a length of 1.851 SD (units of average standard deviation of species turnover). This is a measure of unimodality for the gradient represented by the first DCA axis of the plant order/families data set and 1.359 SD for the Eco-Plant data set. Following Leps and Smilauer (2003), a gradient length less than 3 SD indicates an approximately linear trend in species composition, and the linear response model of the PCA should be used rather than a unimodal response model like (detrended) correspondence analysis (CA/DCA).

5.4 Results

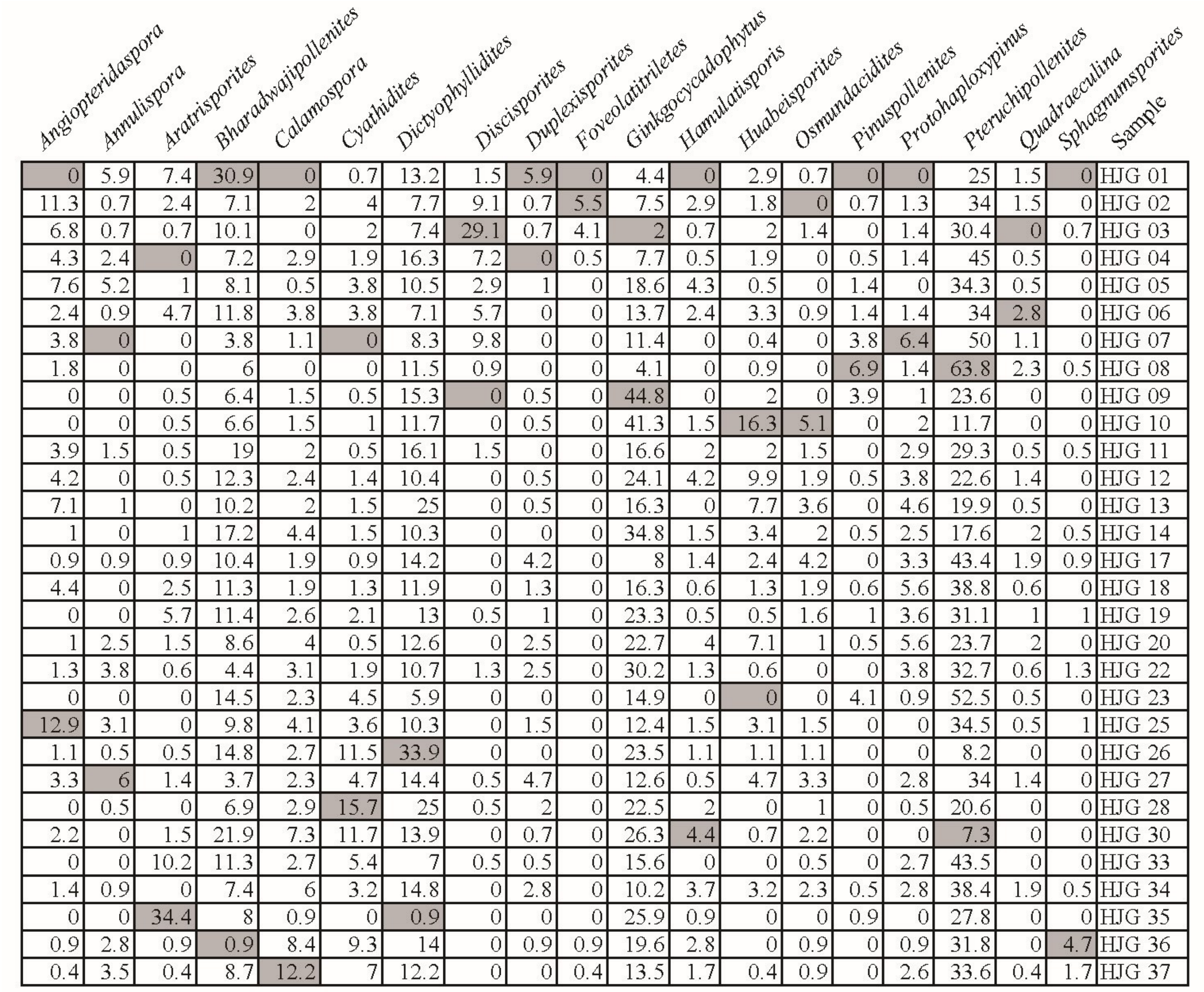
5.4.1 Qualitative analysis

Among the 37 samples, 30 of them preserve abundant palynomorphs. In total, 570 SEM pictures have been taken for identification and assignment to their parent plants as well as 6436 LM pictures for the quantitative analysis. All pictures are stored in the online database ***Sporopollen*** (http://www.sporopollen.com). Finally, 19 genera of palynomorphs have been identified (**Table 5-1**). All recognized palynomorph genera are presented in **Figures 5-2, 3** as SEM and in **Figures 5-4, 5** as LM images. In the following, 18 palynomorph genera are assigned to parent plant orders or families. This is based on information taken from the literature as well as own assignments based on SEM images of the various palynomorphs and the study of the ultrastructure of the palynomorph wall. Furthermore, we allocate the recognized plant order and families to EPH and EPT categories. The relevant plant fossils discovered in this region (Lu and Deng, 2005; Shi et al., 2015; Sun et al., 2010a; Yang et al., 2006) are also listed here (**Table 5-2**). For the identified plants, the fossils of Lycopodiales, Notothyladaceae, and Sphagnales have not been discovered in this region yet. Only one of the recognized genera in the pollen assemblage of the Haojiagou Formation, *Quadraeculina* (**Figures 5-3**-N, **5**-F), could not been assigned to a specific plant order and family. The various plant orders and families are listed below in alphabetical order.

5.4.1.1 Bennettitales

The fossils of *Nilssoniopteris* (Lu and Deng, 2005) and *Otozamites* (Sun et al., 2010a) have been discovered in the Haojiagou Formation. Two pollen genera that have been found in the palynomorph assemblage, *Bharadwajipollenites* (**Figures 5-2**-E-H, **4**-D-E) and *Huabeisporites* (**Figures. 5-3**-F-H, **5**-A), can be assigned to the order of Bennettitales. The only difference between *Huabeisporites* and *Ricciisporites* is that the sculpture of *Huabeisporites* is weaker (Song et al., 2000). *Ricciisporites* was originally thought to be a spore and morphologically comparable with the extant liverwort spore of *Riccia* and the in situ fossil spore of *Ricciopsis* (Balme, 1995). However, based on transmission electron microscope (TEM) and SEM studies of *Ricciisporites* it is obvious that the spore is equipped with a single distal colpus and an ultrastructure of the palynomorph wall characterized by a granular inner sexine as well as an electron-dense laminated nexine (Mander et al., 2012). This demonstrates close morphological resemblance to pollen produced by the in situ bennettitean pollen of *Cycadeoidea dacotensis* (Mander et al., 2012). The sculpture of *Huabeisporites* (**Figure 5-3**-G) is also comparable with the in situ pollen of *Weltrichia setosa* reported by van Konijnenburg-van Cittert (1971). *Bharadwajipollenites* is comparable to the in situ pollen of *Haitingeria krasseri* (Balme, 1995). Furthermore, the sculpture of *Bharadwajipollenites* (**Figures. 5-2**-F, H) is comparable with the in situ pollen of *Cycadeoidea dacotensis* reported by Osborn and Taylor (1995) and Taylor (1973).

Table 5-1 Spore and pollen percentage values from the studied lignite bed of the Haojiagou Formation

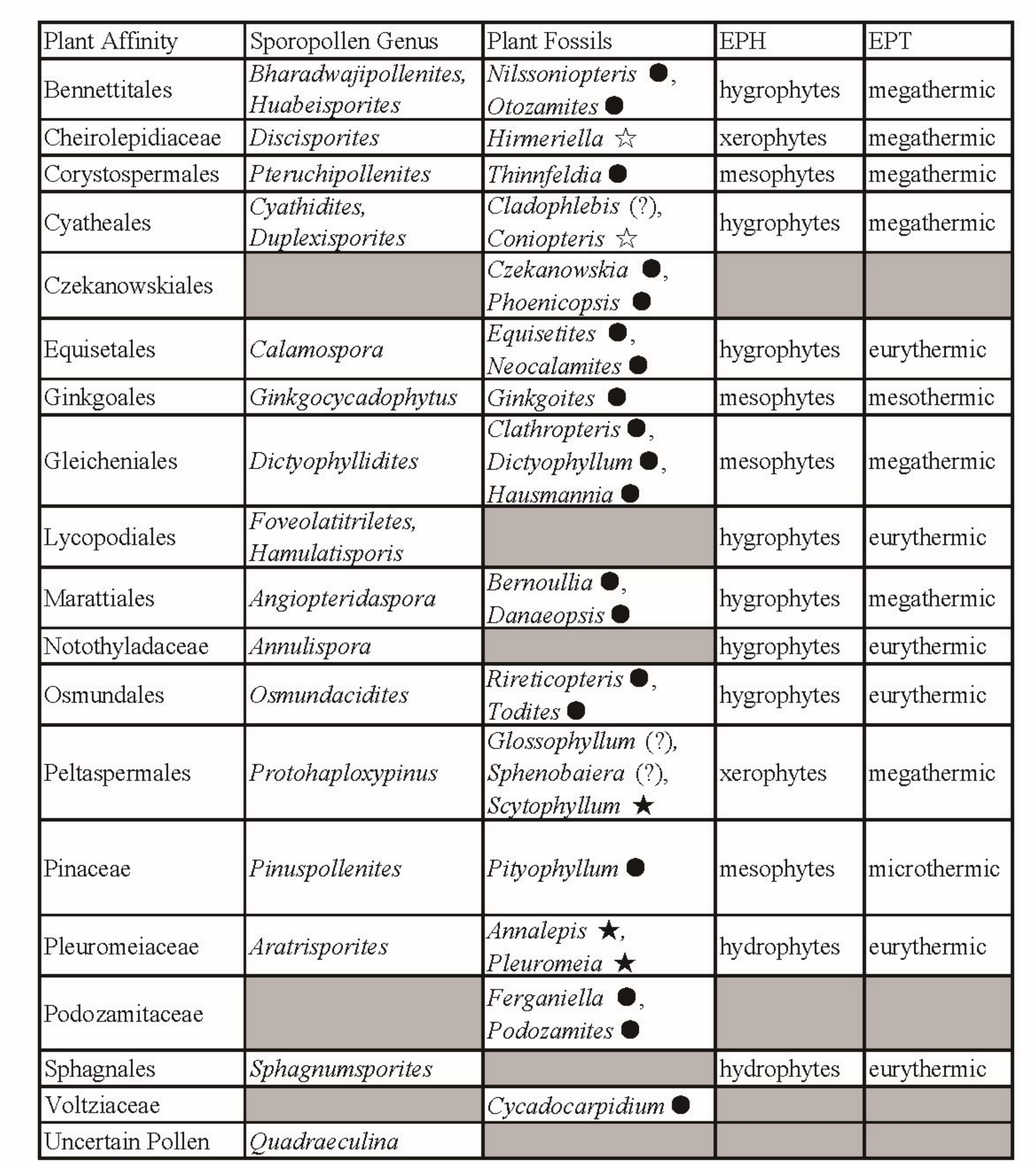


Angiopteridaspora	*Annulispora*	*Aratrisporites*	*Bharadwajipollenites*	*Calamospora*	*Cyathidites*	*Dictyophyllidites*	*Discisporites*	*Duplexisporites*	*Foveolatitriletes*	*Ginkgocycadophytus*	*Hamulatisporis*	*Huabeisporites*	*Osmundacidites*	*Pinuspollenites*	*Protohaploxypinus*	*Pteruchipollenites*	*Quadraeculina*	*Sphagnumsporites*	Sample
0	5.9	7.4	30.9	0	0.7	13.2	1.5	5.9	0	4.4	0	2.9	0.7	0	0	25	1.5	0	HJG 01
11.3	0.7	2.4	7.1	2	4	7.7	9.1	0.7	5.5	7.5	2.9	1.8	0	0.7	1.3	34	1.5	0	HJG 02
6.8	0.7	0.7	10.1	0	2	7.4	29.1	0.7	4.1	2	0.7	2	1.4	0	1.4	30.4	0	0.7	HJG 03
4.3	2.4	0	7.2	2.9	1.9	16.3	7.2	0	0.5	7.7	0.5	1.9	0	0.5	1.4	45	0.5	0	HJG 04
7.6	5.2	1	8.1	0.5	3.8	10.5	2.9	1	0	18.6	4.3	0.5	0	1.4	0	34.3	0.5	0	HJG 05
2.4	0.9	4.7	11.8	3.8	3.8	7.1	5.7	0	0	13.7	2.4	3.3	0.9	1.4	1.4	34	2.8	0	HJG 06
3.8	0	0	3.8	1.1	0	8.3	9.8	0	0	11.4	0	0.4	0	3.8	6.4	50	1.1	0	HJG 07
1.8	0	0	6	0	0	11.5	0.9	0	0	4.1	0	0.9	0	6.9	1.4	63.8	2.3	0.5	HJG 08
0	0	0.5	6.4	1.5	0.5	15.3	0	0.5	0	44.8	0	2	0	3.9	1	23.6	0	0	HJG 09
0	0	0.5	6.6	1.5	1	11.7	0	0.5	0	41.3	1.5	16.3	5.1	0	2	11.7	0	0	HJG 10
3.9	1.5	0.5	19	2	0.5	16.1	1.5	0	0	16.6	2	2	1.5	0	2.9	29.3	0.5	0.5	HJG 11
4.2	0	0.5	12.3	2.4	1.4	10.4	0	0.5	0	24.1	4.2	9.9	1.9	0.5	3.8	22.6	1.4	0	HJG 12
7.1	1	0	10.2	2	1.5	25	0	0.5	0	16.3	0	7.7	3.6	0	4.6	19.9	0.5	0	HJG 13
1	0	1	17.2	4.4	1.5	10.3	0	0	0	34.8	1.5	3.4	2	0.5	2.5	17.6	2	0.5	HJG 14
0.9	0.9	0.9	10.4	1.9	0.9	14.2	0	4.2	0	8	1.4	2.4	4.2	0	3.3	43.4	1.9	0.9	HJG 17
4.4	0	2.5	11.3	1.9	1.3	11.9	0	1.3	0	16.3	0.6	1.3	1.9	0.6	5.6	38.8	0.6	0	HJG 18
0	0	5.7	11.4	2.6	2.1	13	0.5	1	0	23.3	0.5	0.5	1.6	1	3.6	31.1	1	1	HJG 19
1	2.5	1.5	8.6	4	0.5	12.6	0	2.5	0	22.7	4	7.1	1	0.5	5.6	23.7	2	0	HJG 20
1.3	3.8	0.6	4.4	3.1	1.9	10.7	1.3	2.5	0	30.2	1.3	0.6	0	0	3.8	32.7	0.6	1.3	HJG 22
0	0	0	14.5	2.3	4.5	5.9	0	0	0	14.9	0	0	0	4.1	0.9	52.5	0.5	0	HJG 23
12.9	3.1	0	9.8	4.1	3.6	10.3	0	1.5	0	12.4	1.5	3.1	1.5	0	0	34.5	0.5	1	HJG 25
1.1	0.5	0.5	14.8	2.7	11.5	33.9	0	0	0	23.5	1.1	1.1	1.1	0	0	8.2	0	0	HJG 26
3.3	6	1.4	3.7	2.3	4.7	14.4	0.5	4.7	0	12.6	0.5	4.7	3.3	0	2.8	34	1.4	0	HJG 27
0	0.5	0	6.9	2.9	15.7	25	0.5	2	0	22.5	2	0	1	0	0.5	20.6	0	0	HJG 28
2.2	0	1.5	21.9	7.3	11.7	13.9	0	0.7	0	26.3	4.4	0.7	2.2	0	0	7.3	0	0	HJG 30
0	0	10.2	11.3	2.7	5.4	7	0.5	0.5	0	15.6	0	0	0.5	0	2.7	43.5	0	0	HJG 33
1.4	0.9	0	7.4	6	3.2	14.8	0	2.8	0	10.2	3.7	3.2	2.3	0.5	2.8	38.4	1.9	0.5	HJG 34
0	0	34.4	8	0.9	0	0.9	0	0	0	25.9	0.9	0	0	0.9	0	27.8	0	0	HJG 35
0.9	2.8	0.9	0.9	8.4	9.3	14	0	0.9	0.9	19.6	2.8	0	0.9	0	0.9	31.8	0	4.7	HJG 36
0.4	3.5	0.4	8.7	12.2	7	12.2	0	0	0.4	13.5	1.7	0.4	0.9	0	2.6	33.6	0.4	1.7	HJG 37

Note: Minimum and maximum values for each of the sporomorph taxa are marked in grey.

The Bennettitales were distributed from the Triassic to the Cretaceous in both, northern and southern hemispheres and are believed to be 1- to 3-m-tall shrubs (Pott and McLoughlin, 2014; Taylor et al., 2009). They are divided into two separate families: The Williamsoniaceae with mainly Late Triassic and Jurassic representatives and the Cycadeoidaceae (Bennettitaceae) with mainly Cretaceous representatives (Popa, 2019). *Nilssoniopteris* (Zhao et al., 2018) and *Otozamites* (Wang et al., 2008) have been found mainly in the subtropical-tropical climate zone during the Mesozoic. Leaves of the Williamsoniaceae are commonly associated with coaly facies and the parent plants may have been specialized to colonize the surfaces of mires (Pott and McLoughlin, 2014). Therefore, the Bennettitales were generally hygrophytes and megathermic plants.

Table 5-2 Spore and pollen list from the studied lignite bed of the Haojiagou Formation with related plant affinities and Eco-Plant groups that assess the effect of humidity (EPH) and the effect of temperature (EPT).



Plant Affinity	Sporopollen Genus	Plant Fossils	EPH	EPT
Bennettitales	*Bharadwajipollenites,* *Huabeisporites*	*Nilssoniopteris* ●, *Otozamites* ●	hygrophytes	megathermic
Cheirolepidiaceae	*Discisporites*	*Hirmeriella* ☆	xerophytes	megathermic
Corystospermales	*Pteruchipollenites*	*Thinnfeldia* ●	mesophytes	megathermic
Cyatheales	*Cyathidites,* *Duplexisporites*	*Cladophlebis* (?), *Coniopteris* ☆	hygrophytes	megathermic
Czekanowskiales		*Czekanowskia* ●, *Phoenicopsis* ●		
Equisetales	*Calamospora*	*Equisetites* ●, *Neocalamites* ●	hygrophytes	eurythermic
Ginkgoales	*Ginkgocycadophytus*	*Ginkgoites* ●	mesophytes	mesothermic
Gleicheniales	*Dictyophyllidites*	*Clathropteris* ●, *Dictyophyllum* ●, *Hausmannia* ●	mesophytes	megathermic
Lycopodiales	*Foveolatitriletes,* *Hamulatisporis*		hygrophytes	eurythermic
Marattiales	*Angiopteridaspora*	*Bernoullia* ●, *Danaeopsis* ●	hygrophytes	megathermic
Notothyladaceae	*Annulispora*		hygrophytes	eurythermic
Osmundales	*Osmundacidites*	*Rireticopteris* ●, *Todites* ●	hygrophytes	eurythermic
Peltaspermales	*Protohaploxypinus*	*Glossophyllum* (?), *Sphenobaiera* (?), *Scytophyllum* ★	xerophytes	megathermic
Pinaceae	*Pinuspollenites*	*Pityophyllum* ●	mesophytes	microthermic
Pleuromeiaceae	*Aratrisporites*	*Annalepis* ★, *Pleuromeia* ★	hydrophytes	eurythermic
Podozamitaceae		*Ferganiella* ●, *Podozamites* ●		
Sphagnales	*Sphagnumsporites*		hydrophytes	eurythermic
Voltziaceae		*Cycadocarpidium* ●		
Uncertain Pollen	*Quadraeculina*			

Note: ● plant fossils with confirmed affinities found in Haojiagou section of Haojiagou Formation; (?): plant fossils with problematic affinities found in Haojiagou section of Haojiagou Formation; ☆ : plant fossils with confirmed affinities found in the Early-Middle Jurassic Sangonghe Formation in Junggar Basin; ★ : plant fossils with confirmed affinities found in Middle-Late Triassic Karamay Formation in Junggar Basin; the sporomorph affinities are based on this study (see below); the plant fossils are based on literature (e.g., He et al., 2017; Lu and Deng, 2005; Shi et al., 2015; Sun et al., 2010a; Yang et al., 2006).

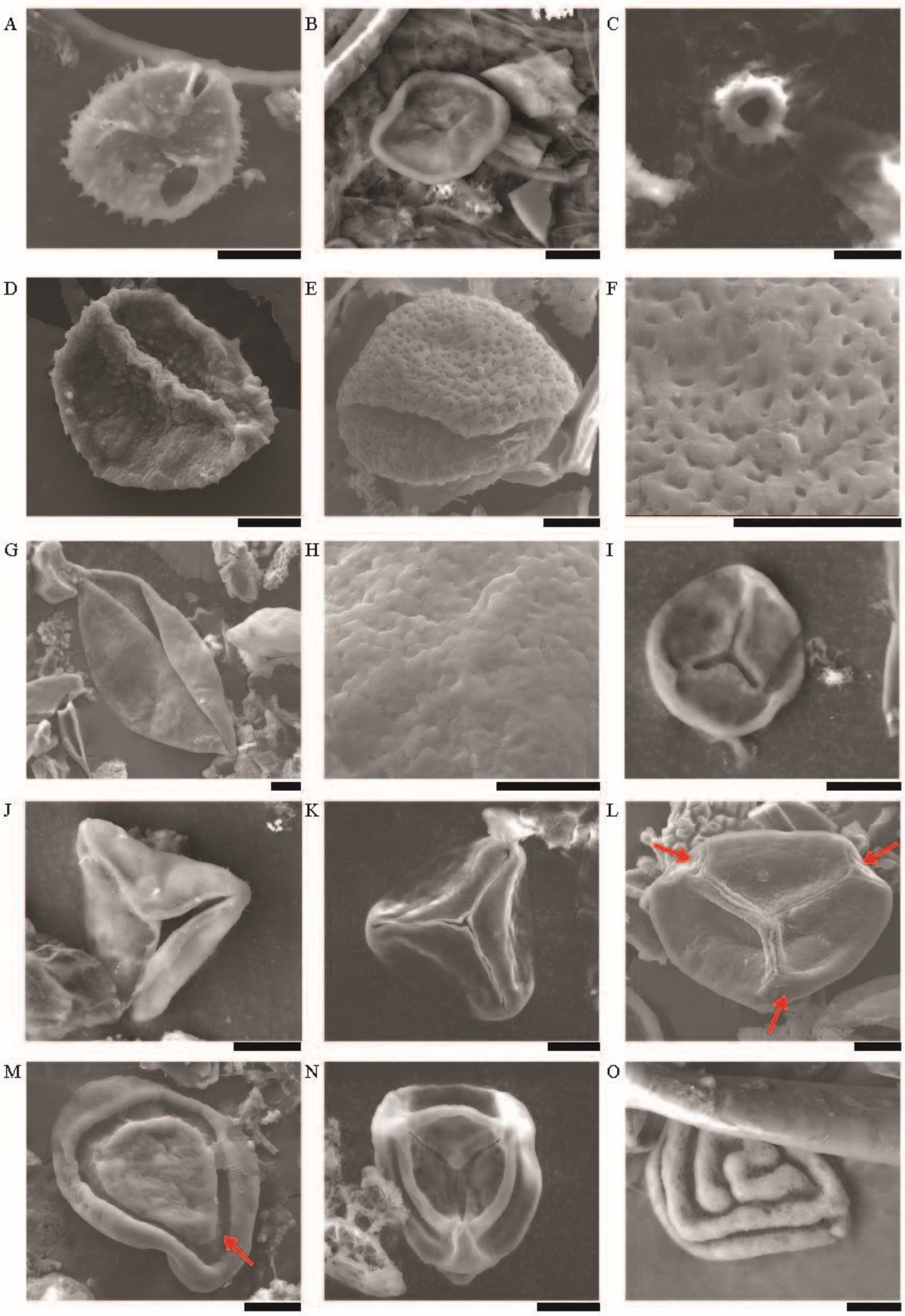


Figure 5-2 Spores and pollen grains under SEM from the studied lignite bed of the Haojiagou Formation: all of the primary images can be visited at: http://www.sporopollen.com/sporepaperpic.php?paper=p3_2020.

Note: **A.** *Angiopteridaspora denticulata* Chang, 1965; **B-C.** *Annulispora folliculosa* (Rogalska) de Jersey, 1959: **B.** proximal view, **C.** distal view; **D.** *Aratrisporites scabratus* Klaus, 1960 coated with gold; **E-H.** *Bharadwajipollenites wielandii* Jain, 1968 coated with gold: **E.** overview of pollen, **F.** detail of exine sculpture of E, **G.** overview of pollen, **H.** detail of exine sculpture of G; **I.** *Calamospora nathorstii* (Halle) Klaus, 1960; **J.** *Cyathidites minor* Couper, 1953; **K.** *Dictyophyllidites harrisii* Couper, 1958; **L-M.** *Discisporites acinosus* Zhang, 1984 coated with gold: **L.** proximal view with laesurae which are branched at the end (red arrows), **M.** distal view with narrow ring of thinner exine (red arrow); **N-O.** *Duplexisporites generalis* Deak 1962 emend. Playford et Dettmann, 1965: **N.** proximal view with crassitude on equator and kyrtome, **O.** distal view with coarse ridges; scale bar: 10μm.

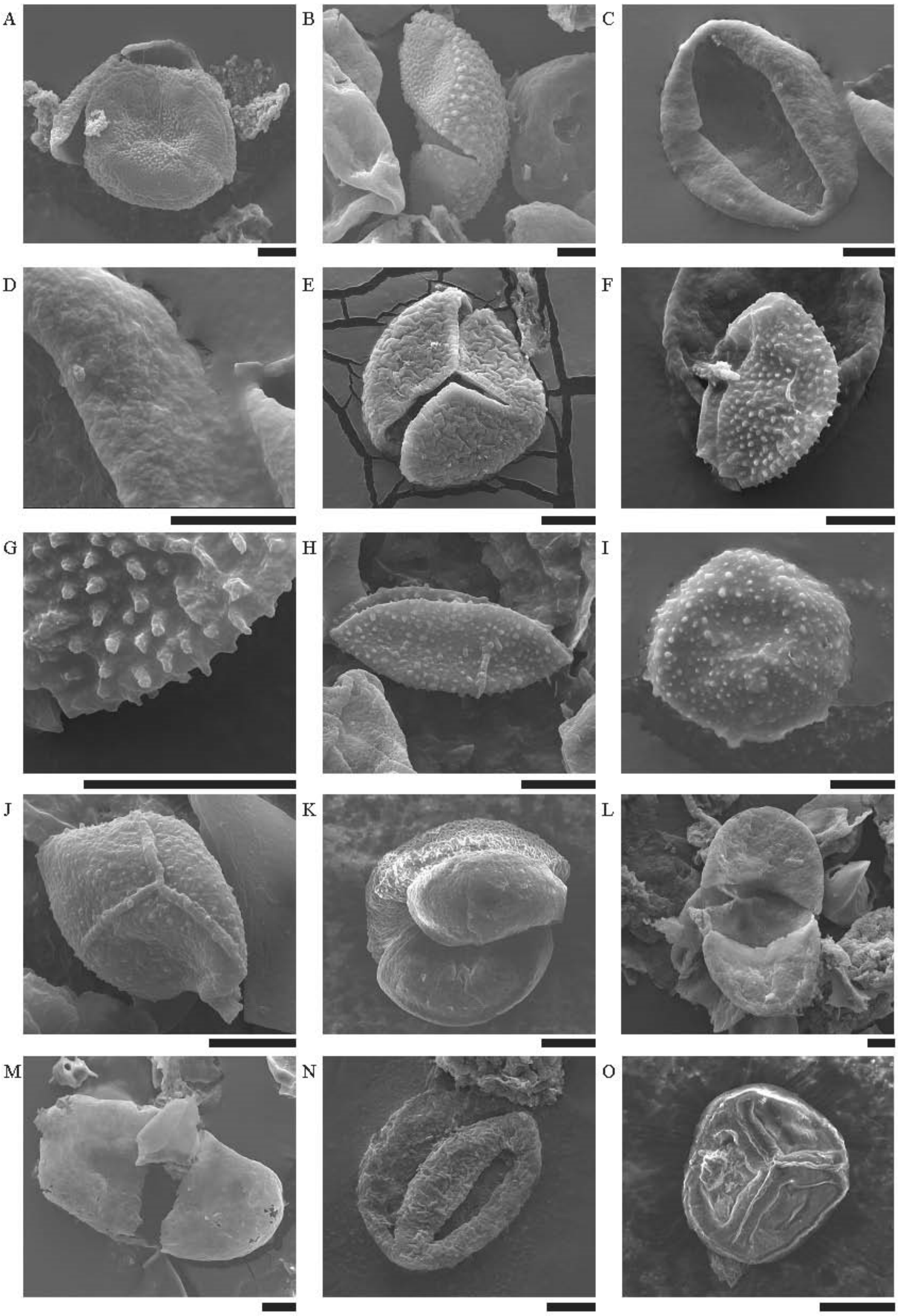


Figure 5-3 Spores and pollen grains under SEM from the studied lignite bed of the Haojiagou Formation: all of the primary images can be visited at: http://www.sporopollen.com/sporepaperpic.php?paper=p3_2020.

Note: A-B. *Foveolatitriletes potoniei* Mädler, 1964 coated with gold; **C-D.** *Ginkgocycadophytus nitidus* (Balme) De Jersey, 1962 coated with gold: **C.** overview of pollen, **D.** detail of exine sculpture of C; **E.** *Hamulatisporis hamulatis* Krutzsch, 1959 coated with gold; **F-H.** *Huabeisporites sp* coated with gold: **F, H.** overview of pollen, **G.** detail of exine sculpture of F; **I-J.** *Osmundacidites alpinus* Klaus, 1960 coated with gold; **K.** *Pinuspollenites alatipollenites* (Rouse) Liu; **L-M.** *Pteruchipollenites thomasii* Couper, 1958 coated with gold; **N.** *Quadraeculina sp.* coated with gold; **O.** *Sphagnumsporites stereoides* (Pot. et Ven) Raatz, 1937; scale bar: 10 µm.

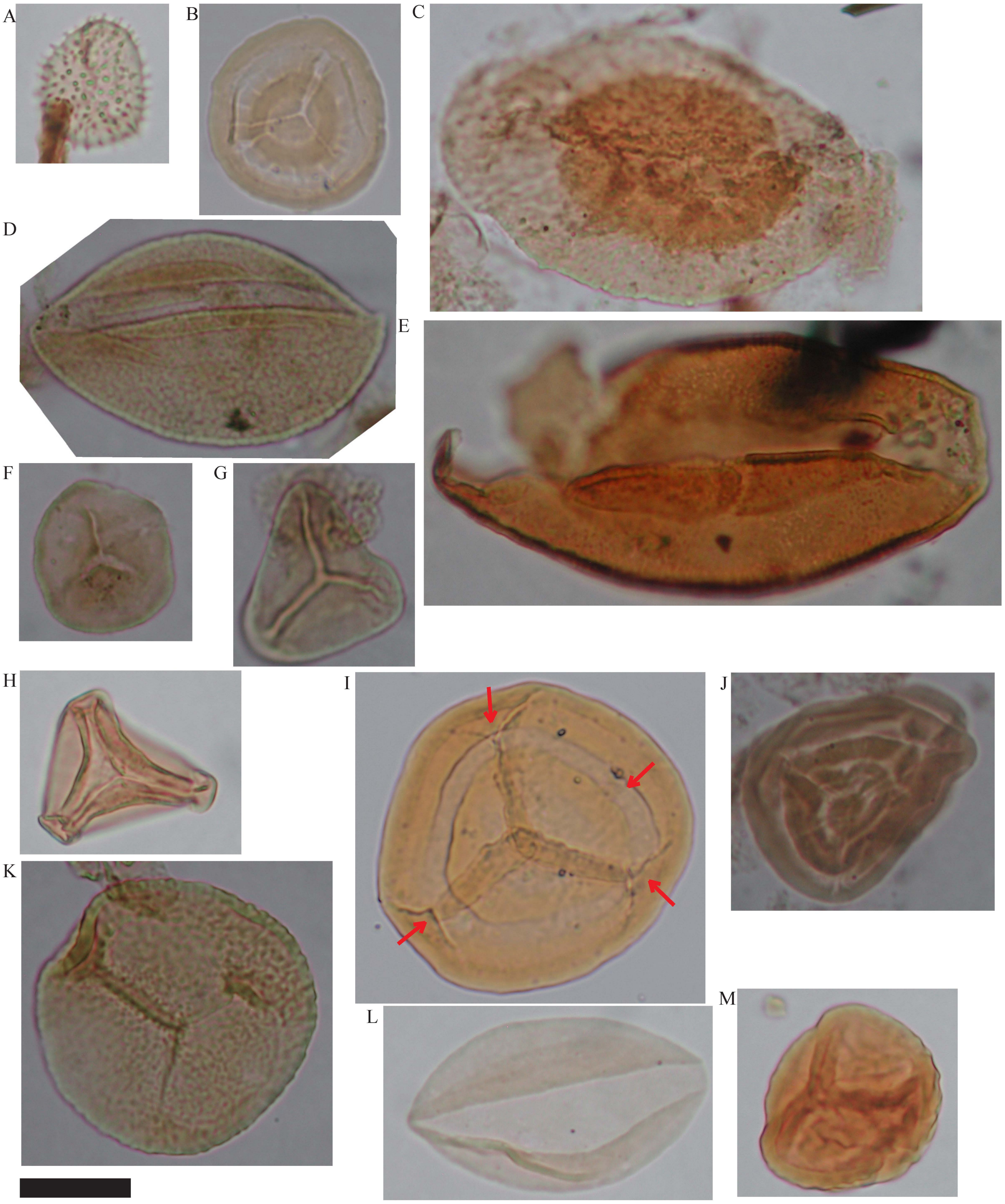


Figure 5-4 Spores and pollen grains under LM from the studied lignite bed of the Haojiagou Formation: all of the primary images can be visited at: http://www.sporopollen.com/sporepaperpic.php?paper=p3_2020.

Note: **A.** *Angiopteridaspora denticulata* Chang, 1965; **B.** *Annulispora folliculosa* (Rogalska) de Jersey, 1959; **C.** *Aratrisporites scabratus* Klaus, 1960; **D-E.** *Bharadwajipollenites wielandii* Jain, 1968: **D.** sculpture with big pit, **E.** sculpture with small pit; **F.** *Calamospora nathorstii* (Halle) Klaus, 1960; **G.** *Cyathidites minor* Couper, 1953; **H.** *Dictyophyllidites harrisii* Couper, 1958; **I.** *Discisporites acinosus* Zhang, 1984: with laesurae which are branched at the end (see red arrows) also with narrow ring of thinner exine (red arrow); **J.** *Duplexisporites generalis* Deak 1962 emend. Playford et Dettmann, 1965: proximal view with crassitude on equator, kyrtome on proximal face, and coarse ridges on distal face; **K.** *Foveolatitriletes potoniei* Mädler, 1964; **L.** *Ginkgocycadophytus nitidus* (Balme) De Jersey, 1962; **M.** *Hamulatisporis hamulatis* Krutzsch, 1959; scale bar: 20 μm.

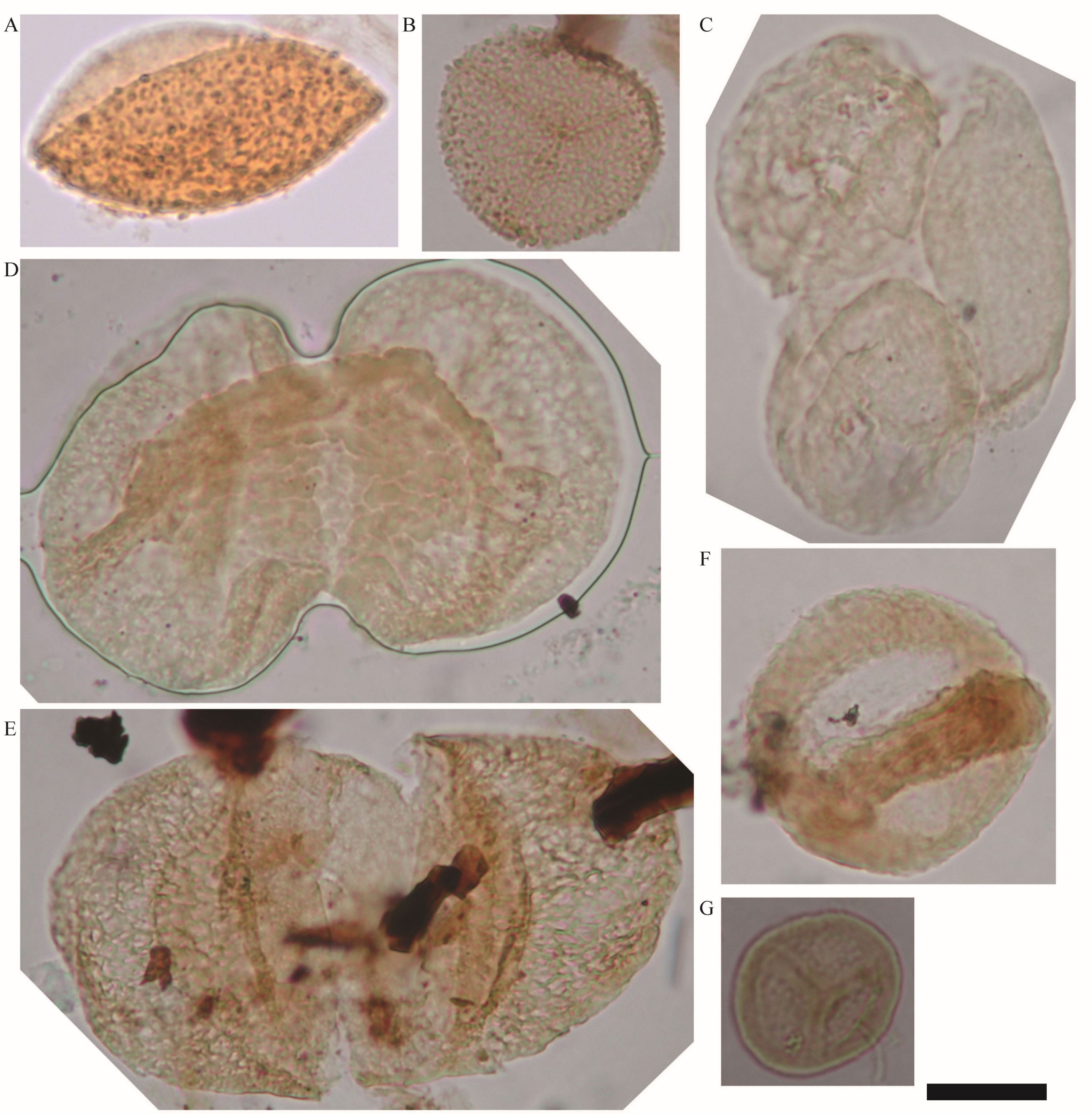


Figure 5-5 Spores and pollen grains under LM from the studied lignite bed of the Haojiagou Formation: all of the primary images can be visited at: http://www.sporopollen.com/sporepaperpic.php?paper=p3_2020.

Note: **A.** *Huabeisporites sp*; **B.** *Osmundacidites alpinus* Klaus, 1960; **C.** *Pinuspollenites alatipollenites* (Rouse) Liu; **D.** *Protohaploxypinus sp.*; **E.** *Pteruchipollenites thomasii* Couper, 1958; **F.** *Quadraeculina sp.*; **G.** *Sphagnumsporites stereoides* (Pot. et Ven) Raatz, 1937; scale bar: 20 µm.

5.4.1.2 Cheirolepidiaceae

Hirmeriella fossils have been found in the Early-Middle Jurassic Sangonghe Formation in this region (Yang et al., 2006). One pollen genus, *Discisporites* (**Figures. 5-2**-L-M, **4**-I), that has been recognized in the palynomorph assemblage can be assigned to the family of Cheirolepidiaceae. *Discisporites* is thought to be comparable with *Classopollis* (Alvin, 1982) and *Circulina* (Norris, 1965). *Classopollis* has been previously reported for the Haojiagou Formation (Huang, 2006).

It is possible that the conifers of the Cheirolepidiaceae are derivative of the *Discisporites* producing plants (Alvin, 1982). Without SEM data, *Discisporites* has also been described as *Limatulasporites* (e.g., Huang, 2006; Lu and Deng, 2009). However, the distal face of *Discisporites* has a narrow ring of a thinner exine which is called operculum (**Figure 5-2**-M), while *Limatulasporites* has a crassitude on the distal face and an equatorial flange called cingulum (Song et al., 2000). Although the difference is remarkable, under LM, it is difficult to distinguish. The operculum (**Figure 5-2**-M), which has never been found on spores, is the most remarkable character for the pollen of Cheirolepidiaceae. However, the Y-mark on a pollen grain is rare. Nevertheless, three cones have been found attached to *Tomaxellia biforme* branches, which yielded *Classopollis* pollen showing proximal folds reproducing a Y-mark (Archangelsky and Gamerro, 1967). The in situ pollen is also comparable to *Discisporites*.

The Cheirolepidiaceae are a large family of Mesozoic conifers, plants of which were large trees, woody shrubs, and possibly herbs (Steart et al., 2014). Evidence from sediments and cuticle morphology, most notably the sunken papillate stomata, indicate that the plants were adapted to xeric habitats and grew in brackish coastal mires as well as on the margins of freshwater rivers and lakes (Alvin, 1982; Steart et al., 2014). Generally, they are drought resistant, thermophilous shrubs and trees with a preference for subtropical to tropical climates, and were never dominant in cool regions (Francis, 1983; Vakhrameev, 1991). They were also adapted to semi-arid and arid low-lying water-margin environments that produce mud flats (Taylor et al., 2009; Vakhrameev, 1991). Therefore, they can be described as xerophytes and megathermic plants.

5.4.1.3 Corystospermales

The fossils of *Thinnfeldia* are known from the Haojiagou Formation (Sun et al., 2010a). One pollen genus, *Pteruchipollenites* (**Figures 5-3**-L-M, **5**-E), that have been found in the palynomorph assemblage can be assigned to the order of Corystospermales. *Pteruchipollenites* is comparable with the in situ pollen of *Pteruchus* (Osborn and Taylor, 1993; Taylor et al., 1984).

The plants of Corystospermales were probably small to large woody shrubs and trees that originated in the late Paleozoic and spread worldwide in the Mesozoic during the climate warming of Late Permian/Early Triassic (Taylor et al., 2006; Taylor et al., 2009). *Dicroidium* apparently originated in the palaeotropics during the late Palaeozoic and subsequently migrated southwards, eventually colonizing the entire extra-tropical region of Gondwana during the Middle and Late Triassic (Kerp et al., 2006). This geographic expansion was accompanied by a remarkable diversification, enhanced by adaptations to different environmental conditions (Bomfleur and Kerp, 2010). The earliest representatives of *Dicroidium* flourished in the palaeotropics under a hot, humid climate with high annual rainfall and short dry seasons (Abu Hamad et al., 2008; Uhl et al., 2007). The stem anatomy of *Cuneumxylon* from Argentina indicates that the plants were well adapted to tolerate prolonged periods of water stress in seasons of drought (Artabe and Brea, 2003). The environment of fossil *Cuneumxylon* correlate with that of an extant subtropical seasonal forest (dry monsoonal forests) (Brea et al., 2008). Although the leaf fossil of *Pachypteris papillosa* from Yorkshire is thought to be a large mangrove shrub forming a thicket beside the river, it should also be noted that the leaf of *Pachypteris lanceolata* from Yorkshire shows no link with marine horizons (Harris, 1983). Therefore, the Corystospermales were mesophytes and megathermic plants.

5.4.1.4 Cyatheales

Cladophlebis fossils have been found in the Haojiagou Formation and *Coniopteris* in the Lower Jurassic Sangonghe Formation (Sun et al., 2010a). Two spore genera, *Duplexisporites* (**Figures 5-2**-N-O, **4**-J) and *Cyathidites* (**Figures 5-2**-J, **4**-G), that have been identified in the palynomorph assemblage can be assigned to the order of Cyatheales. *Duplexisporites* is comparable with the extant spore of *Cibotium* (Potonié, 1967; Srivastava, 1987), whereas *Cyathidites* is probably the in situ spore of *Alsophilites* (Shuklina and Polevova, 2007) as well as the extant spore of *Dicksonia* (Dettmann, 1963).

The foliage of *Cladophlebis* may point either to the Gleicheniales (Yang et al., 1997), Cyatheales (Nagalingum and Cantrill, 2015), or Osmundales (Taylor et al., 2009), but currently spores that are comparable to *Duplexisporites* and *Cyathidites* have never been found as an in situ or extant spore of Gleicheniales or

Osmundales. Therefore, it can be inferred that at least some of the *Cladophlebis* fossils found in the Haojiagou Formation are related to the Cyatheales.

Cyatheales originated as early as the Jurassic (Taylor et al., 2009). Extant species of Cyatheales are tree ferns concentrated in the tropics where they are most numerous in the montane to alpine vegetation. Many species occur in the undergrowth of moist forests, often in ravines. Others prefer more open habitats, even swamps, and some grow preferentially in cleared areas (Kramer and Green, 1990). Therefore, Cyatheales can generally be identified as hygrophytes and megathermic plants.

5.4.1.5 Equisetales

Fossils of *Equisetites* and *Neocalamites* have been found in the Haojiagou Formation (Sun et al., 2010a). One spore genus *Calamospora* (**Figures 5-2**-I, **4**-F) that has been recognized in the palynomorph assemblage can be assigned to the order of Equisetales. *Calamospora* is comparable with the in situ spore of *Equisetites* (Kelber and van Konijnenburg-van Cittert, 1998).

Extant Equisetales consist of a single genus *Equisetum* (Smith et al., 2006), which is a herbaceous perennial plant. The Mesozoic plants of Equisetales are more or less comparable with extant *Equisetum* (Taylor et al., 2009). The mode of fossil *Neocalamites tubulatus* preservation serves to prove the idea that the parent plant, resembling recent *Equisetum* communities, had grown along a lake shore inhabited by a near-water hygrophilous plant community of helophytes (Naugolnykh, 2009). Extensive fossil *Equisetites arenaceus* populations occurred in marginal strips along an anastomosing river system. Dense *Equisetites arenaceus* reeds also invaded the levee belt as well as hygromorphic environments surrounding standing waterbodies in a flood plain (Kelber and van Konijnenburg-van Cittert, 1998). *Equisetum* has been reported from numerous localities worldwide, where they are primarily plants of open, sunny sand banks along river and lake margins, in marshes, and in other wet places (Taylor et al., 2009). Although the greatest concentrations of extant species are found between 40° and 60° northern latitude, *Equisetum* is found around the world from the southern parts of South America and Africa to above the Arctic Circle (Kramer and Green, 1990). Therefore, they are generally hygrophytes and eurythermic plants.

5.4.1.6 Ginkgoales

Ginkgoites fossils have been reported for the Haojiagou Formation (Sun et al., 2010a). One pollen genus *Ginkgocycadophytus* (**Figures. 5-3**-C-D, **4**-L) that has been found in the palynomorph assemblage can be assigned to the order of Ginkgoales. *Ginkgocycadophytus* is comparable with the in situ pollen of ginkgoalean *Allicospermum* (Zavialova et al., 2014).

Ginkgo biloba, the only extant species of the Ginkgoales, is a kind of deciduous tree that can be 30 m in height and 9 m in trunk circumference (Kramer and Green, 1990). Mesozoic ginkgoalean plant fossils are found widely in fossil records, except at the Equator and in Antarctica. After the Cretaceous, ginkgoalean plants began to decline rapidly, their abundance was reduced, and their distribution narrowed to only temperate forests (Wang et al., 2017). In spite of their broad adaptability, however, it appears that ginkgoaleans on the whole were more abundant and diverse in mesic, warm temperate to temperate climates similar to those in the relictual area of their living representative *Ginkgo biloba* (Zhou, 2009). Therefore, they are mesophytes and mesothermic plants.

5.4.1.7 Gleicheniales

Fossils of *Dictyophyllum, Clathropteris,* and *Hausmannia* have been found in the Haojiagou Formation (Lu and Deng, 2005; Sun et al., 2010a). The spore genus *Dictyophyllidites* (**Figures. 5-2**-K, **4**-H) that has been identified in the palynomorph assemblage can be assigned to the order of Gleicheniales. *Dictyophyllidites* is comparable with the in situ spores of *Dictyophyllum* (Dettmann, 1963) and *Phlebopteris* (Cranwell and Srivastava, 2009). *Dictyophyllidites* is also comparable with the extant spores of *Cheiropleuria bicuspis* reported by Wang and Dai (2010) and *Cheiropleuria bicuspus* reported by Tryon and Lugardon (1991).

Gleicheniales can be traced back to the Carboniferous (Taylor et al., 2009). Extant Gleicheniales are terrestrial ferns of rather small to very large sizes (Smith et al., 2006). All of them are heliophilous terrestrial ferns in tropical to subtropical regions and most species occur in open, often strongly disturbed and/or pioneer habitats on damp soils (Kramer and Green, 1990; Qian and Chen, 2006). Some plants, such as *Gleichenites*, *Piazopteris*, and *Weichselia* were adapted to semiarid or arid climates during the Mesozoic (van Konijnenburg-van Cittert, 2002). Of course, this does not imply that all plants of Gleicheniales showed the same ecological adaptations. Therefore, they are generally mesophytes and megathermic plants.

5.4.1.8 Lycopodiales

Two spore genera *Foveolatitriletes* (**Figures 5-3**-A-B, **4**-K) and *Hamulatisporis* (**Figures. 5-3**-E, **4**-M) that have been found in the palynomorph assemblage can be assigned to the order of Lycopodiales. *Foveolatitriletes* is comparable with the extant spore of *Phylloglossum drummondii* reported by Tryon and Lugardon (1991). The remarkable character of *Foveolatitriletes* is that the sculpture on its proximal face is much weaker than on its distal face, which is also the common character of extant spores of Lycopodiales. *Hamulatisporis* is comparable to the extant spore of *Lycopodium* (Traverse and Ames, 1979). Based on our study, the spore of *Hamulatisporis* (**Figure 5-3**-E) is more comparable to the extant spore of *Palhinhaea cernua* reported by Giacosa et al. (2016).

The Lycopodiales includes homosporous, eligulate, usually dichotomously branched herbaceous plants, whose fossils of *Lycopodium* have been described from records ranging from Devonian to Pleistocene (Taylor et al., 2009). Extant species of Lycopodiales are almost cosmopolitan, being absent only from arid areas. The greatest species concentration is in humid, tropical, montane forests and in humid, tropical, alpine vegetation (Kramer and Green, 1990). Therefore, they are generally hygrophytes and eurythermic plants.

5.4.1.9 Marattiales

The fossils of *Bernoullia* and *Danaeopsis* have been discovered in the Haojiagou Formation (Sun et al., 2010a). One spore genus *Angiopteridaspora* (**Figures 5-2**-A, **4**-A) that has been found in the palynomorph assemblage can be assigned to the order of Marattiales. *Angiopteridaspora* is comparable to the extant spore of *Angiopteris* (Kremp et al., 1967). Based on our study, *Angiopteridaspora* (**Figure 5-2**-A) is also comparable with the extant spore of *Protomarattia tonkinensis* reported by Tryon and Lugardon (1991).

Extant Marattiales are terrestrial ferns distributed exclusively in tropical and subtropical regions under primary and secondary wet forests or along the bank of streams (Kramer and Green, 1990). The plants of Mesozoic Marattiales have always lived under rather warm, moist circumstances often probably as understory in forests (van Konijnenburg-van Cittert, 2002). Therefore, they are generally hygrophytes and megathermic plants.

5.4.1.10 Notothyladaceae

One spore genus *Annulispora* (**Figures 5-2**-B, C, **4**-B) that has been found in the palynomorph assemblage can be assigned to the family of Notothyladaceae. This type of microspore is trilete with a considerably thick exine, usually thicker in the distal than in the proximal face. On distal face, there is a characteristic projection which is a hollow circle. *Annulispora* (**Figures 5-2**-B, C) is comparable with the extant spore of *Phaeoceros skottsbergii* reported by Warny et al. (2012). The extant spore of *Notothylas levieri* reported by Chantanaorrapint (2015) is also comparable with *Annulispora,* but on its distal face there is a solid circular projection rather than a hollow circular projection.

Extant Notothyladaceae are a kind of hornwort including *Mesoceros, Notothylas, Paraphymatoceros,* and *Phaeoceros* (Söderström et al., 2016). They can be found in moist soil from warm tropical regions to cold circumboreal regions (Boros and Járai-Komlódi, 1975; Zhang et al., 2006). They are hygrophytes and eurythermic plants.

5.4.1.11 Osmundales

The fossils of *Rireticopteris* and *Todites* have been found in the Haojiagou Formation (Sun et al., 2010a). One spore genus *Osmundacidites* (**Figures 5-3**-I-J, **5**-B) that has been recognized in the palynomorph assemblage can be assigned to the order of Osmundales. *Osmundacidites* is comparable to the extant spore of *Osmunda* or the in situ spore of *Todites* (Dettmann, 1963).

Extant species of Osmundales are terrestrial ferns distributed throughout most temperate and tropical regions in sites with either high edaphic or high atmospheric moisture (or both) (Kramer and Green, 1990; Tryon and Lugardon, 1991). During the Mesozoic, the Osmundales were probably ferns that grew under warm, humid circumstances, either along riverbanks, or in freshwater marshes where they often formed peat resulting in coal (van Konijnenburg-van Cittert, 2002). However, extant species of Osmundales, such as *Osmunda claytoniana,* can also be distributed in the cooler montane regions of the Himalaya and Far East of Russia (Ching and Shing, 1990; Qian and Chen, 2006). Therefore, they are generally hygrophytes and eurythermic plants.

5.4.1.12 Peltaspermales

The fossils of *Glossophyllum* and *Sphenobaiera* have been discovered in the Haojiagou Formation (Sun et al., 2010a), and *Scytophyllum* have been found in the Upper Triassic Karamay Formation from the Junggar Basin (He et al., 2017). One pollen genus *Protohaploxypinus* (**Figure 5-5**-D) that has been identified in the palynomorph assemblage can be assigned to the order of Peltaspermales. It is comparable with the in situ pollen of *Permotheca* (Zavialova and Karasev, 2015) and *Nidpuria* (Balme, 1995). *Glossophyllum* and *Sphenobaiera* are probably plants of the Peltaspermales (Meyen, 1984). However, other authors indicate that they may belong to other plant orders such as the Ginkgoales (Taylor et al., 2009; Zhou, 2009). Nevertheless, the bisaccate pollen of *Protohaploxypinus* is not comparable with any monosulcate pollen of the Ginkgoales. Therefore, at least *Protohaploxypinus* is related with Peltaspermales.

The seed ferns of Peltaspermales are believed to originate from tropical areas during the Late Pennsylvanian and disappeared in the Mesozoic with fossils distributed globally (Taylor et al., 2009; Wan et al., 2016). They might have been shrub-like plants (He et al., 2017). Epidermal features of *Glenopteris splenden*s are consistent with those extant plants adapted to (seasonal) moisture limitation and elevated soil and ground water salinity (Krings et al., 2005). Furthermore, epidermal features indicate that *Peltaspermum martinsii* has been grown in drier or saline influenced biotopes (Poort and Kerp, 1990) and that *Peltaspermum retensorium* has lived in a relatively dry habitat (Naugolnykh and Kerp, 1996). Also plants from the Sobernheim *Autunia conferta* population have been grown in a mineral soil under relatively dry conditions (elevated sandy lake margins, sand and river banks) (Kerp, 1988). Although the sedimentary analysis indicates that the climate was more humid with dry seasons, the thick cuticle, sunken stomata and the papillae surrounding the stomatal aperture indicate that *Scytophyllum karamayense* may have suffered from water stress, with the cuticle being adapted to reducing water loss (He et al., 2017). Generally, the Peltaspermales are therefore xerophytes and megathermic plants.

5.4.1.13 Pinaceae

The fossils of *Pityophyllum* have been found in the Haojiagou Formation (Sun et al., 2010a). One pollen genus *Pinuspollenites* (**Figure 5-3**-K, **5**-C) that has been proven in the palynomorph assemblage can be assigned to the family of Pinaceae. *Pinuspollenites* is comparable with extant pollen of *Pinus* (Song et al., 2000).

The Pinaceae, originated at least from Late Triassic, today are principally a Northern Hemisphere, temperate family and are the largest modern conifer family including shrubs and trees, some up to 100 m tall (Taylor et al., 2009). Most extant species are trees of generally poor, acidic and either wet or rocky habitats, sometimes forming mixed evergreen or evergreen broad-leaved forests, but more often forming extensive monotypic stands over large, north-temperate areas. There are particular concentrations of species in both, North America and in the east of Asia, with a considerable number of endemic species with more restricted range in the Sino-Himalayan region. The limited number of species which spread southward in Central America or in SE Asia, are essentially montane (Kramer and Green, 1990). They are generally mesophytes and microthermic plants.

5.4.1.14 Pleuromeiaceae

Fossils of *Annalepis* and *Pleuromeia* have been found in the Middle-Late Triassic Karamay Formation in the region of Northwestern China (Shi et al., 2015). One spore genus *Aratrisporites* (**Figures 5-2**-D, **4**-C) that has been recognized in the palynomorph assemblage can be assigned to the family of Pleuromeiaceae. *Aratrisporites* is comparable with the in situ spore of *Annalepis* (Grauvogel-Stamm and Duringer, 1983).

Species of Pleuromeiaceae, an exclusively Triassic family, are mostly herbaceous plants (Taylor et al., 2009) that lived in extensive mono-dominant thickets perhaps partly submerged in the bays and lakes of delta systems debouching into coastal lakes, lagoons, or even partly in the water bodies of desert oases (Retallack, 1975; Wang and Wang, 1982). They are widely distributed from low to high palaeolatitudes and are therefore not sensible to temperature variations (Vakhrameev, 1991). Therefore, they are generally hydrophytes and eurythermic plants.

5.4.1.15 Sphagnales

One spore genus *Sphagnumsporites* (**Figures 5-3**-O, **5**-G) that has been found in the palynomorph assemblage can be assigned to the order of Sphagnales. *Sphagnumsporites* is identical with the extant spore of *Sphagnum* (Potonié, 1956). *Sphagnumsporites* from the Haojiagou Formation (**Figure 5-3**-O) is more comparable with the extant spore of *Sphagnum cuspidatum* reported by Zhang et al. (2006).

The extant Sphagnaceae are a monogeneric family of peat moss based on the extant genus *Sphagnum* (Goffinet and Buck, 2004). Species are nearly cosmopolitan, most of them are found in circumboreal regions in bogs, wetlands, or swamp forests (Boros et al., 1993; Gao, 1994). They are generally hydrophytes and eurythermic plants.

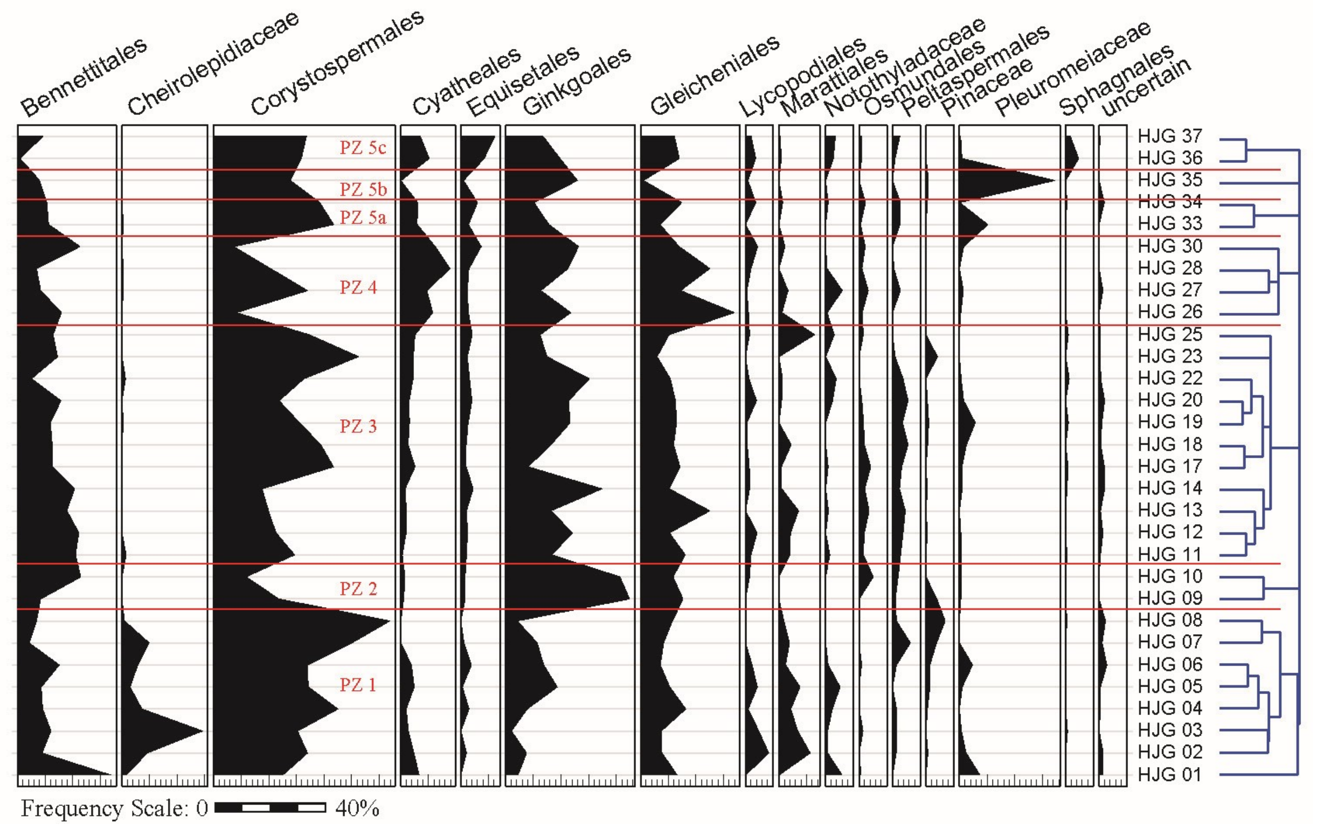


Figure 5-6 Pollen diagram of the studied 10 m thick lignite seam of the Haojiagou Formation (see **Figure 5-1**) showing the abundance of 15 plant orders or families. The zonation is based on constrained cluster analysis using the unweighted pair-group average (UPGMA) method and a Euclidean distance.

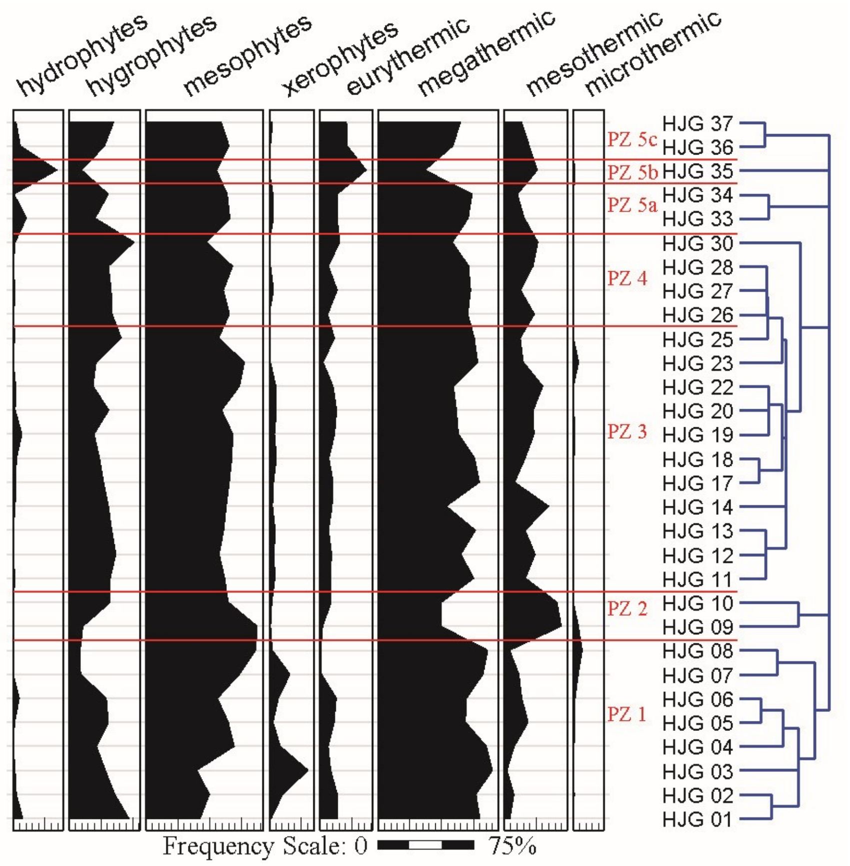


Figure 5-7 Pollen diagram of the studied 10 m thick lignite seam of the Haojiagou Formation (see **Figure 5-1**) showing the abundance of 5 Eco-Plant groups that assess the effect of humidity and the effect of temperature. The zonation is based on constrained cluster analysis of the abundance of 15 plant orders or families presented in **Figure 5-6**.

5.4.2 Quantitative analysis

The abundance diagrams of plant orders/families (**Figure 5-6**) and Eco-Plant (**Figure 5-7**) show that several taxa vary significantly in frequency throughout the studied section. Based on constrained cluster analysis five palynozones (PZ) can be recognized. They are characterized by distinct palynomorph assemblages.

5.4.2.1 Palynozone PZ 1

The 8 samples HJG_01 to HJG_08 can be assigned to PZ 1. The zone is generally characterized by the high abundances of pollen for the Corystospermales with an average value of 39.6% (**Figure 5-6**). It shows an increase in abundance from the base to the top of the zone. While at the base a value of 25% is reached, the values increase up to 63.8% in sample HJG_08. Other common elements in PZ 1 are the pollen of the Bennettitales (12.3% on average) and Ginkgoales (8.7% on average) as well as the spores of the Gleicheniales (10.3% on average). Only the Bennettitales achieve their maximum in the entire succession with 33.8% in HJG_01.

Less frequently and with decreasing values from the base to the top of the PZ other spores such as those of Cyatheales and Marattiales begin to appear. The Marattiales in sample HJG_02 reach 11.3% and thus the second highest value in the whole succession; whereas, in sample HJG_08 they occur with only 1.8%. The spores of the Cyatheales, in HJG_01 with a value of 6.6%, disappear completely at the top of the PZ.

However, the most striking feature of PZ 1 is the appearance of pollen of the Cheirolepidiaceae, which are represented at the base of the PZ with only 1.5%. Subsequently, the values increase up to 29.1%, but decrease to 0.9% towards the top of the PZ. Nonetheless, the pollen of these conifers is almost exclusively restricted to PZ 1 and appear in the succeeding PZs only with single pollen grains in the palynomorph assemblages. In the PCA of plant orders/families (**Figure 5-8**), PZ 1 is due to the occurrence of the Cheirolepidiaceae, clearly separated from the other PZs. The samples plot in the upper left corner of the ordination space with a small overlap with PZ 3.

Due to the high abundances of plants such as the Cheirolepidiaceae and Corystospermales among the EPT the megathermic plants and among the EPH the mesophytes and xerophytes are the prevailing Eco-Plant groups. Between 68.7% and 89.9% of the palynomorphs belong to megathermic plants with an average abundance of 79.9%, while between 39.8% and 86.3% are mesophytes with an average abundance of 60.3%. The xerophytes reach their maximum within the succession in PZ 1. Due to the high values of megathermic plants and xerophytes, the samples of PZ 1 are also separated from most other samples in the PCA of the Eco-Plant and plot at the negative side of PCA axis 2 (**Figure 5-9**).

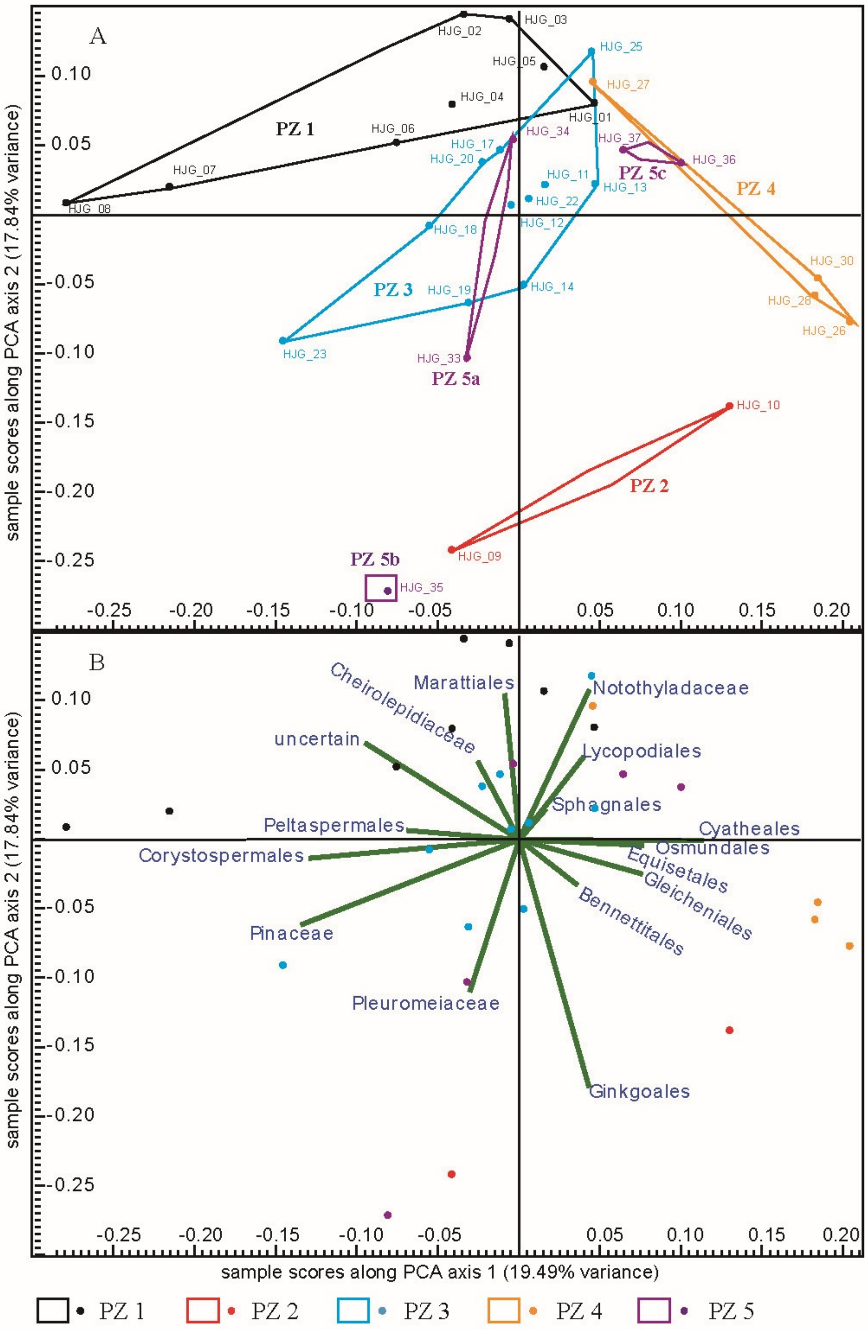


Figure 5-8 Principal Component Analysis of the plant order/family data set showing the biplot of the first two axes.

Note: **A.** Scatter plot of the first two axes (19.49/17.84% variance) showing the arrangement of samples. The different colors represent samples from different palynozones; **B.** Scatter plot of the first two PCA axes showing the arrangement of taxa. The dots show the arrangement of samples (see view **Figure 5-8**-A).

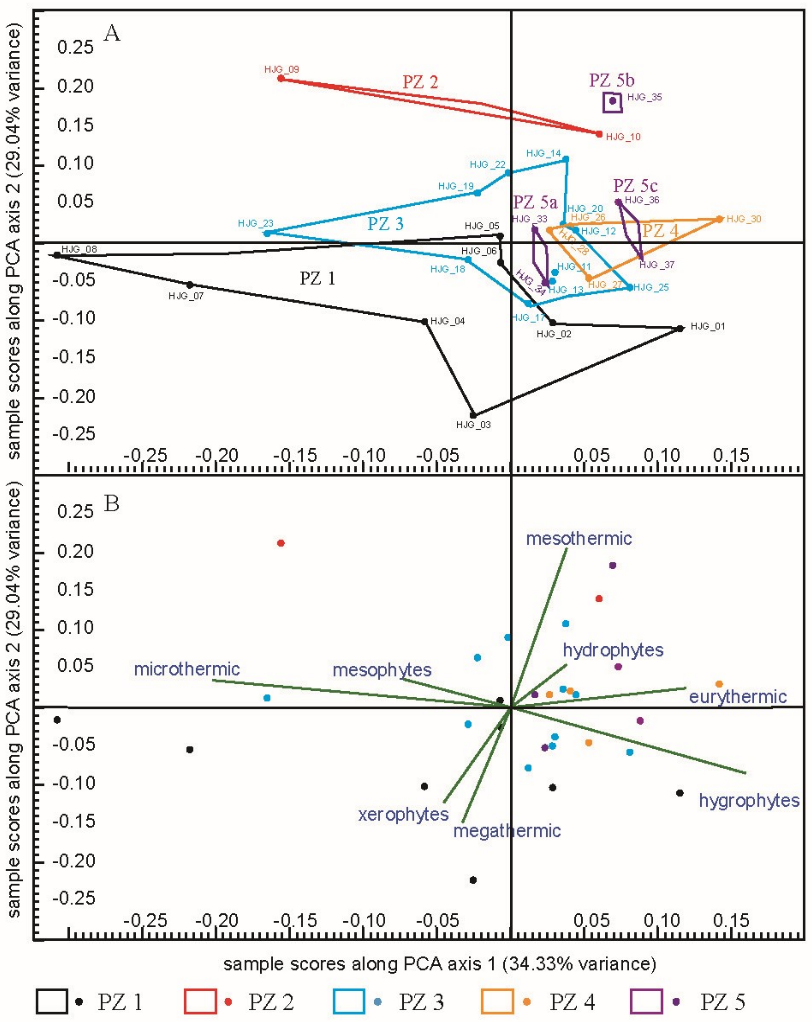


Figure 5-9 Principal Component Analysis of the Eco Plant data set showing the biplot of the first two axes.

Note: **A.** Scatter plot of the first two axes (34.33/29.04% variance) showing the arrangement of samples. The different colors represent samples from different palynozones; **B.** Scatter plot of the first two PCA axes showing the arrangement of Eco Plant groups. The dots show the arrangement of samples (see view **Figure 5-9**-A).

5.4.2.2 Palynozone PZ 2

This zone is composed of only two samples (HJG_09, HJG_10), which, have a significantly different composition of the palynomorph assemblages compared to all other PZs (**Figure 5-6**). Therefore, the two samples are clearly separated from all other samples in the PCA of the plant orders/families and plot in the lower right corner of the ordination space (**Figure 5-8**). The separation is due to a significant increase in pollen from the Ginkgoales and Bennettitales. The Ginkgoales reach their maximum in the entire succession with values of more than 41% in the two samples. Compared to PZ 1, the increase of pollen of the Bennettitales up to 22.9% is significant. Accordingly, beside the mass occurrence in the basal sample, the second highest value for the entire succession is reached.

In contrast, the strong decrease of pollen of the Corystospermales from 63.8% in PZ 1 to 11.7% in PZ 2 is distinctive. The pollen of the Cheirolepidiaceae, which are common elements in PZ 1, completely disappears in PZ 2. All other taxa remain nearly unchanged in their abundance compared to PZ 1.

With the strong increase of the Ginkgoales, there is a strong abundance change in the dominance of the Eco-Plant (**Figure 5-7**). After the occurrence of xerophytes in PZ 1, mesophytes become increasingly dominant among the EPH with an average abundance of 76.2%. Also among the EPT, there is a clear change represented by the significant increase of mesothermic plants with an average abundance of 43.1%. At the same time the proportion of megathermic plants decreases significantly from 86.3% at the top of PZ 1 to 49.3% in PZ 2 with an average abundance of 49.6%. The PCA of the Eco-Plant illustrates this strong change, since PZ 2 is plotted at the positive end of PCA axis 2 and thus opposite to the samples of PZ 1, which are on the negative end of the axis (**Figure 5-9**).

5.4.2.3 Palynozone PZ 3

A total of 11 samples from the central part of the studied succession are included in PZ 3 (HJG_11 to HJG_25). In the PCA of the plant orders/families, the samples are plotted at the centre of the ordination space separated from most of the samples of the other PZ (**Figure 5-8**). PZ 3 is again characterized by the high abundances of pollen from the Corystospermales, which appear with strong frequency fluctuations. Nevertheless, a superimposed gradual increase up to 52.5% to the top of PZ 3 is recognizable. In addition to the Corystospermales, the pollen of the Ginkgoales is also widespread. However, by reaching only a maximum of 34.8%, the abundance is decreased compared to PZ 2. The pollen of the Bennettitales as well as the spores of the Gleicheniales are represented with consistently high values of more than 10% in PZ 3.

After the decline at the top of PZ 1 and the almost complete absence in PZ 2, the spores of tree ferns of the Cyatheales and also the spores of the Marattiales increase again. The values for the Cyatheales increase continuously to the top of PZ 3 to more than 5%, while the Marattiales show up with 12.9% which is their maximum for the entire succession.

Among the Eco-Plant, the mesophytes with an average abundance of 64.8% dominated the EPH due to the common abundance of Corystospermales and Ginkgoales. In almost all samples values of more than 57% are reached which is intermediate between PZ 1 and PZ 2. Among the EPT the megathermic plants are prevailing and reach between 53.5% and 79.7% with an average abundance of 69.4%. In addition to a clear separation of PZ 2 and PZ 3, the PCA of the Eco-Plant also shows a separation to the samples of PZ 1, but with a small overlapping area (**Figure 5-9**).

5.4.2.4 Palynozone PZ 4

The 4 samples HJG_26 to HJG_30 can be assigned to PZ 4. In the PCA of plant orders/families the samples are plotted at the positive side of PCA axis 1 and are thus clearly separated from the other samples (**Figure 5-8**). PZ 4 is characterized in particular by the strong propagation of fern spores of the Cyatheales and Gleicheniales. The Cyatheales, which already show increasing values in PZ 3, now reach their maximum for the complete succession with up to 17.7%. The Gleicheniales also show their overall maximum with 33.9%.

Due to the increasing values for the Gleicheniales, the mesophytes are still the dominant elements among the EPH with an average value of 60.6%, but the hygrophytes still show a significant increase compared to PZ 3. Among the EPT, the megathermic plants are still the most abundant elements with an average value of 68.3%. Therefore, in the PCA of Eco Plant (**Figure 5-9**), PZ 4 is, together with samples of PZ 5c, separated from the other zones especially due to the higher values of hygrophytes.

5.4.2.5 Palynozone PZ 5

The 5 samples HJG_33 to HJG_37 can be assigned to PZ 5. However, due to strong abundance changes of some taxa, PZ 5 can further be subdivided in three subzones PZ 5a (samples HJG_33-34), 5b (sample HJG_35) and 5c (samples HJG_36-37). In the PCA of plant orders/families (**Figure 5-8**) the two samples of PZ 5a are plotted together with the samples of PZ 3 in the centre of the ordination space. PZ 5b is plotted at the negative end of PCA axis 2, distinctly separated from the other samples of the succession, whereas the two samples of PZ 5c can be found in the upper right corner of the ordination space in the area of PZ 4.

In PZ 5a the values for the spores of the Cyatheales and Gleicheniales, which showed their peak abundance in the preceding PZ 4, clearly decline. Instead, the pollen of the Corystospermales is once again characterized by high abundances. Additionally, the spores of the Pleuromeiaceae occur with a significant increase and reach 10.2% in PZ 5a. In the succeeding PZ 5b, these spores show, with 34.4%, their main distribution; however, they disappear nearly completely in PZ 5c. Instead, spores of the Sphagnales appear with values up to 4.5%.

Among the Eco-Plant, the composition in PZ 5a does not change much compared to PZs 3 and 4. Accordingly, PZ 5a is plotted in the PCA (**Figure 5-9**) together with samples of PZ 3 in the centre of the ordination space. Due to the high abundance of Pleuromeiaceae, the proportion of hydrophytes among the EPH increase to more than 10% in PZ 5a and to 34% in PZ 5b. This leads to a significant separation of PZ 5b in the PCA, since sample HJG_35 is plotted in the upper right corner far away from all other samples (**Figure 5-9**). With the decreasing number of hydrophytes but due to the relatively high abundance of Sphagnales, PZ 5c is separated from the other samples of PZ 5 in the PCA and shows similarities to samples of PZ 4.

5.5. Discussion

5.5.1 Palaeoenvironment and Palaeoclimate

In our record of the lignite (10 m in thickness), 19 sporomorph genera have been recognized, which are abundant and can be presented in the pollen diagram. We found most of the genera reported by Ashraf et al. (1999; 2010; 2001). However, most genera reported in Lu and Deng (2005) and Huang (2006) are missing. This is probably due to the fact that we studied with 10 m, only a small section of the 290 m thick whole Haojiagou Formation. Therefore, the number of 19 genera recognized in the studied lignite seam of the Haojiagou Formation seems to be representative only for a short section within the complete formation and a specific environment. However, in both studies, many genera have been described whose abundances are generally less than 2% (Huang, 2006; Lu and Deng, 2005). Related to the entire Haojiagou Formation, these taxa are extremely rare and often disappear. For our purpose, they play only a minor role in presenting general statements on the composition of the vegetation and the interpretation, e.g., of the climatic conditions. The number of 19 genera, which are generally common in the Haojiagou Formation, may therefore also be representative for predicting the overall composition of the vegetation in the entire formation.

The palynological samples of the Haojiagou Formation belong to the *Concavisporites-Duplexisporites problematicus-Ricciisporites tuberculatus* zone, which has been shown repeatedly in Iran, Afghanistan and Germany indicating that all these basins belong to the same phytogeographic province (Ashraf et al., 1999; Ashraf et al., 2010; Ashraf et al., 2001). However, the Corystospermales are a relatively small group of plants which have a primarily Gondwanan distribution and are known from Triassic localities in Antarctica, South Africa, Australia, Argentina, Tasmania, and India (Artabe and Brea, 2003; Taylor et al., 2009). The discovery of the plant fossil *Thinnfeldia* by Sun et al. (2010a) and the high abundance of pollen related to the Corystospermales indicate that the Haojiagou flora is also associated with the Gondwanan flora of the Late Triassic. The palynological samples of the Haojiagou Formation also belong to the *Concavisporites-Dictyophyllidites-Chasmatosporites-Cycadopites* assemblage, which is comparable to the Late Triassic palynological assemblage of the Ipswich Coalfield of Australia (Huang, 2006). Therefore, it can be estimated that the Late Triassic Haojiagou flora is a mixed flora with both Eurasian and Gondwanan elements.

Generally, the 5 pollen zones, which can be distinguished by cluster analysis and NMDS, are qualitatively very similar in composition. However, there are significant quantitative changes within the palynomorph assemblages. Since all samples are taken from lignites of the coal-bearing part of the Haojiagou Formation they reflect a similar depositional environment. Although the coal-bearing part is intercalated with an about 1 m thick sandy bed (**Figure 5-1**-C), the bed is laterally not continuous. All the samples are taken from the continuous coal-bearing part (**Figure 5-1**-D). There is no lithofacies change for the sampled coal-bearing part. The type of vegetation is governed by two principal controls: sea (lake)-level fluctuations and climate (Abbink et al., 2004b). However, sedimentary study reveals that there are no significant lake-level fluctuations for the sampled coal-bearing part (Hornung and Hinderer, 2011). Therefore, quantitative changes within the palynomorph assemblages may probably point to climate changes. The Eco-Plant model depicts and confirms these climate trends in high resolution. Thus, the pollen zones reveal the evolution of vegetation and climate during the deposition of the lignite deposits of the Haojiagou Formation in 5 phases.

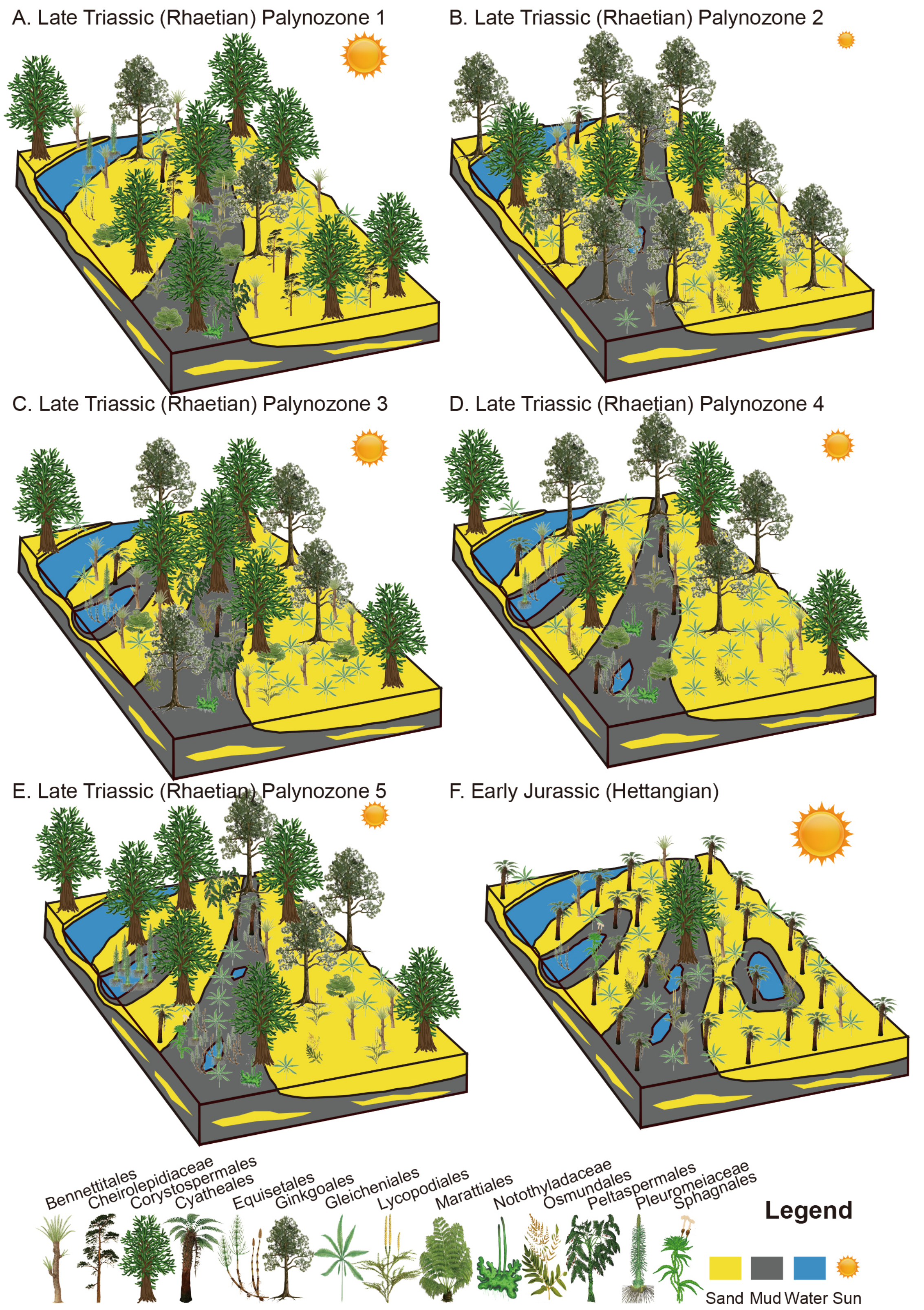


Figure 5-10 Reconstruction of the palaeoenvironment and vegetation for the Late Triassic Rhaetian (Haojiagou Formation) based on this study and the Early Jurassic Hettangian (basal Badaowan Formation) after Lu and Deng (2005). The area of water indicates the relative humidity and the size of the sun indicates the relative temperature. Due to low abundance, the plants of Pinaceae are not depicted.

5.5.1.1 Warm and dry/wet subtropical phase 1 (Palynozone 1)

The palynomorph assemblage in PZ 1 (**Figure 5-10**-A) reflects the driest and hottest conditions among all PZs**,** since it is characterized by the highest average abundance of megathermic plants and highest average abundance of xerophytes. The flora is mainly composted by plants of Corystospermales, Bennettitales, and Gleicheniales (**Figure 5-6**).

As shrubs or trees, Corystospermales and Bennettitales were elements of the canopy and sub-canopy vegetation. The shrubs or trees of Cheirolepidiaceae are almost exclusively distributed in this PZ. Extant Gleicheniales are heliophilous terrestrial ferns which are today distributed under the forest canopy. The heliophilous trait and high abundance of the Gleicheniales may therefore indicate that the forest canopy was not dense, and sunlight frequently reached the forest floor. This is also confirmed by the appearance of the Cyatheales, which often occur in the undergrowth of moist forests or open habitats (Kramer and Green, 1990). Therefore, an open vegetation was widespread in the vicinity of the peat-forming swamps (**Figure 5-10**-A).

Corystospermales, Bennettitales, and Gleicheniales are all megathermic plants. Furthermore, the ferns of the Marattiales, which reach their maximum in PZ 1, occur exclusively in tropical and subtropical regions (Kramer and Green, 1990). Extant species of Cyatheales are tree ferns concentrated in the tropics (Kramer and Green, 1990). The dominant megathermic plants point therefore to a tropical or subtropical climate. However, Mesozoic ginkgoalean plant fossils are found widely in fossil records, except at the Equator and in Antarctica (Wang et al., 2017). The considerable abundances of Ginkgoales together with the high abundance of the megathermic plants indicate that the climate condition during the deposition of PZ 1 was more subtropical than tropical. This is confirmed by Triassic palaeolatitudes of this region between 23.3° N to 31.1° N (Li et al., 1999).

Due to the high abundance of Cheirolepidiaceae pollen, which is nearly restricted to PZ 1, the xerophytes show a high average abundance of 9.9% with peak values up to 30.5%. Nevertheless, hygrophytes also occur in this zone with an average of 26.4 % and peak values up to 47%, which are more common than the xerophytes. Therefore, a climate with both drought and wet periods is indicated. This can explain that fibre coal is particularly common in the lignite deposits which was formed almost exclusively by forest fires (Hornung and Hinderer, 2011; Ligouis, 2001). However, the abundant mesophytes such as the ferns of the Gleicheniales could not resist long term drought and show that the drought periods may have occurred often but were apparently short. Also, the extant species of Cyatheales cannot resist long periods of drought as tree ferns in the undergrowth of moist forests (Kramer and Green, 1990). Therefore, wet periods may have been longer than drought periods.

The hygrophytes decrease throughout PZ 1, whereas mesophytes increase to the top of PZ 1. This indicates an overall change of the climate that climaxed in the succeeding PZ 2.

5.5.1.2 Cooler subtropical phase 2 (Palynozone 2)

In the short phase represented by the two samples of PZ 2, the strong increase of pollen of Bennettitales and Ginkgoales is noteworthy (**Figure 5-10**-B). This indicates a quantitative change in the composition of the forest. However, the flora is mainly composed by plants of Ginkgoales and Corystospermales. The average abundance of Ginkgoales is higher than that of Corystospermales. During the Mesozoic, plants of the Ginkgoales were associated with plants that were adapted to different climates ranging from hot and dry, to wet and temperate in coastal plain and lowland to inland riparian/swamp environments (Zhou, 2009). However, as mesothermic plants, they preferred mesic habitats in temperate regions in mixed conifer-broadleaved forests (Kramer and Green, 1990). Therefore, the abundant pollen of the Ginkgoales may indicate a climate change to slightly cooler temperatures during PZ 2. This is also confirmed by the strong decrease of megathermic plants such as the Cheirolepidiaceae and the ferns of the Marattiales, which both completely disappear in PZ 2.

The average abundance of megathermic plants such as the Corystospermales significantly decreased in PZ 2. The increase of deciduous trees such as the Ginkgoales therefore indicates a cooler climate with strong seasonality (Kramer and Green, 1990; Zhou, 2009). Although mesothermic plants had their highest average abundance in PZ 2, they did not reach the values of megathermic plants. It can be inferred that the climate of PZ 2 is still subtropical with the MAT above 20 °C, but the MAT is probably lower compared to PZ 1.

5.5.1.3 Subtropical phase 3 (Palynozone 3)

The change in the composition of the floras between PZ 1 and PZ 2 is followed by a further change within the vegetation during PZ 3 (**Figure 5-10**-C). The flora is mainly composed by the plants of Corystospermales, Ginkgoales, and Bennettitales. The Corystospermales gradually increase, indicated by the increasing values of their pollen within PZ 3. Along with this, the values for the Bennettitales and Ginkgoales are gradually decreasing from the base to the top of PZ 3. However, both plant orders are more abundant compared to most parts of PZ 1 indicating that they were important parts of the vegetation during PZ 3. The gradual appearance of the tree ferns of the Cyatheales is also notable. Other ferns such as the Gleicheniales, which have the highest abundance among all ferns within the flora, or Osmundales and Marattiales, are relatively common and point to an open forest community.

The frequency trends of the palynomorphs, such as the increase of pollen of the Corystospermales or the decrease of pollen of the Ginkgoales indicate a gradual warming. The temperature-related Eco-Plant model clearly reveals this trend, because the megathermic plants are generally dominant. However, the opposite abundance trends of Corystospermales and Bennettitales pollen (megathermic plants) show that besides a temperature increase, humidity changes may have also had an influence on the composition of the vegetation.

In general, due to the dominance of the megathermic plants, a subtropical climate is indicated during the deposition of PZ 3. However, the values for the megathermic plants are not as high as in PZ 1. On the other hand, the proportions of the mesothermic plants in PZ 3 are significantly higher than in PZ 1. Therefore, the high temperatures that have occurred during PZ 1 are probably not reached in PZ 3. Nevertheless, they were higher than during PZ 2. In conclusion, a MAT of *c.* 20 °C can be assumed.

During PZ 3 hygrophytes reach higher values than in PZ 2, indicating that PZ 3 was more humid than PZ 2. However, the dominant mesophytes, such as the Ginkgoales, also point to strong seasonality and less humid periods during the season.

5.5.1.4 Subtropical phase 4 (Palynozone 4)

The vegetation during PZ 4 is still dominated by plants of Ginkgoales and Corystospermales. Furthermore, the PZ is characterized by the increased occurrence of spores of the Cyatheales and the Gleicheniales (**Figure 5-10**-D). This may indicate increasingly open habitats. In particular, the tree ferns of the Cyatheales are widespread within the vegetation of PZ 4. Therefore, the abundance trend among these ferns, which has already started with the gradual increase of values within PZ 3, continues. As hygrophytes, which cannot resist longer periods of draught, they point to increasingly humid conditions.

The values for megathermic and mesothermic plants are nearly unchanged compared to their occurrence in PZ 3. Therefore, they point still to very warm temperatures and subtropical climate with a MAT above 20 °C.

5.5.1.5 Wet subtropical phase 5 (Palynozone 5)

During PZ 5, the forest is dominated by plants of Gleicheniales, Ginkgoales, and Corystospermales. However, the palaeoenvironmental changes in the depositional area are strengthened, as indicated by strong frequency fluctuations within the palynomorph assemblages (**Figure 5-10**-E), which leads to the separation of PZ 5 into three sub-zones. Principally, the common occurrence of hydrophytes points to increasingly humid conditions during the deposition of PZ 5 with a rising water level or increasing areas with open water that were settled by submerged plants such as the Pleuromeiaceae. In PZ 5 they appear with higher values, but peaked in PZ 5b. The Pleuromeiaceae are replaced in PZ 5c by the Sphagnales. The modern *Sphagnum* (peat moss) is the dominant plant type in modern ombrotrophic bogs and adapted to acidic, waterlogged and nutrient-limited environments (Clymo, 1984; van Breemen, 1995). The *Sphagnum*-type spores that can be found in the Haojiagou Formation thus indicate significant changes in the local hydrology and nutrient conditions. Modern

Sphagnum is an important plant of raised bogs indicating the end of lignite deposition (Inglis et al., 2015). In the studied seam of the Haojiagou Formation an ombrogenous peat bog maintained by growth of Sphagnales had been formed in association with a variety of ferns such as those of the Gleicheniales and Cyatheales. In conclusion, during PZ 5, changes in hydrological conditions (e.g., by increased precipitation) are responsible for changes within the vegetation and less changes in temperature.

The dominance of megathermic plants such as the Corystospermales indicates persistently very warm temperatures and a MAT above 20 °C. However, the decreasing values for the megathermic plants in PZ 5b may point to slightly cooler conditions as in PZ 4.

5.5.2 The Triassic/Jurassic boundary

The Triassic-Jurassic boundary in Northwestern China is characterized by the disappearance of the marker taxa of *Aratrisporites, Chordasporites, Taeniaesporites* and *Bharadwajapollenites,* which occur at the base of the Lower Jurassic Badaowan Formation in this section (Ashraf et al., 2010; Lu and Deng, 2005). They separately represent Bennettitales (*Bharadwajapollenites*), Peltaspermales (*Chordasporites* and *Taeniaesporites*), and Pleuromeiaceae (*Aratrisporites*). Plants of the Bennettitales were distributed from the Triassic to the Cretaceous in both hemispheres (Taylor et al., 2009). *Densoisporites* related with Pleuromeiaceae has been discovered at the base of the Lower Jurassic Badaowan Formation in this section with abundances up to 46.3% (Lu and Deng, 2009). Peltaspermales were extinct at the Triassic-Jurassic boundary. *Classopollis* related with Cheirolepidiaceae was the dominant pollen at the base of the Lower Jurassic Badaowan Formation (Lu and Deng, 2009). Both, Cheirolepidiaceae and Peltaspermales are xerophytes and megathermic plants. In the studied lignite bed of the Haojiagou Formation, which are considerably below the Triassic-Jurassic boundary, the abundances of Peltaspermales are already rare (<6.4%). Hence, it may be estimated that the Peltaspermales were replaced by Cheirolepidiaceae during the Late Triassic by slow competition rather than sudden disaster.

Pollen percentages are influenced by both, different pollen production within a genus, and by differences in the relative pollen production of taxa within different vegetation assemblages. Nevertheless, data on the relative abundances of different taxa of pollen in present day surface sediments of eastern North America can be compared directly with forestry data on the abundance of trees of the same species in forests close to the surface sediment sources (Delcourt and Delcourt, 1985). Based on the low pollen abundance of Peltaspermales, it can be estimated that the abundances of these plants in the Haojiagou flora were also low. In comparison, the pollen abundance of Cheirolepidiaceae in the sampled lignite bed can reach up to 29.1%.

Although among the 15 plant orders and families that were distributed throughout the studied part of the Haojiagou Formation, 14 of them passed the Triassic-Jurassic boundary; their abundances changed significantly. Different authors separately reported that changes in the abundance of pollen and spores in the Haojiagou Formation are relatively gentle, but significant at the Triassic-Jurassic boundary (Ashraf et al., 2010; Lu and Deng, 2009). The generally similar values of δ^{13} C_{org} for the whole Haojiagou Formation indicate that there was no significant climate change (Lu and Deng, 2009). In this case, the studied samples taken from lignites of the coal-bearing part of the Haojiagou Formation, can also give an overall view on the palaeoclimate of the whole Haojiagou Formation, although detailed palynological study for the whole formation is still needed. Although some fluctuations in humidity and temperature are indicated, the five palynozones generally reveal a variable, but general subtropical climate with seasonal changes of both wet and drought periods. The drought periods were shorter compared to the wet periods.

A spike in the abundance of fern spores, mainly composed by *Cyathidites* (54.9%) and *Deltoidospora* (7%), in the basal Badaowan Formation (Hettangian) in the studied section has been reported by Lu and Deng (2005, 2009). The high abundance of *Cyathidites* and the very low abundance of *Cycadopites* (7. 1%) in the Badaowan flora indicates that the Late Triassic shrub and tree forests, as revealed in the Haojiagou flora with a dominance of Bennettitales, Cheirolepidiaceae, Corystospermales, Ginkgoales, and Peltaspermales were replaced by a flora dominated by tree ferns of Cyatheales in the Early Jurassic (**Figure 5-10**-F). The deciduous trees such as the Ginkgoales indicate a cooler climate with strong seasonality during the late Triassic (Kramer and Green, 1990; Zhou, 2009). The increase of hygrophytes and megathermic plants such as Cyatheales and the decrease of the mesothermic plants such as the Ginkgoales indicate that the climate of the basal Badaowan Formation of the Early Jurassic (Hettangian) was much hotter and wetter than in the Late Triassic (Rhaetian). In addition, it may be inferred, that the seasonal change in the basal Badaowan Formation of the Early Jurassic (Hettangian) was not remarkable. In the layer of the fern spore spike in the Badaowan Formation, the significant negative deviation of $\delta^{13}C_{org}$ to a value lower than the regular value of 24.5‰ also indicates a change to a much hotter and wetter climate (Lu and Deng, 2009).

The strong climate change between the Late Triassic (Rhaetian) and the Early Jurassic (Hettangian) is also confirmed by the fact that huge and economically important lignite seams together with Fe-rich (especially ironstone rich) sediments occur in the basal Badaowan Formation. As the lignite beds in the Haojiagou Formation are generally relatively thin, the occurrence of thick lignite seams in the Badaowan Formation point to warmer and probably even more humid conditions during the Early Jurassic which is favorable for the long-lasting growth of a peat-forming vegetation (Ashraf et al., 2010).

The abundance spike in fern spores across the Triassic/Jurassic boundary has also been found in Greenland, northern France, northeastern US, southern Spain, and Austria (Heunisch et al., 2010; van de Schootbrugge et al., 2009), was also found to be related to changes in climate, such as increasing global temperatures and humidity (Michalik et al., 2010). It can be concluded that the climate change across the Triassic/Jurassic boundary in Haojiagou section is part of the global climate change event.

5.6 Conclusions

This study presents the first detailed high-resolution palynoflora and vegetation patterns of a 10 m thick lignite seam from the Late Triassic terrestrial Haojiagou Formation (Rhaetian). It revealed 5 palynozones each characterized by specific palynomorph assemblages that indicate changes within peat forming vegetation. At the beginning of peat formation, plants of the Cheirolepidiaceae and the Corystospermales, and to a lesser extent plants of the Bennettitales, Ginkgoales and Peltaspermales, formed the forest canopy in the depositional area; whereas, ferns of the Gleicheniales and Cyatheales, inhabited the forest floors and open habitats. The plants point to a subtropical climate. Later the increase of pollen of the Ginkgoales indicates stronger seasonality and a climate change to cooler conditions, but still with a predominantly subtropical climate. At the end of peat formation a shift to more humid conditions can be noticed. The overall climate was subtropical with seasonal changes of both wet and drought periods. The drought periods were shorter compared to the wet periods. The overall trend to a wetter climate is proven by the changes in abundance of xerophytes, hygrophytes, and hydrophytes. However, the distribution of spores of the Sphagnales shows that not only climate change was responsible for changes within the vegetation, but also hydrological conditions and the availability of nutrients. Compared to the following Lower Jurassic Badaowan Formation (Hettangian), the strong changes in the composition of the vegetation indicate that the climate was much hotter and wetter in the region than in the Late Triassic, which mimics the global signal.

The use of the Eco-Plant model that assesses the effect of humidity as well as the effect of temperature turned out to be an important tool for revealing climate variations in the record. In general, the model analyzes diverse plant associations in relation to their principal habitat preferences with high sensitivity. Hence, the model is also a suitable method for other Mesozoic microfloras which do not show a major turnover in species composition within their palynomorph assemblages. However, for robust palaeoenvironmental analyses using the Eco-plant model, the accurate identification of parent plants is required, which is more problematic the older the record is. This was done with a combination of LM and SEM that allowed the assignment of 18 out of 19 recognized palynomorph genera to their parent plant orders and genera, which was assisted by our online database ***Sporopollen*** (http://www.sporopollen.com). In conclusion, to get a precise affinity and Eco-Plant, detailed SEM studies are crucial.

In view of the rarity of similar studies of terrestrial records from the Mesozoic basins in Northwestern China, this study should be seen as an initial step in the recognition of palaeoecological and climatic variations during this period. Therefore, it is necessary to identify and study more terrestrial records in higher resolution to get a deeper insight into the dynamics and controls of palaeoenvironmental changes.

6. Summary

The new database ***Sporopollen*** (http://www.sporopollen.com) focused mainly on Mesozoic sporomorphs is created. Currently, it has collected **100,610** sporomorph pictures, **59, 498** plant pictures, **31, 922** sporomorph descriptions. At the same time, from **63, 035** references, it has collected **2, 215, 162** occurrences for both sporomorph and non-sporomorph fossils. The collected plant data include **32, 972** genera from **946** families. The collected sporomorph pictures include **5, 857** genera. They can be queried in the form of a map or dataset. It collects illustrations, descriptions, occurrences, and the taxonomy of sporomorphs. Different user-friendly interfaces are created for:

- Data query both on a map and in datasets
- Sporomorph identification
- Stratigraphic analysis
- Linking sporomorphs to their parent plants

With the help of the database, based on literature and the unique outline and structure/sculpture of the sporomorph wall, 861 dispersed Mesozoic sporomorph genera of Bryophytes, Pteridophytes, and Gymnosperms are reviewed by comparing the unique outline and structure/sculpture of the sporomorph wall with that of modern plants and *in situ* fossil plants. 474 of them can be linked to their closest parent plants and Eco-Plant model at family or order level. 387 of them can not because of the lack of detailed ultrastructure descriptions. The presented eco-groups for dispersed Mesozoic sporomorphs provide the possibility to identify the detailed plant and palaeoenvironmental change in the Mesozoic, especially in the context of climate change. We can also get the following conclusions:

- The use of LM for determination is one of the main reasons that some dispersed sporomorphs cannot be linked precisely to their parent plants.
- In the Mesozoic, both spore-producing plants and pollen-producing plants are adapted to different kinds of humidity.
- The concept to use the spore/pollen ratio to reflect the hygrophytes/xerophytes ratio is questionable.

A new interface (http://www.sporopollen.com/sporemesozoicsegs.php?opencode=paper1) was created based on the reviewed result to quickly link the dispersed sporomorphs to past vegetation patterns and climatic changes. Users can upload their data to the database and in return get quick results. It can automatically link all of the Mesozoic and Cenozoic sporomorphs to their possible parent plants at phylum, order, or family level. It can also automatically link all of the Triassic and Jurassic sporomorphs to the Eco-Plant model to assess the effect of humidity (EPH) and the effect of temperature (EPT). The new interface is:

- A useful tool for using the Eco-Plant model to reconstruct Triassic and Jurassic humidity and temperature.
- A useful tool for palaeoenvironmental reconstruction.
- A useful tool for high-resolution quantitative palynomorph study.

As a case study, the Eco-Plant model and the sporomorphs of a 10 m thick lignite bed from the Upper Triassic Haojiagou Formation (Rhaetian) are used to discuss the palaeovegetation and palaeoenvironment of a peat-forming wetland near the Triassic-Jurassic boundary. The result shows that the palynoflora contains both Eurasian and Gondwanan elements, and is dominated by the spores and pollen of Bennettitales, Corystospermales, Ginkgoales, and Gleicheniales. At the Triassic/Jurassic boundary (Hettangian), the

palynoflora significantly changes as Cyatheales spores become the dominant elements. We analyse assemblages in terms of an Eco-Plant model, which assigns the parent plants of the palynomorphs into five groups based on humidity and four groups based on temperature, and uses multivariate statistical analyses to infer palaeoclimate and palaeoenvironmental conditions. Results suggest that the palaeoclimate of the Rhaetian was generally wet and subtropical with short seasonal drought periods. Our analysis shows that an Eco-Plant model may be a useful tool to reveal past vegetation patterns and climate changes, applicable to other Mesozoic assemblages.

References

Abbink, O., Targarona, J., Brinkhuis, H., and Visscher, H., 2001, Late Jurassic to earliest Cretaceous palaeoclimatic evolution of the southern North Sea: Global and Planetary Change, v. 30, p. 231-256.

Abbink, O.A., Van Konijnenburg-Van Cittert, J.H.A., Van der Zwan, C.J., and Visscher, H., 2004a, A sporomorph ecogroup model for the Northwest European Jurassic Lower Cretaceous II : Application to an exploration well from the Dutch North Sea: Netherlands Journal of Geosciences-Geologie En Mijnbouw, v. 83, p. 81-91.

Abbink, O.A., Van Konijnenburg-Van Cittert, J.H.A., and Visscher, H., 2004b, A sporomorph ecogroup model for the Northwest European Jurassic - Lower Cretaceousi: concepts and framework: Netherlands Journal of Geosciences-Geologie En Mijnbouw, v. 83, p. 17-31.

Abu Hamad, A., Kerp, H., Voerding, B., and Bandel, K., 2008, A late Permian flora with Dicroidium from the Dead Sea region, Jordan: Review of Palaeobotany and Palynology, v. 149, p. 85-130.

Alvin, K.L., 1982, Cheirolepidiaceae - Biology, Structure and Paleo-Ecology: Review of Palaeobotany and Palynology, v. 37, p. 71-98.

Ames, H.T., and Spackman, W., 1981, Catalog of fossil spores and pollen Volume 42: Cretaceous Spores and Pollen from the U.S.A. and the U.S.S.R. , University Park, Pennsylvania.

—, 1985, Catalog of fossil spores and pollen Volume 44: Tertiary and Upper Cretaceous Spores and Pollen from Africa, Europe, Canada, Australia and New Zealand, University Park, Pennsylvania.

Ames, H.T., Traverse, A., and Spackman, W., 1976, Catalog of fossil spores and pollen Volume 40: Triassic - Cretaceous Spores and Pollen, University Park, Pennsylvania.

Aranbarri, J., Gonzalez-Samperiz, P., Valero-Garces, B., Moreno, A., Gil-Romera, G., Sevilla-Callejo, M., Garcia-Prieto, E., Di Rita, F., Mata, M.P., Morellon, M., Magri, D., Rodriguez-Lazaro, J., and Carrion, J.S., 2014, Rapid climatic changes and resilient vegetation during the Lateglacial and Holocene in a continental region of south-western Europe: Global and Planetary Change, v. 114, p. 50-65.

Archangelsky, A., Phipps, C.J., Taylor, T.N., and Taylor, E.L., 1999, Paleoazolla, a new heterosporous fern from the Upper Cretaceous of Argentina: American Journal of Botany, v. 86, p. 1200-1206.

Archangelsky, S., 1966, New gymnosperms from the Ticó flora, Santa Cruz Province, Argentina: Bulletin of the British Museum (Natural History), Geology, v. 13, p. 259-295.

—, 1994, Comparative ultrastructure of three early cretaceous gymnosperm pollen grains: Araucariacites, Balmeiopsis and Callialasporites: Review of Palaeobotany and Palynology, v. 83, p. 185-198.

—, 2009, Biogeographic implications of Albian Mohria-like spores (Family Anemiaceae) in SW Gondwana (Patagonia): Review of Palaeobotany and Palynology, v. 157, p. 301-308.

Archangelsky, S., and Archangelsky, A., 2006, Putative Early Cretaceous pteridaceous spores from the offshore Austral Basin in Patagonia, Argentina: Cretaceous Research, v. 27, p. 473-486.

Archangelsky, S., and Cuneo, R., 1987, Ferugliocladaceae, a new conifer family from the Permian of Gondwana: Review of Palaeobotany and Palynology, v. 51, p. 3-30.

Archangelsky, S., and Gamerro, J.C., 1967, Pollen grains found in coniferous cones from the lower cretaceous of patagonia (Argentina): Review of Palaeobotany and Palynology, v. 5, p. 179-182.

Archangelsky, S., and Seoane, L.V.d., 2005, Estudios palinológicos del Grupo Baqueró (Cretácico Inferior), provincia de Santa Cruz, Argentina. IX polen bisacado de Podocarpaceae: Revista Española de Paleontología, v. 20, p. 37-56.

Artabe, A., and Brea, M., 2003, A new approach to Corystospermales based on Triassic permineralized stems from Argentina: Alcheringa, v. 27, p. 209-229.

Ash, S., 1994, First occurrence of Czekanowskia (Gymnospermae, Czekanowskiales) in the United States: Review of Palaeobotany and Palynology, v. 81, p. 129-140.

Avramenko, A.S., and Polevova, S.V., 2013, Morphology and ultrasctructure of spores Klukia tyganensis Krassilov (Schizaeaceae, Filicales) from the Berriassian of the Tyrma Depression (Russian Far East): Paleontological Journal, v. 47, p. 439-453.

Axsmith, B.J., Krings, M., and Taylor, T.N., 2001, A filmy fern from the upper triassic of North Carolina (USA): American Journal of Botany, v. 88, p. 1558-1567.

Baeza, S., Lezama, F., Pineiro, G., Altesor, A., and Paruelo, J.M., 2010, Spatial variability of above-ground net primary production in Uruguayan grasslands: a remote sensing approach: Applied Vegetation Science, v. 13, p. 72-85.

Baldoni, A.M., and Taylor, T.N., 1982, The Ultrastructure of Trisaccites Pollen from the Cretaceous of Southern Argentina: Review of Palaeobotany and Palynology, v. 38, p. 23-33.

Balme, B.E., 1995, Fossil in situ spores and pollen grains: an annotated catalogue: Review of Palaeobotany and Palynology, v. 87, p. 81-323.

Barale, G., Marron, T.F., and Ramis, C.A., 1988, Étude de cônes mâles de Frenelopsis Schenk emend.Reymanówna & Watson, 1976 (Cheirolepidiaceae) du Crétacé supérieur de Torrelaguna (Province de Madrid-Espagne): Geobios, v. 21, p. 187-199.

Barreda, V., Palazzesi, L., and Marenssi, S., 2009, Palynological record of the Paleogene Rio Leona Formation (southernmost South America): Stratigraphical and paleoenvironmental implications: Review of Palaeobotany and Palynology, v. 154, p. 22-33.

Bashforth, A.R., Cleal, C.J., Gibling, M.R., Falcon-Lang, H.J., and Miller, R.F., 2014, Paleoecology of Early Pennsylvanian vegetation on a seasonally dry tropical landscape (Tynemouth Creek Formation, New Brunswick, Canada): Review of Palaeobotany and Palynology, v. 200, p. 229-263.

Batten, D.J., 2009, An unusual megaspore of uncertain systematic affinity from Lower Cretaceous deposits in south-east England and its biostratigraphic and palaeoenvironmental significance: Grana, v. 48, p. 270-280.

—, 2012, Taxonomic implications of exospore structure in selected Mesozoic lycopsid megaspores: Palynology, v. 36, p. 144-160.

Batten, D.J., and Collinson, M.E., 2001, Revision of species of Minerisporites, Azolla and associated plant microfossils from deposits of the Upper Palaeocene and Palaeocene/Eocene transition in the Netherlands, Belgium and the USA: Review of Palaeobotany and Palynology, v. 115, p. 1-32.

Batten, D.J., and Dutta, R.J., 1997, Ultrastructure of exine of gymnospermous pollen grains from Jurassic and basal Cretaceous deposits in Northwest Europe and implications for botanical relationships: Review of Palaeobotany and Palynology, v. 99, p. 25-54.

Batten, D.J., and Ferguson, D.J.P., 1987, Cabochonicus, a new genus for species of gemmate megaspores previously referred to Verrutriletes: Journal of Micropalaeontology, v. 6, p. 65-75.

Batten, D.J., and Koppelhus, E.B., 1993, Morphological Reassessment of Some Zonate and Coronate Megaspore Genera of Mainly Postpaleozoic Age: Review of Palaeobotany and Palynology, v. 78, p. 19-40.

Batten, D.J., Zavattieri, A.M., and Collinson, M.E., 2011, Megaspores from the upper Maastrichtian of the eastern Spanish Pyrenees and their biostratigraphic, palaeogeographic and palaeoenvironmental significance: Review of Palaeobotany and Palynology, v. 167, p. 156-172.

Bek, J., Oplustil, S., and Drabkova, J., 2001, Two species of Selaginella cones and their spores from the Bohemian Carboniferous continental basins of the Czech Republic: Review of Palaeobotany and Palynology, v. 114, p. 57-81.

Bharadwaj, D.C., and Dwivedi, A., 1981, Sporae dispersae of the Barakar sediments from South Karanpura Coalfield, Bihar, India: Palaeobotanist, v. 21(1), p. 21-94.

Bolchovitina, N.A., 1967, The fossil spores of the family Gleicheniaceae (morphology and taxonomy): Review of Palaeobotany and Palynology, v. 3, p. 59-64.

Bomfleur, B., and Kerp, H., 2010, Dicroidium diversity in the Upper Triassic of north Victoria Land, East Antarctica: Review of Palaeobotany and Palynology, v. 160, p. 67-101.

Boros, Á., and Járai-Komlódi, M., 1975, An Atlas of Recent European Moss Spores: Budapest Hungery, Scientia Publishing.

Boros, Á., Járai-Komlódi, M., Tóth, Z., Nilsson, S., and Pócs, T., 1993, An Atlas of Recent European Moss Spores, Scientia Publishing, 321 p.

Bozukov, V., Utescher, T., and Ivanov, D., 2009, Late Eocene to early Miocene climate and vegetation of Bulgaria: Review of Palaeobotany and Palynology, v. 153, p. 360-374.

Brea, M., Artabe, A., and Spalletti, L., 2008, Ecological reconstruction of a mixed Middle Triassic forest from Argentina: Alcheringa, v. 32, p. 365-393.

Breckon, G.J., and Falk, R.H., 1974, External Spore Morphology and Taxonomic Affinities of Phylloglossum Drummondii Kunze (Lycopodiaceae): American Journal of Botany, v. 61, p. 481-485.

Brenner, G.J., 1963, The spores and pollen of the Potomac Group of Maryland, State of Maryland, Board of Natural Resources, Department of Geology, Mines, and Water Resources.

Cantrill, D.J., and Webb, J.A., 1998, Permineralized pleuromeid lycopsid remains from the early Triassic Arcadia formation, Queensland, Australia: Review of Palaeobotany and Palynology, v. 102, p. 189-211.

Cavagnetto, C., and Anadon, P., 1996, Preliminary palynological data on floristic and climatic changes during the Middle Eocene Early Oligocene of the eastern Ebro Basin, northeast Spain: Review of Palaeobotany and Palynology, v. 92, p. 281-305.

Césari, S.N., 2006, Aptian ferns with in situ spores from the South Shetland Islands, Antarctica: Review of Palaeobotany and Palynology, v. 138, p. 227-238.

Césari, S.N., and Colombi, C., 2016, Palynology of the Late Triassic Ischigualasto Formation, Argentina: Paleoecological and paleogeographic implications: Palaeogeography Palaeoclimatology Palaeoecology, v. 449, p. 365-384.

Césari, S.N., Panti, C., Pujana, R.R., Francis, J.E., and Marenssi, S.A., 2015, The late Oligocene flora from the Rio Leona Formation, Argentinian Patagonia: Review of Palaeobotany and Palynology, v. 216, p. 143-158.

Chambers, T.C., Drinnan, A.N., and McLoughlin, S., 1998, Some morphological features of wollemi pine (Wollemia nobilis : Araucariaceae) and their comparison to Cretaceous plant fossils: International Journal of Plant Sciences, v. 159, p. 160-171.

Chantanaorrapint, S., 2015, Taxonomic studies on Thai Anthocerotophyta II. The genus Notothylas (Notothyladaceae): Cryptogamie Bryologie, v. 36, p. 251-266.

Ching, R.-C., and Shing, K., 1990, Flora of China, Volume 3(1), Science Press (in chinese), 305 p.

Ching, R., 2006, Flora Reipublicae Popularis Sinicae, Volume 2: Beijing, Science Press (in chinese).

Christenhusz, M.J.M., Reveal, J.L., Farjon, A., Gardner, M.F., Mill, R.R., and Chase, M.W., 2011, A new classification and linear sequence of extant gymnosperms: Phytotaxa, v. 19, p. 55-70.

Clement-Westerhof, J.A., 1984, Aspects of Permian Paleobotany and Palynology .IV. The Conifer Ortiseia Florin from the Val Gardena Formation of the Dolomites and the Vicentinian Alps (Italy) with Special Reference to a Revised Concept of the Walchiaceae (Goppert) Schimper: Review of Palaeobotany and Palynology, v. 41, p. 51-166.

—, 1987, Aspects of permian palaeobotany and palynology, VII. the majonicaceae, a new family of late permian conifers: Review of Palaeobotany and Palynology, v. 52, p. 375-402.

Clement-Westerhof, J.A., and van Konijnenburg-van Cittert, J.H.A., 1991, Hirmeriella muensteri - New Data on the Fertile Organs Leading to a Revised Concept of the Cheirolepidiaeae: Review of Palaeobotany and Palynology, v. 68, p. 147-179.

Collinson, M.E., Batten, D.J., Scott, A.C., and Ayonghe, S.N., 1985, Palaeozoic, Mesozoic and contemporaneous megaspores from the Tertiary of southern England: indicators of sedimentary provenance and ancient vegetation: Journal of the Geological Society, v. 142, p. 375-395.

Cottnam, C.F., Hemsley, A.R., Rossler, R., Collinson, M.E., and Brain, A.P.R., 2000, Diversity of exine structure in Upper Carboniferous (Westphalian) selaginellalean megaspores: Review of Palaeobotany and Palynology, v. 109, p. 33-44.

Crandall-Stotler, B.J., Stotler, R.E., Doyle, W.T., and Forrest, L.L., 2008, Part Eight: Hornworts Chapter Nineteen: Phaeoceros proskaueri sp. nov., a New Species of the Phaeoceros hallii (Austin) Prosk.—Phaeoceros pearsonii (M. Howe) Prosk. Complex and the Systematic Affinities of Paraphymatoceros Hässel: Fieldiana Botany, p. 213–238.

Crane, P.R., 1996, The fossil history of the gnetales: International Journal of Plant Sciences, v. 157, p. S50-S57.

Cranwell, L.M., and Srivastava, S.K., 2009, An Early Cretaceous (Hauterivian) Spore-Pollen Assemblage from Southern Chile: Palynology, v. 33, p. 241-280.

De Klerk, P., and Joosten, H., 2007, The difference between pollen types and plant taxa: a plea for clarity and scientific freedom: E&G Quaternary Sci. J., v. 56, p. 162-171.

de Seoane, L.V., and Archangelsky, S., 2008, Taxonomy and biostratigraphy of Cretaceous megaspores from Patagonia, Argentina: Cretaceous Research, v. 29, p. 354-372.

Decombeix, A.L., Bomfleur, B., Taylor, E.L., and Taylor, T.N., 2014, New insights into the anatomy, development, and affinities of corystosperm trees from the Triassic of Antarctica: Review of Palaeobotany and Palynology, v. 203, p. 22-34.

Del Fueyo, G.M., and Archangelsky, S., 2005, A new araucarian pollen cone with in situ Cyclusphaera Elsik from the Aptian of Patagonia, Argentina: Cretaceous Research, v. 26, p. 757-768.

Deng, S.H., 2002, Ecology of the Early Cretaceous ferns of Northeast China: Review of Palaeobotany and Palynology, v. 119, p. 93-112.

Dettmann, M.E., 1963, Upper Mesozoic microfloras from South-Eastern Australia: Proceedings of the Royal Society of Victoria, v. 77, p. 1-148.

Dino, R., Pocknall, D.T., and Dettmann, M.E., 1999, Morphology and ultrastructure of elater-bearing pollen from the Albian to Cenomanian of Brazil and Ecuador: implications for botanical affinity: Review of Palaeobotany and Palynology, v. 105, p. 201-235.

Eklund, H., Cantrill, D.J., and Francis, J.E., 2004, Late cretaceous plant mesofossils from Table Nunatak, Antarctica: Cretaceous Research, v. 25, p. 211-228.

El-Ghazaly, G., Rowley, J., and Hesse, M., 1998, Polarity, aperture condition and germination in pollen grains of Ephedra (Gnetales): Plant Systematics and Evolution, v. 213, p. 217-231.

Figueiral, I., Mosbrugger, V., Rowe, N.P., Ashraf, A.R., Utescher, T., and Jones, T.P., 1999, The Miocene peat-forming vegetation of northwestern Germany: an analysis of wood remains and comparison with previous palynological interpretations: Review of Palaeobotany and Palynology, v. 104, p. 239-266.

Francis, J.E., 1983, The Dominant Conifer of the Jurassic Purbeck Formation, England: Palaeontology, v. 26, p. 277-294.

Friis, E.M., and Pedersen, K.R., 1996, Eucommiitheca hirsuta, a new pollen organ with Eucommiidites pollen from the early Cretaceous of Portugal: Grana, v. 35, p. 104-112.

Friis, E.M., Pedersen, K.R., and Crane, P.R., 2009, Early Cretaceous Mesofossils from Portugal and Eastern North America Related to the Bennettitales-Erdtmanithecales-Gnetales Group: American Journal of Botany, v. 96, p. 252-283.

—, 2014, Welwitschioid diversity in the Early Cretaceous: evidence from fossil seeds with pollen from Portugal and eastern North America: Grana, v. 53, p. 175-196.

Gao, C., 1994, Flora Bryophytorum Sinicorum Vol.1 Sphagnales Andreaeales Archidiales Dicranales, Science Press (in chinese), 368 p.

Gao, C., Li, X., Li, Z., Li, P., and Gao, T., 1996, Flora Bryophytarum Sinicorum, Volume 2: Fissidentales Pottiales Beijing, Science Press (in chinese).

Gastony, G.J., 1982, Spore Morphology in the Dicksoniaceae. II. The Genus Cibotium: Canadian Journal of Botany-Revue Canadienne De Botanique, v. 60, p. 955-972.

Germeraad, J.H., Hopping, C.A., and Muller, J., 1968, Palynology of Tertiary Sediments from Tropical Areas: Review of Palaeobotany and Palynology, v. 6, p. 189-+.

Giacosa, J.P.R., Morbelli, M.A., Giudice, G.E., and Gorrer, D.A., 2016, Spore morphology and wall ultrastructure of Lycopodiaceae from northwest Argentina: Review of Palaeobotany and Palynology, v. 225, p. 84-94.

Glasspool, I., 2000, Megaspores from the Late Permian, Lower Whybrow coal seam, Sydney Basin, Australia: Review of Palaeobotany and Palynology, v. 110, p. 209-227.

Godin, V.N., 2017, Sexual forms and their ecological correlates of flowering plants in Siberia: Russian Journal of Ecology, v. 48, p. 433-439.

Goffinet, B., and Buck, W.R., 2004, Systematics of the Bryophyta (Mosses): From molecules to a revised classification, Molecular Systematics of Bryophytes, Missouri Botanical Garden Press, p. 205-239.

Gomankov, A.V., 2009, Pollen Evolution in Cordaites and Early Conifers: Paleontological Journal, v. 43, p. 1245-1252.

Gosling, W.D., Miller, C.S., and Livingstone, D.A., 2013, Atlas of the tropical West African pollen flora: Review of Palaeobotany and Palynology, v. 199, p. 1-135.

Grauvogel-Stamm, L., 1993, Pleuromeia sternbergii (Munster) Corda from the Lower Triassic of Germany - Further Observations and Comparative Morphology of Its Rooting Organ: Review of Palaeobotany and Palynology, v. 77, p. 185-212.

Grauvogel-Stamm, L., and Duringer, P., 1983, Annalepis zeilleri Fliche 1910 emend., un organe reproducteur de Lycophyte de la Lettenkohle de l'Est de la France. Morphologie, spores in situ et paléoécologie: Geologische Rundschau, v. 72, p. 23-51.

Grauvogel-Stamm, L., and Lugardon, B., 2009, Phylogeny and evolution of the horsetails: Evidence from spore wall ultrastructure: Review of Palaeobotany and Palynology, v. 156, p. 116-129.

Grimsson, F., and Zetter, R., 2011, Combined LM and SEM study of the Middle Miocene (Sarmatian) palynoflora from the Lavanttal Basin, Austria: Part II. Pinophyta (Cupressaceae, Pinaceae and Sciadopityaceae): Grana, v. 50, p. 262-310.

Guignard, G., Wang, Y.D., Ni, Q., Tian, N., and Jiang, Z.K., 2009, A dipteridaceous fern with in situ spores from the Lower Jurassic in Hubei, China: Review of Palaeobotany and Palynology, v. 156, p. 104-115.

Harris, T.M., 1938, The British Rhaetic Flora: London.

—, 1964, The Yorkshire Jurassic Flora Vol. II: Caytoniales, Cycdales & Pteridosperms: London, Trustees of the British Museum (Natural History), 191 p.

—, 1983, The Stem of Pachypteris papillosa (Thomas and Bose) Harris: Botanical Journal of the Linnean Society, v. 86, p. 149-159.

Harris, T.M., and Museum, B., 1969, The Yorkshire Jurassic Flora Vol. III: Bennettitales, Trustees of the British Museum (Natural History), 192 p.

He, X.Z., Shi, T.M., Wan, M.L., Wang, S.J., Hilton, J., Tang, P., and Wang, J., 2017, Peltaspermalean seed ferns with preserved cuticle from the Upper Triassic Karamay Formation in the Junggar Basin, northwestern China: Review of Palaeobotany and Palynology, v. 247, p. 68-82.

Hemsley, A.R., 1989, The Ultrastructure of the Spore Wall of the Triassic Bryophyte Naiadita lanceolata: Review of Palaeobotany and Palynology, v. 61, p. 89-99.

Hermsen, E.J., Taylor, T.N., and Taylor, E.L., 2007, A voltzialean pollen cone from the Triassic of Antarctica: Review of Palaeobotany and Palynology, v. 144, p. 113-122.

Hesse, M., Buchner, R., Svojtka, M., and Frosch-Radivo, A., 2018, Illustrated Pollen Terminology, Springer, Cham.

Hesse, M., Halbritter, H., Weber, M., Buchner, R., Zetter, R., Ulrich, S., and Frosch-Radivo, A., 2009, Pollen Terminology: An illustrated handbook: Austria, Springer, 266 p.

Heunisch, C., Luppold, F.W., Reinhardt, L., and Röhling, H.-G., 2010, Palynofazies, Bio- und Lithostratigrafie im Grenzbereich Trias/Jura in der Bohrung Mariental 1 (Lappwaldmulde, Ostniedersachsen): Zeitschrift der Deutschen Gesellschaft für Geowissenschaften, v. 161, p. 51-98.

Hieger, T.J., Serbet, R., Harper, C.J., Taylor, T.N., Taylor, E.L., and Gulbranson, E.L., 2015, Cheirolepidiaceous diversity: An anatomically preserved pollen cone from the Lower Jurassic of southern Victoria Land, Antarctica: Review of Palaeobotany and Palynology, v. 220, p. 78-87.

Hill, C.R., 1990, Ultrastructure of In situ Fossil Cycad Pollen from the English Jurassic, with a Description of the Male Cone Androstrobus-Balmei sp-nov: Review of Palaeobotany and Palynology, v. 65, p. 165-173.

Hill, R.S., 2017, History of the Australian Vegetation Cretaceous to Recent, The University of Adelaide Press, 443 p.

Hochuli, P.A., and Vigran, J.O., 2010, Climate variations in the Boreal Triassic - Inferred from palynological records from the Barents Sea: Palaeogeography Palaeoclimatology Palaeoecology, v. 290, p. 20-42.

Hofmann, C.C., 2002, Pollen distribution in sub-recent sedimentary environments of the Orinoco Delta (Venezuela) - an actuo-palaeobotanical study: Review of Palaeobotany and Palynology, v. 119, p. 191-217.

Horton, D.G., 1978, Bryobrittonia-Longipes, an Earlier Name for Bryobrittonia-Pellucida (Encalyptaceae, Musci): Brittonia, v. 30, p. 16-20.

Huang, H., Pérez-Pinedo, D., Morley, R.J., Dupont-Nivet, G., Philip, A., Win, Z., Aung, D.W., Licht, A., Jardine, P.E., and Hoorn, C., 2021, At a crossroads: The late Eocene flora of central Myanmar owes its composition to plate collision and tropical climate: Review of Palaeobotany and Palynology, v. 291, p. 104441.

Huang, P., 2008, Palaeontologia Sinica:Triassic sporopollen assemblages from Santanghu Basin, Xinjiang: Beijing, Science Press (in chinese), 240 p.

Huang, W., Dilcher, D.L., Wang, H., Na, Y.L., Li, Y.F., Li, T., and Sun, C.L., 2017, First record of Sphenarion (Czekanowskiales) with epidermal structures from the Middle Jurassic of Inner Mongolia, China: Palaeoworld, v. 26, p. 510-518.

Hui Ho, R., and Sziklai, O., 1973, Fine structure of the pollen surface of some taxodiaceae and cupressaceae species: Review of Palaeobotany and Palynology, v. 15, p. 17-26.

Jiang, D., Robbins, E.I., Wang, Y., and Yang, H., 2016, Petrolipalynology, Springer, 263 p.

Joosten, H., and de Klerk, P., 2002, What's in a name? Some thoughts on pollen classification, identification, and nomenclature in Quaternary palynology: Review of Palaeobotany and Palynology, v. 122, p. 29-45.

Kar, R.K., and Sah, S.C.D., 1969, Palynological investigation of the Gondwana outcrop from Vemavaram with remarks on the age of the bed: Palaeobotanist, v. 18(2), p. 103-117.

Katagiri, T., and Hagborg, A., 2015, Validation of ordinal and family names for a Triassic fossil liverwort, Naiadita (Naiaditaceae, Marchantiopsida): Phytotaxa, v. 222, p. 165-166.

Kelber, K.P., and van Konijnenburg-van Cittert, J.H.A., 1998, Equisetites arenaceus from the Upper Triassic of Germany with evidence for reproductive strategies: Review of Palaeobotany and Palynology, v. 100, p. 1-26.

Kern, A.K., Harzhauser, M., Soliman, A., Piller, W.E., and Gross, M., 2012, Precipitation driven decadal scale decline and recovery of wetlands of Lake Pannon during the Tortonian: Palaeogeography Palaeoclimatology Palaeoecology, v. 317, p. 1-12.

Kerp, H., Abu Hamad, A., Vording, B., and Bandel, K., 2006, Typical Triassic Gondwanan floral elements in the Upper Permian of the paleotropics: Geology, v. 34, p. 265-268.

Kerp, J.H.F., 1988, Aspects of Permian palaeobotany and palynology. X. The West- and Central European species of the genus Autunia Krasser emend. Kerp (Peltaspermaceae) and the form-genus Rhachiphyllum Kerp (Callipterid Foliage): Review of Palaeobotany and Palynology, v. 54, p. 249-360.

Kerp, J.H.F., Poort, R.J., Swinkels, H.A.J.M., and Verwer, R., 1990, Aspects of Permian Palaeobotany and Palynology. IX. Conifer-dominated Rotliegend floras from the Saar-Nahe basin (? Late carboniferous-early permian; SW-Germany) with special reference to the reproductive biology of early conifers: Review of Palaeobotany and Palynology, v. 62, p. 205-248.

Kershaw, P., and Wagstaff, B., 2001, The southern conifer family Araucariaceae: History, status, and value for paleoenvironmental reconstruction: Annual Review of Ecology and Systematics, v. 32, p. 397-414.

Klaus, W., 1963, Sporen aus dem südalpinen Perm, Jahrbuch Geologische Bundesanstalt Austria.

Kramer, K.U., and Green, P.S., 1990, The Families and Genera of Vascular Plants:Pteridophytes and Gymnosperms, Springer, 404 p.

Krassilov, V., 1972, Mesozoic flora of the Bureya River. Ginkgoales and Czekanowskiales: Moscow, Akad. Nauk SSSR Izd. Nauk (in Russian).

Krassilov, V.A., 1977, Contributions to The Knowledge of Caytoniales: Review of Palaeobotany and Palynology, v. 24, p. 155-178.

—, 2009, Diversity of Mesozoic Gnetophytes and the First Angiosperms: Paleontological Journal, v. 43, p. 1272-1280.

Krassilov, V.A., Afonin, S.A., and Naugolnykh, S.V., 1999, Permotheca with in situ pollen grains from the Lower Permian of the Urals: Palaeobotanist, v. 49(1), p. 19-25.

Krassilov, V.A., and Zakharov, Y.D., 1975, Pleuromeia from the lower triassic of the far east of the U.S.S.R: Review of Palaeobotany and Palynology, v. 19, p. 221-232.

Kremp, G.O.W., and Ames, H.T., 1959, Catalog of fossil spores and pollen Volume 5: Cretaceous spores, University Park, Pennsylvania.

—, 1961a, Catalog of fossil spores and pollen Volume 13: Carboniferous and Permian Spores, University Park, Pennsylvania.

—, 1961b, Catalog of fossil spores and pollen Volume 14: Mesozoic and Tertiary Spores and Pollen, University Park, Pennsylvania.

—, 1962a, Catalog of fossil spores and pollen Volume 15: Tertiary and Cretaceous Spores and Pollen, University Park, Pennsylvania.

—, 1962b, Catalog of fossil spores and pollen Volume 16: Mesozoic and Lower Tertiary Spores and Pollen University Park, Pennsylvania.

—, 1965a, Catalog of fossil spores and pollen Volume 23: Spores and Pollen of the Upper Cretaceous and Cretaceous-Tertiary Boundary University Park, Pennsylvania.

—, 1965b, Catalog of fossil spores and pollen Volume 24: Mesozoic Spores and Pollen University Park, Pennsylvania.

Kremp, G.O.W., Ames, H.T., and Grebe, H., 1957a, Catalog of fossil spores and pollen Volume 1: Cretaceous and Tertiary Spores and Pollen, University Park, Pennsylvania, 182 p.

—, 1957b, Catalog of fossil spores and pollen Volume 2: Mesozoic and Tertiary Spores and Pollen, University Park, Pennsylvania.

Kremp, G.O.W., Ames, H.T., and Kovar, A.J., 1958, Catalog of fossil spores and pollen Volume 4: Cretaceous and Tertiary spores and pollen, University Park, Pennsylvania.

—, 1959, Catalog of fossil spores and pollen Volume 8: Cretaceous spores and Pollen, University Park, Pennsylvania.

—, 1960a, Catalog of fossil spores and pollen Volume 9: Triassic and Jurassic spores and pollen, University Park, Pennsylvania.

—, 1960b, Catalog of fossil spores and pollen Volume 10: Jurassic and Cretaceous Spores and Pollen, University Park, Pennsylvania.

Kremp, G.O.W., Spackman, W., and Ames, H.T., 1966, Catalog of fossil spores and pollen Volume 25: Mesozoic and Tertiary Spores and Pollen, University Park, Pennsylvania.

Kremp, G.O.W., Spackman, W., Traverse, A., and Ames, H.T., 1967, Catalog of fossil spores and pollen Volume 26: Permian-Triassic Transition and Mesozoic Spores and Pollen University Park, Pennsylvania.

—, 1968, Catalog of fossil spores and pollen Volume 28: Mesozoic Megaspores, Microspores and Pollen University Park, Pennsylvania.

Krings, M., Klavins, S.D., DiMichele, W.A., Kerp, H., and Taylor, T.N., 2005, Epidermal anatomy of Glenopteris splendens Sellards nov emend., an enigmatic seed plant from the Lower Permian of Kansas (USA): Review of Palaeobotany and Palynology, v. 136, p. 159-180.

Kurmann, M.H., 1991, Pollen Ultrastructure in Elatides-Williamsonii (Taxodiaceae) from the Jurassic of North Yorkshire: Review of Palaeobotany and Palynology, v. 69, p. 291-298.

Kustatscher, E., Hemsley, A., and Van Konijnenburg-van Cittert, J.H.A., 2009, Lugardonia paradoxa gen. et sp nov., a new strobilus from the Anisian flora of Kuhwiesenkopf, the Dolomites, Italy and its affinities with emphasis on spore ultrastructure: Review of Palaeobotany and Palynology, v. 156, p. 90-97.

Kustatscher, E., Kelber, K.P., and van Konijnenburg-van Cittert, J.H.A., 2012, Danaeopsis Heer ex Schimper 1869 and its European Triassic species: Review of Palaeobotany and Palynology, v. 183, p. 32-49.

Kvacek, J., Daskova, J., and Renata, P., 2006, A new schizaeaceous fern, Schizaeopsis ekrtii sp nov., and its in situ spores from the Upper Cretaceous (Cenomanian) of the Czech Republic: Review of Palaeobotany and Palynology, v. 140, p. 51-60.

Kvacek, J., and Pacltova, B., 2001, Bayeritheca hughesii gen. et sp nov., a new Eucommiidites-bearing pollen organ from the Cenomanian of Bohemia: Cretaceous Research, v. 22, p. 695-704.

Labiak, P.H., Mickel, J.T., and Hanks, J.G., 2015, Molecular phylogeny and character evolution of Anemiaceae (Schizaeales): Taxon, v. 64, p. 1141-1158.

Leslie, A.B., Herendeen, P.S., and Crane, P.R., 2009, Upatoia barnardii gen. et sp nov., an araucarian pollen cone with in situ pollen from the Late Cretaceous (Santonian) of Georgia, USA: Grana, v. 48, p. 128-135.

Li, L.Q., and Wang, Y.D., 2016, Late Triassic palynofloras in the Sichuan Basin, South China: Synthesis and perspective: Palaeoworld, v. 25, p. 212-238.

Li, L.Q., Wang, Y.D., Liu, Z.S., Zhou, N., and Wang, Y., 2016, Late Triassic palaeoclimate and palaeoecosystem variations inferred by palynological record in the northeastern Sichuan Basin, China: Palaeontologische Zeitschrift, v. 90, p. 327-348.

Li, T., Cao, H., Kang, M., Zhang, Z., Zhao, N., and Zhang, H., 2011, Pollen Flora of China Woody Plants by SEM, Science Press (in chinese), 1233 p.

Li, W.B., and Batten, D.J., 1986, The Early Cretaceous Megaspore Arcellites and Closely Associated Crybelosporites Microspores from Northeast Inner-Mongolia, Pr China: Review of Palaeobotany and Palynology, v. 46, p. 189-208.

Litwin, R.J., 1985, Fertile Organs and In situ Spores of Ferns from the Late Triassic Chinle Formation of Arizona and New-Mexico, with Discussion of the Associated Dispersed Spores: Review of Palaeobotany and Palynology, v. 44, p. 101-146.

Liu, Z., 2003, Palaeontologia Sinica:Triassic and Jurassic Sporopollen Assemblages from the Kuqa Depression, Tarim Basin of Xinjiang, NW China: Beijing, Science Press (in chinese), 244 p.

Liu, Z.H., Li, C.S., and Hilton, J., 2001, Fertile pinnules of Danaeites rigida Gu and Zhi (Marattiales) from the Upper Permian of South China: Botanical Journal of the Linnean Society, v. 136, p. 107-117.

Lugardon, B., Grauvogel-Stamm, L., and Dobruskina, I., 1999, The microspores of Pleuromeia rossica Neuburg (Lycopsida; Triassic): comparative ultrastructure and phylogenetic implications: Comptes Rendus De L Academie Des Sciences Serie Ii Fascicule a-Sciences De La Terre Et Des Planetes, v. 329, p. 435-442.

—, 2000, Comparative ultrastructure of the megaspores of the Triassic lycopsid Pleuromeia rossica Neuburg: Comptes Rendus De L Academie Des Sciences Serie Ii Fascicule a-Sciences De La Terre Et Des Planetes, v. 330, p. 501-508.

Lupia, R., Schneider, H., Moeser, G.M., Pryer, K.M., and Crane, P.R., 2000, Marsileaceae sporocarps and spores from the Late Cretaceous of Georgia, USA: International Journal of Plant Sciences, v. 161, p. 975-988.

Mander, L., Collinson, M.E., Chaloner, W.G., Brain, A.P.R., and Long, D.G., 2012, The Ultrastructure and Botanical Affinity of the Problematic Mid-Mesozoic Palynomorph Ricciisporites Tuberculatus Lundblad: International Journal of Plant Sciences, v. 173, p. 429-440.

McKellar, J.L., 1974, Jurassic miospores from the upper Evergreen Formation, Hutton Sandstone and basal Injune Creek Group, north-eastern Surat Basin, Geological Survey of Queensland.

McLoughlin, S., Pott, C., and Sobbe, I.H., 2018, The diversity of Australian Mesozoic bennettitopsid reproductive organs: Palaeobiodiversity and Palaeoenvironments, v. 98, p. 71-95.

Mendes, M.M., Barron, E., Batten, D.J., and Pais, J., 2017, A new species of the spore genus Costatoperforosporites from Early Cretaceous deposits in Portugal and its taxonomic and palaeoenvironmental significance: Grana, v. 56, p. 401-409.

Mendes, M.M., Friis, E.M., and Pais, J., 2008, Erdtmanispermum juncalense sp nov., a new species of the extinct order Erdtmanithecales from the Early Cretaceous (probably Berriasian) of Portugal: Review of Palaeobotany and Palynology, v. 149, p. 50-56.

Mendes, M.M., Pais, J., Pedersen, K.R., and Friis, E.M., 2010, Erdtmanitheca portucalensis, a new pollen organ from the Early Cretaceous (Aptian-Albian) of Portugal with Eucommiidites-type pollen: Grana, v. 49, p. 26-36.

Meyen, S.V., 1984, Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record: The Botanical Review, v. 50, p. 1.

—, 1997, Permian conifers of Western Angaraland: Review of Palaeobotany and Palynology, v. 96, p. 351-447.

Mickel, J.T., 1982, The Genus Anemia (Schizaeaceae) in Mexico: Brittonia, v. 34, p. 388-413.

Mohr, B.A.R., Bernardes-de-Oliveira, M.E.C., Loveridge, R., Pons, D., Sucerquia, P.A., and Castro-Fernandes, M.C., 2015, Ruffordia goeppertii (Schizaeales, Anemiaceae) - A common fern from the Lower Cretaceous Crato Formation of northeast Brazil: Cretaceous Research, v. 54, p. 17-26.

Moisan, P., and Voigt, S., 2013, Lycopsids from the Madygen Lagerstatte (Middle to Late Triassic, Kyrgyzstan, Central Asia): Review of Palaeobotany and Palynology, v. 192, p. 42-64.

Moller, M., Mill, R.R., Glidewell, S.M., Masson, D., Williamson, B., and Bateman, R.M., 2000, Comparative biology of the pollination mechanisms in Acmopyle pancheri and Phyllocladus hypophyllus (Podocarpaceae s. l.): Annals of Botany, v. 86, p. 149-158.

Morbelli, M.A., 1990, Austral South-American Jurassic Megaspores: Review of Palaeobotany and Palynology, v. 65, p. 209-216.

Mueller, S., Krystyn, L., and Kurschner, W.M., 2016, Climate variability during the Carnian Pluvial Phase - A quantitative palynological study of the Carnian sedimentary succession at Lunz am See, Northern Calcareous Alps, Austria: Palaeogeography Palaeoclimatology Palaeoecology, v. 441, p. 198-211.

Muller, J., 1981, Fossil Pollen Records of Extant Angiosperms: Botanical Review, v. 47, p. 1-&.

Naugolnykh, S.V., 2009, A new fertile Neocalamites from the Upper Permian of Russia and equisetophyte evolution: Geobios, v. 42, p. 513-523.

—, 2012, Vetlugospermum and Vetlugospermaceae: A new genus and family of peltasperms from the Lower Triassic of Moscow syneclise (Russia): Geobios, v. 45, p. 451-462.

—, 2013a, The heterosporous lycopodiophyte Pleuromeia rossica Neuburg, 1960 from the Lower Triassic of the Volga River basin (Russia): organography and reconstruction according to the 'Whole-Plant' concept: Wulfenia, v. 20, p. 1-16.

—, 2013b, New male reproductive organs of gymnosperms Permotheca colovratica sp nov from the Lower Permian of the Ural Mountains: Paleontological Journal, v. 47, p. 114-126.

—, 2014, A new genus of male cones of voltzialean affinity, Uralostrobus voltzioides nov. gen., nov. sp., from the Lower Permian of the Urals (Russia): Geobios, v. 47, p. 315-324.

Naugolnykh, S.V., and Kerp, H., 1996, Aspects of Permian palaeobotany and palynology. XV. On the oldest known peltasperms with radially symmetrical ovuliferous discs from the Kungurian (uppermost Lower Permian) of the Fore-Urals (Russia): Review of Palaeobotany and Palynology, v. 91, p. 35-62.

Nemejc, F., and Pacltova, B., 1972, Hepaticae in the senonian of South Bohemia: Palaeobotanist, v. 21(1), p. 23-26.

Norris, G., 1965, Triassic and Jurassic miospores and acritarchs from the Beacon and Ferrar groups, Victoria land, Antarctica: New Zealand Journal of Geology and Geophysics, v. 8, p. 236-277.

Nowak, M.D., and Lupia, R., 2005, Reinvestigation of Ariadnaesporites varius Hall and Peake, 1968 emend. Hall, 1975: Review of Palaeobotany and Palynology, v. 135, p. 41-59.

Osborn, J.M., 1994, The morphology and ultrastructure of Caytonanthus: Canadian Journal of Botany, v. 72, p. 1519-1527.

Osborn, J.M., and Taylor, T.N., 1993, Pollen Morphology and Ultrastructure of the Corystospermales - Permineralized in-Situ Grains from the Triassic of Antarctica: Review of Palaeobotany and Palynology, v. 79, p. 205-219.

—, 1995, Pollen Morphology and Ultrastructure of the Bennettitales - in-Situ Pollen of Cycadeoidea: American Journal of Botany, v. 82, p. 1074-1081.

Pacyna, G., Barbacka, M., Zdebska, D., Ziaja, J., Fijalkowska-Mader, A., Boka, K., and Sulej, T., 2017, A new conifer from the Upper Triassic of southern Poland linking the advanced voltzialean type of ovuliferous scale with Brachyphyllum-Pagiophyllum-like leaves: Review of Palaeobotany and Palynology, v. 245, p. 28-54.

Pattemore, G.A., and Rozefelds, A.C., 2019, Palissya – absolutely incomprehensible or surprisingly interpretable: a new morphological model, affiliations and phylogenetic insights: Acta Palaeobotanica, v. 59, p. 181-214.

Pedersen, K.R., Crane, P.R., and Friis, E.M., 1989, Pollen Organs and Seeds with Eucommiidites Pollen: Grana, v. 28, p. 279-294.

Pedersen, K.R., Friis, E.M., and Crane, P.R., 1993, Pollen Organs and Seeds with Decussosporites Brenner from Lower Cretaceous Potomac Group Sediments of Eastern USA: Grana, v. 32, p. 273-289.

Pigg, K.B., and Rothwell, G.W., 1983, Megagametophyte Development in the Chaloneriaceae Fam. Nov., Permineralized Paleozoic Isoetales (Lycopsida): Botanical Gazette, v. 144, p. 295-302.

Pocknall, D.T., 1981a, Pollen Morphology of the New-Zealand Species of Libocedrus Endlicher (Cupressaceae) and Agathis Salisbury (Araucariaceae): New Zealand Journal of Botany, v. 19, p. 267-272.

—, 1981b, Pollen morphology of the New Zealand species of Dacrydium Selander, Podocarpus L'Heritier, and Dacrycarpus Endlicher (Podocarpaceae): New Zealand Journal of Botany, v. 19, p. 67-95.

Pocock, S.A.J., Vasanthy, G., and Venkatachala, B.S., 1990, Pollen of Circumpolles - an Enigma or Morphotrends Showing Evolutionary Adaptation: Review of Palaeobotany and Palynology, v. 65, p. 179-193.

Poort, R.J., and Kerp, J.H.F., 1990, Aspects of Permian palaeobotany and palynology. XI. On the recognition of true peltasperms in the Upper Permian of Western and Central Europe and a reclassification of species formerly included in Peltaspermum Harris: Review of Palaeobotany and Palynology, v. 63, p. 197-225.

Popa, M., 2019, Review of the bennettitalean genus Weltrichia: Journal of Palaeogeography-English, v. 8.

Popescu, S.M., Krijgsman, W., Suc, J.P., Clauzon, G., Marunteanu, M., and Nica, T., 2006, Pollen record and integrated high-resolution chronology of the early Pliocene Dacic Basin (southwestern Romania): Palaeogeography Palaeoclimatology Palaeoecology, v. 238, p. 78-90.

Potonié, R., 1956, Synopsis der Gattungen der Sporae dispersae I.Teil:Sporites, Hannover : Amt für Bodenforschung, 103 p.

—, 1958, Synopsis der Gattungen der Sporae dispersae II.Teil:Sporites (Nachtraege), Saccites, Aletes, Preacolpates, Polyplicates, Monocolpates: Hannover, Amt für Bodenforschung, 114 p.

—, 1960, Synopsis der Gattungen der Sporae dispersae III.Teil:Naechtrage Sporites, Forstetzung Pollenites Mit Generalregister zu Teil I-III: Hannover, Amt für Bodenforschung, 189 p.

—, 1966, Synopsis der Gattungen der Sporae dispersae IV. Teil: Nachtraege zu allen gruppen(Turmae): Hannover, Amt für Bodenforschung, 244 p.

—, 1967a, New phylogenetic facts on fossil spores: Review of Palaeobotany and Palynology, v. 1, p. 75-82.

—, 1967b, Versuch der Einordnung der fossilen Sporae dispersae in das phylogenetische System der Pflanzenfamilien: Köln, Westdeutscher Verlag, 310 p.

—, 1970, Synopsis der Gattungen der Sporae dispersae V.Teil:Nachtraege zu allen gruppen(Turmae): Hannover, Amt für Bodenforschung, 156 p.

Potonié, R., 1967, Versuch der Einordnung der fossilen Sporae dispersae in das phylogenetische System der Pflanzenfamilien: Köln, Westdeutscher Verlag, 310 p.

Potonié, R., and Kremp, G.O.W., 1970, Synopsis der Gattungen der Sporae dispersae VI. Teil: Hannover, Amt für Bodenforschung, 76 p.

Potonié, R., and Schweitzer, H.J., 1960, Der Pollen von Ullmannia frumentaria: Paläontologische Zeitschrift, v. 34, p. 27-39.

Pott, C., and McLoughlin, S., 2014, Divaricate growth habit in Williamsoniaceae (Bennettitales): unravelling the ecology of a key Mesozoic plant group: Palaeobiodiversity and Palaeoenvironments, v. 94, p. 307-325.

Povilauskas, L., 2012, Palynology of the Monte Chico formation (late cretaceous) from Santa Cruz Province, Argentina: Pollen of gymnosperms: Revista Brasileira de Paleontologia v. 15, p. 85-94.

Puebla, G.G., Pramparo, M.B., and Gandolfo, M.A., 2015, Aquatic ferns from the Upper Cretaceous Loncoche Formation, Mendoza, central-western, Argentina: Plant Systematics and Evolution, v. 301, p. 577-588.

Punt, W., Hoen, P.P., Blackmore, S., Nilsson, S., and Le Thomas, A., 2007, Glossary of pollen and spore terminology: Review of Palaeobotany and Palynology, v. 143, p. 1-81.

Qian, C., and Chen, H., 2006, Flora of China, Volume 2, Science Press (in chinese), 406 p.

Rattanamanee, S., and Chantanaorrapint, S., 2015, Note on Notothylas yunannensis (Notothyladaceae, Anthocerotophyta), a little known species of hornwort: Songklanakarin Journal of Science and Technology (SJST), v. 37, p. 271-274.

Rees, P.M., 1993, Caytoniales in Early Jurassic Floras from Antarctica: Geobios, v. 26, p. 33-42.

Retallack, G., 1975, The life and times of a Triassic lycopod: Alcheringa, v. 1, p. 3-29.

Roghi, G., Gianolla, P., Minarelli, L., Pilati, C., and Preto, N., 2010, Palynological correlation of Carnian humid pulses throughout western Tethys: Palaeogeography Palaeoclimatology Palaeoecology, v. 290, p. 89-106.

Rossler, R., and Buschmann, B., 1994, Some Herbaceous Lycopods from the Westphalian-D of Germany: Review of Palaeobotany and Palynology, v. 80, p. 259-275.

Rothwell, G.W., Mapes, G., Hilton, J., and Hollingworth, N.T., 2007, Pollen cone anatomy of Classostrobus crossii sp nov (Cheirolepidiaceae): International Journal of Coal Geology, v. 69, p. 55-67.

Rothwell, G.W., and Stockey, R.A., 1994, The Role of Hydropteris pinnata gen. et. sp. nov. in Reconstructing the Cladistics of Heterosporous Ferns: American Journal of Botany, v. 81, p. 479-492.

Rydin, C., and Friis, E.M., 2005, Pollen germination in Welwitschia mirabilis Hook. f.: differences between the polyplicate pollen producing genera of the Gnetales: Grana, v. 44, p. 137-141.

Saxena, R.K., and Trivedi, G.K., 2009, Palynological investigation of the Kopili Formation (Late Eocene) in North Cachar Hills, Assam, India: Acta Palaeobotanica, v. 49, p. 253-277.

Scafati, L., Melendi, D.L., and Volkheimer, W., 2009, A Danian subtropical lacustrine palynobiota from South America (Bororo Formation, San Jorge Basin, Patagonia - Argentina): Geologica Acta, v. 7, p. 35-61.

Scheuring, B.W., 1974, On the type material of Accinctisporites Leschik, Succinctisporites Leschik, Rimaesporites Leschik and Sahnisporites Bharadwaj: Review of Palaeobotany and Palynology, v. 17, p. 205-216.

Schimper, A.F.W., 1898, Pflanzen-geographie auf physiologischer Grundlage: Jena, Verlag von Gustav Fischer, 876 p.

Schrank, E., 2010, Pollen and spores from the Tendaguru Beds, Upper Jurassic and Lower Cretaceous of southeast Tanzania: palynostratigraphical and paleoecological implications: Palynology, v. 34, p. 3-42.

—, 2017, Palynology of the Albian Makhtesh Qatan site, northern Negev (Israel), with descriptions of two new pollen species: Review of Palaeobotany and Palynology, v. 246, p. 185-215.

Schuettpelz, E., Schneider, H., Smith, A.R., Hovenkamp, P., Prado, J., Rouhan, G., Salino, A., Sundue, M., Almeida, T.E., Parris, B., Sessa, E.B., Field, A.R., de Gasper, A.L., Rothfels, C.J., Windham, M.D., Lehnert, M., Dauphin, B., Ebihara, A., Lehtonen, S., Schwartsburd, P.B., Metzgar, J., Zhang, L.B., Kuo, L.Y., Brownsey, P.J., Kato, M., Arana, M.D., Assis, F.C., Barker, M.S., Barrington, D.S., Chang, H.M., Chang, Y.H., Chao, Y.S., Chen, C.W., Chen, D.K., Chiou, W.L., Dittrich, V.A.D., Duan, Y.F., Dubuisson, J.Y., Farrar, D.R., Fawcett, S., Galan, J.M.G.Y., Goes-Neto, L.A.D., Grant, J.R., Grusz, A.L., Haufler, C., Hauk, W., He, H., Hennequin, S., Hirai, R.Y., Huiet, L., Kessler, M., Korall, P., Labiak, P.H., Larsson, A., Leon, B., Li, C.X., Li, F.W., Link-Perez, M., Liu, H.M., Lu, N.T., Meza-Torres, E.I., Miao, X.Y., Moran, R., Mynssen, C.M., Nagalingum, N., Ollgaard, B., Paul, A.M., Pereira, J.B.D., Perrie, L.R., Ponce, M., Ranker, T.A., Schulz, C., Shinohara, W., Shmakov, A., Sigel, E.M., de Souza, F.S., Sylvestre, L.D., Testo, W., Triana-Moreno, L.A., Tsutsumi, C., Tuomisto, H., Valdespino, I.A., Vasco, A., Viveros, R.S., Weakley, A., Wei, R., Weststrand, S., Wolf, P.G., Yatskievych, G., Xu, X.G., Yan, Y.H., Zhang, L., Zhang, X.C., Zhou, X.M., and Grp, P.P., 2016, A community-derived classification for extant lycophytes and ferns: Journal of Systematics and Evolution, v. 54, p. 563-603.

Schwendemann, A.B., Wang, G., Mertz, M.L., McWilliams, R.T., Thatcher, S.L., and Osborn, J.A., 2007, Aerodynamics of saccate pollen and its implications for wind pollination: American Journal of Botany, v. 94, p. 1371-1381.

Scott, A.C., and Playford, G., 1985, Early Triassic Megaspores from the Rewan Group, Bowen Basin, Queensland: Alcheringa, v. 9, p. 297-323.

Serbet, R., and Stockey, R.A., 1991, Taxodiaceous Pollen Cones from the Upper Cretaceous (Horseshoe Canyon Formation) of Drumheller, Alberta, Canada: Review of Palaeobotany and Palynology, v. 70, p. 67-76.

Seyfullah, L.J., Kustatscher, E., and Taylor, W.A., 2013, The first discovery of in situ Verrucosisporites applanatus spores from the Middle Triassic flora from Bromsgrove (Worcestershire, UK): Review of Palaeobotany and Palynology, v. 197, p. 15-25.

Shang, Y., 2011, Palaeontologia Sinica:Late Triassic Palynology of Yunnan and Guizhou, China: Beijing, Science Press (in chinese), 363 p.

Sheremetov, R.T., and Sheremetova, S.A., 2017, The effect of the hydrothermal conditions of the Tom River Basin on the ecological structure of flora: Contemporary Problems of Ecology, v. 10, p. 119-130.

Shu, O.Y., and Norris, G., 1988, Spores and Pollen from the Lower Triassic Heshanggou Formation, Shaanxi Province, North China: Review of Palaeobotany and Palynology, v. 54, p. 187-231.

—, 1999, Earliest Triassic (Induan) spores and pollen from the Junggar Basin, Xinjiang, northwestern China: Review of Palaeobotany and Palynology, v. 106, p. 1-56.

Shuklina, A.S., and Polevova, S.V., 2007, Spores in situ and problems of the classification of Mesozoic tree ferns: Paleontological Journal, v. 41, p. 312-318.

Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H., and Wolf, P.G., 2006, A classification for extant ferns: Taxon, v. 55, p. 705-731.

Söderström, L., Hagborg, A., von Konrat, M., Bartholomew-Began, S., Bell, D., Briscoe, L., Brown, E., Cargill, D.C., Costa, D.P., Crandall-Stotler, B.J., Cooper, E.D., Dauphin, G., Engel, J.J., Feldberg, K., Glenny, D., Gradstein, S.R., He, X., Heinrichs, J., Hentschel, J., Ilkiu-Borges, A.L., Katagiri, T., Konstantinova, N.A., Larraín, J., Long, D.G., Nebel, M., Pócs, T., Puche, F., Reiner-Drehwald, E., Renner, M.A.M., Sass-Gyarmati, A., Schäfer-Verwimp, A., Moragues, J.G.S., Stotler, R.E., Sukkharak, P., Thiers, B.M., Uribe, J., Váňa, J., Villarreal, J.C., Wigginton, M., Zhang, L., and Zhu, R.-L., 2016, World checklist of hornworts and liverworts: PhytoKeys, p. 1-828.

Song, Z., Wang, Y., Liu, Z., Huang, B., Wang, J., Qian, L., Du, B., and Zhang, D., 1999, Fossil Spores and Pollen of China:The Late Cretaceous and Tertiary Spores and Pollen: Beijing, Science Press (in chinese), 910 p.

—, 2000, Fossil Spores and Pollen of China: The Mesozoic Spores and Pollen: Beijing, Science Press (in chinese), 710 p.

Song, Z.C., Wang, W.M., and Huang, F., 2004, Fossil pollen records of extant angiosperms in China: Botanical Review, v. 70, p. 425-458.

Specht, R.L., Dettmann, M.E., and Jarzen, D.M., 1992, Community Associations and Structure in the Late Cretaceous Vegetation of Southeast Australasia and Antarctica: Palaeogeography Palaeoclimatology Palaeoecology, v. 94, p. 283-309.

Srivastava, S.K., 1971, Systematic Revision of Genus Styx Norton Et Hall, 1967: Review of Palaeobotany and Palynology, v. 11, p. 297-+.

—, 1987, Jurassic Spore-Pollen Assemblages from Normandy (France) and Germany: Geobios, v. 20, p. 5-79.

—, 1994, Evolution of Cretaceous Phytogeoprovinces, Continents and Climates: Review of Palaeobotany and Palynology, v. 82, p. 197-224.

Steart, D.C., Spencer, A.R.T., Garwood, R.J., Hilton, J., Munt, M.C., Needham, J., and Kenrick, P., 2014, X-ray Synchrotron Microtomography of a silicified Jurassic Cheirolepidiaceae (Conifer) cone: histology and morphology of Pararaucaria collinsonae sp nov.: Peerj, v. 2, p. 1-29.

Suc, J.P., and Fauquette, S., 2012, The use of pollen floras as a tool to estimate palaeoaltitude of mountains: The eastern Pyrenees in the Late Neogene, a case study: Palaeogeography Palaeoclimatology Palaeoecology, v. 321, p. 41-54.

Sun, K., Cui, J., and Wang, S., 2010, Fossil Flora of China (vol 2): Fossil Pteridophytyes in China, Higher Education Press (in chinese), 438 p.

Taylor, E.L., and Taylor, T.N., 2006, Mesozoic seed ferns: Old paradigms, new discoveries: Journal of the Torrey Botanical Society, v. 133, p. 62-82.

—, 2009, Seed Ferns from the Late Paleozoic and Mesozoic: Any Angiosperm Ancestors Lurking There?: American Journal of Botany, v. 96, p. 237-251.

Taylor, E.L., Taylor, T.N., Kerp, H., and Hermsen, E.I., 2006, Mesozoic seed ferns: Old paradigms, new discoveries: Journal of the Torrey Botanical Society, v. 133, p. 62-82.

Taylor, E.L., Taylor, T.N., and Krings, M., 2009, Paleobotany:The Biology and Evolution of Fossil Plants: London, Academic Press, 1252 p.

Taylor, T.N., 1973, A consideration of the morphology, ultrastructure and multicellular microgametophyte of Cycadeoidea dacotensis pollen: Review of Palaeobotany and Palynology, v. 16, p. 157-164.

Taylor, T.N., Cichan, M.A., and Baldoni, A.M., 1984, The Ultrastructure of Mesozoic Pollen - Pteruchus dubius (Thomas) Townrow: Review of Palaeobotany and Palynology, v. 41, p. 319-327.

Taylor, T.N., and Grauvogel-Stamm, L., 1995, The Ultrastructure of Voltzialean Pollen: Review of Palaeobotany and Palynology, v. 84, p. 281-303.

Tekleva, M., 2016, Pollen morphology and ultrastructure of several Gnetum species: an electron microscopic study: Plant Systematics and Evolution, v. 302, p. 291-303.

Tekleva, M.V., and Krassilov, V.A., 2009, Comparative pollen morphology and ultrastructure of modern and fossil gnetophytes: Review of Palaeobotany and Palynology, v. 156, p. 130-138.

Tekleva, M.V., Polevova, S.V., and Zavialova, N.E., 2007, On some peculiarities of sporoderm structure in members of the Cycadales and Ginkgoales: Paleontological Journal, v. 41, p. 1162-1178.

Tekleva, M.V., and Roghi, G., 2018, Lagenella martini from the Triassic of Austria – Exine structure and relationships with other striate palynomorphs: Review of Palaeobotany and Palynology, v. 258, p. 13-21.

Thomas, H.H., and Seward, A.C., 1925, VI. The caytoniales, a new group of angiospermous plants from the Jurassic Rocks of Yorkshire: Philosophical Transactions of the Royal Society of London. Series B, Containing Papers of a Biological Character, v. 213, p. 299-363.

Townrow, J.A., 1962, On Some Disaccate Pollen Grains of Permian to Middle Jurassic Age: Grana, v. 3, p. 13-44.

Traverse, A., 2007, Paleopalynology Second Edition: The Netherlands, Springer, 813 p.

Traverse, A., and Ames, H.T., 1968, Catalog of fossil spores and pollen Volume 29: Mesozoic and Cenozoic Spores, Pollen and Other Microfossils University Park, Pennsylvania.

—, 1969, Catalog of fossil spores and pollen Volume 30: Mesozoic and Cenozoic Spores and Pollen University Park, Pennsylvania.

—, 1971, Catalog of fossil spores and pollen Volume 33: Cretaceous Pollen and Spores University Park, Pennsylvania.

—, 1972, Catalog of fossil spores and pollen Volume 35: Permian Pollen and Spores, University Park, Pennsylvania.

—, 1979, Catalog of fossil spores and pollen Volume 41: Late Cretaceous and Early Tertiary Spores and Pollen from the U.S.A. and the U.S.S.R., University Park, Pennsylvania.

Traverse, A., Ames, H.T., and Spackman, W., 1973a, Catalog of fossil spores and pollen Volume 36: Cretaceous Pollen and Spores University Park, Pennsylvania.

—, 1973b, Catalog of fossil spores and pollen Volume 37: Paleozoic Megaspores and Miospores, University Park, Pennsylvania.

—, 1974, Catalog of fossil spores and pollen Volume 38: Mesozoic Pollen and Spores, University Park, Pennsylvania.

—, 1975, Catalog of fossil spores and pollen Volume 39: Mesozoic Pollen and Spores, University Park, Pennsylvania.

Traverse, A., Spackman, W., and Ames, H.T., 1969, Catalog of fossil spores and pollen Volume 31: Mesozoic and Cenozoic Spores and Pollen University Park, Pennsylvania.

Tryon, A.F., and Lugardon, B., 1991, Spores of the Pteridophyta, Springer, 648 p.

Uhl, D., Abu Hamad, A., Kerp, H., and Bandel, K., 2007, Evidence for palaeo-wildfire in the Late Permian palaeotropics - charcoalified wood from the Um Irna Formation of Jordan: Review of Palaeobotany and Palynology, v. 144, p. 221-230.

Vakhrameev, V.A., 1987, Climates and the distribution of some gymsosperms in Asia during the Jurassic and Cretaceous: Review of Palaeobotany and Palynology, v. 51, p. 205-212.

—, 1991, Jurassic and Cretaceous Floras and Climates of the Earth: Cambridge, Cambridge University Press, 318 p.

Van der Eem, J.G.L.A., 1983, Aspects of Middle and Late Triassic Palynology .6. Palynological Investigations in the Ladinian and Lower Karnian of the Western Dolomites, Italy: Review of Palaeobotany and Palynology, v. 39, p. 189-300.

van Konijnenburg-van Cittert, J.H.A., 1971, In Situ Gymnosperm Pollen from Middle Jurassic of Yorkshire: Acta Botanica Neerlandica, v. 20, p. 1-&.

—, 1978, Osmundaceous Spores In situ from Jurassic of Yorkshire, England: Review of Palaeobotany and Palynology, v. 26, p. 125-141.

—, 1981, Schizaeaceous Spores In situ from the Jurassic of Yorkshire, England: Review of Palaeobotany and Palynology, v. 33, p. 169-181.

—, 1989, Dicksoniaceous Spores In situ from the Jurassic of Yorkshire, England: Review of Palaeobotany and Palynology, v. 61, p. 273-301.

—, 1992, An Enigmatic Liassic Microsporophyll, Yielding Ephedripites Pollen: Review of Palaeobotany and Palynology, v. 71, p. 239-254.

—, 2002, Ecology of some Late Triassic to Early Cretaceous ferns in Eurasia: Review of Palaeobotany and Palynology, v. 119, p. 113-124.

van Konijnenburg-van Cittert, J.H.A., Kustatscher, E., Pott, C., Dutsch, G., and Schmeissner, S., 2017, First record of the pollen-bearing reproductive organ Hydropterangium from the Rhaetian of Germany (Wustenwelsberg, Upper Franconia): Neues Jahrbuch Fur Geologie Und Palaontologie-Abhandlungen, v. 284, p. 139-151.

Van Konijnenburg-van Cittert, J.H.A., Pott, C., Schmeißner, S., Dütsch, G., and Kustatscher, E., 2021, The Rhaetian flora of Wüstenwelsberg, Bavaria, Germany: Description of selected gymnosperms (Ginkgoales, Cycadales, Coniferales) together with an ecological assessment of the locally prevailing vegetation: Review of Palaeobotany and Palynology, v. 288, p. 104398.

Veisberg, E.I., 2017, Species structure of plant groupings in the shallow coastal zone of piedmont lake Bolshoe Miassovo (Southern Urals): Inland Water Biology, v. 10, p. 275-285.

Verma, P.K., Rawat, K.K., and Kumar, R., 2014, Anthoceros subtilis Steph: A Rare Disjunct Species, New to North East India from Brahmaputra Valley: Proceedings of the National Academy of Sciences, India Section B: Biological Sciences, v. 84, p. 811-813.

Villarreal, J.C., Cargill, C., Söderström, L., Hagborg, A., and Konrat, M.v., 2015, Notes on Early Land Plants Today. 70. Nomenclatural notes in hornworts (Anthocerotophyta): Phytotaxa, v. 208, p. 92-96.

Visscher, H., and van der Zwan, C.J., 1981, Palynology of the circum-mediterranean triassic: Phytogeographical and palaeoclimatological implications: Geologische Rundschau, v. 70, p. 625-634.

Vitt, D.H., and Hamilton, C.D., 1974, A scanning electron microscope study of the spores and selected peristomes of the North American Encalyptaceae (Musci): Canadian Journal of Botany, v. 52, p. 1973-1981.

Volkheimer, W., and Scafati, L., 2007, Palynology of a Danian warm climatic wetland in Central Northern Patagonia, Argentina: Revista española de micropaleontología, v. 39, p. 117-134.

Wan, M.L., Zhou, W.M., He, X.Z., Liu, L.J., and Wang, J., 2016, A typical Euramerican floral element from the Shanxi Formation (Cisuralian, lower Permian) in the Wuda Coal Field, Inner Mongolia, North China: Palaeobiodiversity and Palaeoenvironments, v. 96, p. 507-515.

Wan, Z.H., and Basinger, J.F., 1992, On the Fern Pectinangium Li Et-Al, Emend (Marattiales), with Spores Insitu from the Permian of Southern China: Review of Palaeobotany and Palynology, v. 75, p. 219-238.

Wang, C.S., Feng, Z.G., Zhang, L.M., Huang, Y.J., Cao, K., Wang, P.J., and Zhao, B., 2013, Cretaceous paleogeography and paleoclimate and the setting of SKI borehole sites in Songliao Basin, northeast China: Palaeogeography Palaeoclimatology Palaeoecology, v. 385, p. 17-30.

Wang, Q., and Dai, X., 2010, Spores of Polypodiales (Filicales) from China, Science Press (in chinese), 262 p.

Wang, Y.-D., Ni, Q., Jiang, Z.-K., and Tian, N., 2008, Diversity variation and tempo-spatial distribution of Otozamites (Bennettitales) in the Mesozoic of China: Palaeoworld, v. 17, p. 222-234.

Wang, Y.D., 1999a, Fertile organs and in situ spores of Marattia asiatica (Kawasaki) Harris (Marattiales) from the Lower Jurassic Hsiangchi Formation in Hubei, China: Review of Palaeobotany and Palynology, v. 107, p. 125-144.

Wang, Y.D., Mosbrugger, V., and Zhang, H., 2005, Early to Middle Jurassic vegetation and climatic events in the Qaidam Basin, northwest China: Palaeogeography Palaeoclimatology Palaeoecology, v. 224, p. 200-216.

Wang, Y.D., Yang, X.J., Guignard, G., Deng, S.H., Tian, N., and Jiang, Z.K., 2009, The fossil Gleicheniaceous ferns of China: Biodiversity, systematics, spore ultrastructure and evolution: Review of Palaeobotany and Palynology, v. 156, p. 139-156.

Wang, Z., 2012, A bizarre Palissya ovulate organ from Upper Triassic strata of the Zixing coal field, Hunan Province, China: Science Bulletin, v. 57, p. 1169-1177.

Wang, Z.Q., 1999b, Gigantonoclea: An enigmatic Permian plant from North China: Palaeontology, v. 42, p. 329-373.

Wang, Z.Q., and Wang, L.X., 1982, A New Species of the Lycopsid Pleuromeia from the Early Triassic of Shanxi, China, and Its Ecology: Palaeontology, v. 25, p. 215-225.

Wang, Z.X., Sun, F.K., Jin, P.H., Chen, Y.Q., Chen, J.W., Deng, P., Yang, G.L., and Sun, B.N.A., 2017, A New Species of Ginkgo with Male Cones and Pollen Grains in situ from the Middle Jurassic of Eastern Xinjiang, China: Acta Geologica Sinica-English Edition, v. 91, p. 9-21.

Warming, E., 1895, Plantesamfund - Grundtræk af den økologiske Plantegeografi, Clarendon Press, Oxford, 335 p.

Warny, S., Jarzen, D.M., Evans, A., Hesp, P., and Bart, P., 2012, Environmental significance of abundant and diverse hornwort spores in a potential submerged Paleoindian site in the Gulf of Mexico: Palynology, v. 36, p. 234-253.

Wetschnig, W., and Depisch, B., 1999, Pollination biology of Welwitschia mirabilis HOOK. f. (Welwitschiaceae, Gnetopsida): Phyton-Annales Rei Botanicae, v. 39, p. 167-183.

White, J.M., Jessop, C.M., Scotese, C.R., Lai, G., and da Roza, R.J., 2009, Depicting Biostratigraphical Data from Palynodata: Experiments and Questions in Data Presentation and Manipulation: Palynology, v. 33, p. 157-174.

Wilde, V., and Hemsley, A.R., 2000, Morphology, ultrastructure and affinity of barremian (lower cretaceous) megaspores dijkstraisporites and paxillitriletes from Brilonnehden, Germany: Palynology, v. 24, p. 217-230.

Worobiec, E., 2009, Middle Miocene palynoflora of the Legnica lignite deposit complex, Lower Silesia, Poland: Acta Palaeobotanica, v. 49, p. 5-133.

Yang, G.X., Sheng, A.X., and Wang, H.S., 1997, A new species: Szea (Cladophlebis) henanense sp nov in Henan Province and its evolutional significance: Chinese Science Bulletin, v. 42, p. 1023-1028.

Yang, X.J., 2008, A male cone of Pseudofrenelopsis dalatzensis with in situ pollen grains from the Lower Cretaceous of Northeast China: Geobios, v. 41, p. 689-698.

Yang, Z.P., Gao, J.X., Zhao, L., Xu, X.L., and Ouyang, H., 2013, Linking thaw depth with soil moisture and plant community composition: effects of permafrost degradation on alpine ecosystems on the Qinghai-Tibet Plateau: Plant and Soil, v. 367, p. 687-700.

Yao, Z.Q., and Taylor, T.N., 1988, On a New Gleicheniaceous Fern from the Permian of South China: Review of Palaeobotany and Palynology, v. 54, p. 121-134.

Yurtsev, B.A., 2001, The Pleistocene "Tundra-Steppe" and the productivity paradox: the landscape approach: Quaternary Science Reviews, v. 20, p. 165-174.

Zavada, M.S., 1990, The ultrastructure of three monosulcate pollen grains from the triassic chinle formation, western United States Palynology, v. 14, p. 41-51.

Zavada, M.S., and Crepet, W.L., 1986, Pollen Grain Wall Structure of Caytonanthus-Arberi (Caytoniales): Plant Systematics and Evolution, v. 153, p. 259-264.

Zavialova, N., Buratti, N., and Roghi, G., 2010, The ultrastructure of some Rhaetian Circumpolles from southern England: Grana, v. 49, p. 281-299.

Zavialova, N., Gordenko, N., Nosova, N., and Polevova, S., 2014, The fine morphology of pollen grains from the pollen chamber of a supposed ginkgoalean seed from the Middle Jurassic of Uzbekistan (Angren locality): Plant Systematics and Evolution, v. 300, p. 1995-2008.

Zavialova, N., and Karasev, E., 2015, Exine ultrastructure of in situ Protohaploxypinus from a Permian peltasperm pollen organ, Russian Platform: Review of Palaeobotany and Palynology, v. 213, p. 27-41.

Zavialova, N., Markevich, V., Bugdaeva, E., and Polevova, S., 2011, The ultrastructure of fossil dispersed monosulcate pollen from the Early Cretaceous of Transbaikalia, Russia: Grana, v. 50, p. 182-201.

Zavialova, N., and van Konijnenburg-van Cittert, J.H.A., 2011, Exine ultrastructure of in situ peltasperm pollen from the Rhaetian of Germany and its implications: Review of Palaeobotany and Palynology, v. 168, p. 7-20.

—, 2012, Exine ultrastructure of in situ pollen from the cycadalean cone Androstrobus prisma Thomas et Harris 1960 from the Jurassic of England: Review of Palaeobotany and Palynology, v. 173, p. 15-22.

—, 2016, Exine ultrastructure of in situ pollen from the cycadalean cone Androstrobus manis Harris, 1941 from the Jurassic of England: Review of Palaeobotany and Palynology, v. 225, p. 33-42.

Zavialova, N.E., and Gomankov, A.V., 2009, Occurrence of angiosperm-like ultrastructural features in gymnosperm pollen from the Permian of Russia: Review of Palaeobotany and Palynology, v. 156, p. 79-89.

Zavialova, N.E., and Roghi, G., 2005, Exine morphology and ultrastructure of Duplicisporites from the Triassic of Italy: Grana, v. 44, p. 337-342.

Zavialova, N.E., Tekleva, M.V., Polevova, S.V., and Bogdanov, A.G., 2018, Electron microscopy for morphology of pollen and spores: Moscow:, RIPOL Classic Press, 334 p.

Zeng, J., and Huo, C., 2004, Flora of China, Volume 6(3), Science Press (in chinese), 313 p.

Zetter, R., Farabee, M.J., Pigg, K.B., Manchester, S.R., DeVore, M.L., and Nowak, M.D., 2011, Palynoflora of the late Paleocene silicified shale at Almont, North Dakota, USA: Palynology, v. 35, p. 179-211.

Zhang, J., Lenz, O.K., Hornung, J., Wang, P., Ebert, M., and Hinderer, M., 2020, Palynology and the Eco-Plant model of peat-forming wetlands of the Upper Triassic Haojiagou Formation in the Junggar Basin, Xinjiang, NW China: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 556, p. 109888.

Zhang, J., Lenz, O.K., Wang, P., Gao, Y., and Hornung, J., 2021a, Database-based Eco-Plant analysis for Mesozoic dispersed sporomorphs: MethodsX, v. 8, p. 101329.

Zhang, J., Lenz, O.K., Wang, P., and Hornung, J., 2021b, The Eco-Plant model and its implication on Mesozoic dispersed sporomorphs for Bryophytes, Pteridophytes, and Gymnosperms: Review of Palaeobotany and Palynology, v. 293, p. 104503.

Zhang, Y., Wu, P., Wang, C., Jia, Y., Luo, J., and Lin, B., 2006, Spore Morphology of Chinese Bryophytes: Qingdao, Qindao Press (in chinese), 339 p.

Zhao, J., Wan, X.Q., Xi, D.P., Jing, X., Li, W., Huang, Q.H., and Zhang, J.Y., 2014, Late Cretaceous palynology and paleoclimate change: Evidence from the SK1 (South) core, Songliao Basin, NE China: Science China-Earth Sciences, v. 57, p. 2985-2997.

Zhao, Y., Lu, Y.Z., Shang, P., Deng, S.H., and Wang, X.L., 2018, An amended species, Nilssoniopteris neimenguensis nom. nov., from the Lower Jurassic of the Xilinhot Basin, Inner Mongolia, northern China, with a reexamination of Nilssoniopteris species: Review of Palaeobotany and Palynology, v. 255, p. 22-34.

Zhou, Z.-Y., 2009, An overview of fossil Ginkgoales: Palaeoworld, v. 18, p. 1-22.

Appendix

Appendix 3-1 Uncertain dispersed spores and pollen

A. Uncertain Pteridophytes

The following 249 dispersed spore genera can not be linked to any specific extant or fossil plants:

Acanthosporis Mädler, ***Agastospora*** Zhang, ***Anemiidites*** Ross, ***Anulatizonites*** Mädler, ***Apicrassizonosporites*** Kedves & Rákosy, ***Apiculatisporis*** Potonié & Kremp, ***Asbeckiasporites*** Brelie, ***Auritulina*** Malyavkina, ***Baculareticulosporis*** Singh, Srivastava & Roy, ***Baculatitriletes*** Brelie, ***Baldurnisporites*** Delcourt & Sprumont, ***Biglobosisporites*** Döring, ***Bocciaspora*** Eem, ***Boseisporites*** Bharadwaj & Kumar, ***Bothriotriletes*** Fuglewicz, ***Bracteolina*** Malyavkina, ***Bucculina*** Malyavkina, ***Bulbella*** Malyavkina, ***Bullasporis*** Krutzsch, ***Buttinia*** Boltenhagen, ***Caliendrina*** Malyavkina, ***Callispora*** (Sukh) Bharadwaj et Kumar, ***Camarozonotriletes*** Naumova, ***Camerozonosporites*** Pant ex Potonié, ***Cardioangulina*** Malyavkina emend. Potonié, ***Cardiocolliculina*** Malyavkina, ***Cardiolina*** Malyavkina, ***Cardiosectella*** Malyavkina, ***Catenulasporites*** Zhang, ***Cingulatisporites*** Thomson, ***Cingulatizonites*** Mädler, ***Cingutriletes*** Pierce emend. Dettmann, ***Cladophlebites*** Malyavkina, ***Clavatosporis*** Song et Zhang, ***Colliculina*** Malyavkina, ***Compactisporites*** Lu & Wang, ***Conbaculatisporites*** Klaus, ***Concavisporites*** (Pflug) Delcourt & Sprumont, ***Concavitriletes*** Krutzsch, ***Conipollenites*** Cameron, ***Converrucosisporites*** Potonié & Kremp, ***Corculina*** Malyavkina, ***Corollisporites*** Lu & Wang, ***Coronatispora*** Dettmann, ***Cosmosporites*** Nilsson, ***Crassimonoletes*** Singh, Srivastava & Roy, ***Craterisporites*** de Jersey, ***Cyclina*** Malyavkina, ***Cyclinasporites*** Nilsson, ***Cyclosporites*** Cookson & Dettmann, ***Cyclotriletes*** Mädler, ***Cycloverrutriletes*** Schulz, ***Cymbellina*** Malyavkina, ***Datongsporites*** Liu, ***Deltoidisporites*** Danzé-Corsin & Laveine, ***Deltoidospora*** (Miner) Potonié, ***Didecitriletes*** Venkatachala & Kar, ***Dipteridaceaeauritulina*** Malyavkina, ***Distaverrusporites*** Muller, ***Divaricina*** Malyavkina, ***Dongbeispora*** Pu et Wu, ***Dulhuntyispora*** (Potonié) Balme et Hennelly, ***Duplosporis*** Pflug, ***Echinatisporites*** Krutzsch, ***Echizonospora*** Bai, ***Equisetacites*** Malyavkina, ***Equisetosporites*** (Daugherty) Singh, ***Exinella*** Malyavkina, ***Filtrotriletes*** van Hoecken-Klinkenberg, ***Flabellisporites*** Marcinkiewicz, ***Foveoinaperturites*** Pierce, ***Foveolatisporites*** Bhardwaj, ***Foveotriletes*** Hammen ex Potonié, ***Gemmatriletes*** (Hammen) Pierce, ***Glabrina*** Malyavkina, ***Globulisporis*** Mädler, ***Gradisporites*** Döring, ***Granulatisporites*** (Ibrahim) Potonié & Kremp, ***Granulatosporites*** (Imgrund) Dybová & Jachowicz, ***Grebespora*** Jansonius, ***Gordonispora*** van der Eem, ***Guangdongspora*** Song, Li et Zhong, ***Gushanispora*** Li, ***Guttatisporites*** Visscher, ***Gyrina*** Malyavkina, ***Gyrinella*** Malyavkina, ***Habrozonosporites*** Lu et Wang, ***Halosphaeropsis*** Mädler, ***Hekousporites*** Yu, Zhang, Zhao et Song, ***Hsuisporites*** Zhang, ***Hunanispora*** Shang, ***Hymenoreticulisporites*** Döring, ***Hystrichosporis*** Pacltová, ***Ingentosporites*** Busnardo et Taugourdeau, ***Intertriletes*** Anderson, ***Interulobites*** Phillips, ***Intrapunctatosporis*** Krutzsch, ***Intrapunctosporis*** Krutzsch, ***Ischyosporites*** Balme, ***Jerseyiaspora*** Kar, Kieser & Jain, ***Keuperisporites*** Schulz, ***Krutzschisporites*** Kedves, ***Laevigatosporites*** Ibrahim, ***Laevizonosporites*** Döring, ***Lapposisporites*** Visscher, ***Leiotriletes*** (Naumova) Potonie & Kremp, ***Leschikisporis*** Potonié, ***Levisporites*** Ilina, ***Liaoxisporis*** Pu et Wu, ***Limatulasporites*** Helby et Foster, ***Lobosporites*** Nilsson, ***Lunzisporites*** Bharadwaj & Singh, ***Lygodiumidites*** Malyavkina, ***Maculatasporites*** Tiwari, ***Maexisporites*** Potonié, ***Matthesisporites*** Döring, ***Medullina*** Malyavkina, ***Mesozoicisporites*** Schulz, ***Mitraesporites*** Zhang, ***Monoleiotriletes*** Krutzsch, ***Monoletella*** Malyavkina, ***Monolites*** Cookson ex Potonié, ***Muerrigerisporis*** Krutzsch, ***Murospora*** Somers, ***Narkisporites*** Kannegieser & Kozur, ***Neotuberculatisporites*** Zhang, ***Obtusisporis*** (Krutzsch) Pocock, ***Occultosporites*** Khlonova, ***Ocultosporites*** Chlonova, ***Orbella*** Malyavkina, ***Orbipatella*** Malyavkina, ***Orientalisporites*** Zhang, ***Ornatisporites*** Nagy, ***Otynisporites*** Fuglewicz, ***Palaeospongisporis*** Schulz, ***Papillotriletes*** Mädler, ***Paraconcavisporites*** Klaus, ***Paradoxisporites*** Huang, ***Paraklukisporites*** Mädler, ***Paralundbladispora*** Visscher, ***Partina*** Malyavkina, ***Patellisporites*** Ouyang, ***Perinosporites*** Schulz, ***Periplecotriletes*** Naumova, ***Peromonoletes*** Couper, ***Peromonolites*** Couper, ***Placulina*** Malyavkina, ***Polaneuletes*** Marcinkiewicz, ***Politusella*** Malyavkina, ***Pollinaria*** Malyavkina, ***Polypodiaceoisporites*** Potonié, ***Polypodiacites*** Malyavkina, ***Polypodiumidites*** Malyavkina, ***Poroplanites*** Pflug, ***Prikaspisporites*** Kozur, ***Propterisispora*** Ouyang & Li, ***Psilamonoletes*** Hammen, ***Pterina*** Malyavkina, ***Pterinella*** Malyavkina, ***Pterosphaeridia*** Mädler, ***Punctatosporites*** Ibrahim, ***Punctatriletes*** Pierce, ***Pusulosporites*** Fuglewicz,

Pyramidella (Malyavkina) Potonié, ***Radialisporis*** Krutzsch, ***Radiorugoisporites*** Zhang, ***Radisporis*** Bai, ***Reticuloidisporites*** Busnardo et Taugourdeau, ***Reticuloidosporites*** Pflug, ***Retioulatisporites*** Brenner, ***Retiverrucispora*** Liu, ***Rogalskaisporites*** Danzé-Corsin & Laveine, ***Rotinella*** Malyavkina, ***Rotverrusporites*** Döring, ***Rugospora*** Neves & Owens, ***Rugutriletes*** (Hammen) Potonié, ***Sagittella*** Malyavkina, ***Santanghusporites*** Huang et Xu, ***Scabratriletes*** Hammen ex Potonié, ***Schizoplanites*** Pflug, ***Scortea*** Chlonova, ***Seductisporites*** Chlonova, ***Sellaspora*** Eem, ***Semisporis*** Pflug, ***Seritriletes*** Zhang, ***Sexaneuletes*** (Fuglewicz)Marcinkiewicz, ***Simozonotriletes*** (Naumova) Potonié et Kremp, ***Simplicesporites*** Leschik, ***Skarbysporites*** Erve, ***Sphaerina*** (Malyavkina) Delcourt et Sprumont, ***Sphaerinella*** Malyavkina, ***Spinotriletes*** Mädler, ***Spongiosisporis*** Krutzsch, ***Sporopollenites*** (Erdtman) Thiergart, ***Stellisporites*** Alpern, ***Stenozonotriletes*** Naumova, ***Stoverisporites*** Norvick & Burger, ***Stratexinis*** Stach, ***Striatisporis*** Krutzsch, ***Striatisporites*** Leschik, ***Striatizonites*** Mädler, ***Striatriletes*** Hammen ex Potonié, ***Styxisporites*** Cookson & Dettmann, ***Tabellina*** Malyavkina, ***Talchirella*** Pant & Srivastava, ***Tappanispora*** Srivastava, ***Tenerina*** Krutzsch, ***Tenuicontactosporites*** (Han) Yu et Han, ***Thiergartisporis*** Mädler, ***Thomsonisporites*** Leschik, ***Thuringiatrilites*** Schulz, ***Tigrisporites*** Klaus, ***Toripustulatisporites*** Krutzsch, ***Trachysporites*** Nilsson, ***Trachytriletes*** Naumova, ***Transbaculisporites*** Döring, ***Triancoraesporites*** Schulz, ***Triangulina*** Malyavkina, ***Triaristella*** Malyavkina, ***Triassisporis*** Schulz, ***Trichomanidites*** Malyavkina, ***Triletes*** (Erdtman) Potonié, ***Trilites*** Cookson ex Couper, ***Trilobozonosporites*** (Pant) Potonié, ***Tripartites*** (Schemel) Potonié et Kremp, ***Triplanosporites*** Pflug, ***Trizonatisporites*** Leschik, ***Trizonites*** Mädler, ***Tuberculatosporites*** Imgrund, ***Tuberella*** Malyavkina, ***Tumulispora*** Staplin & Jansonius, ***Tympanea*** Malyavkina, ***Umbosporites*** Newman, ***Undulatisporites*** Pflug, ***Undulatosporites*** Leschik, ***Undulipollis*** Krutzsch, ***Vallizonosporites*** Döring, ***Velamensporites*** Brelie, ***Velatisporites*** Döring, ***Verexinis*** Stach, ***Verreticulisporis*** Krutzsch, ***Verrucatotriletes*** van Hoeken-Klinkenberg, ***Verrucingulatisporites*** Kedves, ***Verrucosisporites*** (Ibrahim) Potonie & Kremp, ***Viburamegaspora*** Zhang, ***Volucellina*** Malyavkina, ***Waltzispora*** Staplin, ***Wulongspora*** Yu et Zhang, and ***Zlivispors*** Pacltova ex Gupta.

B. Uncertain Gymnospermae

The following 138 dispersed pollen genera can not be linked to any specific extant or fossil plant:

Abieticedripites Malyavkina, ***Acuminella*** Malyavkina, ***Aggerella*** Malyavkina, ***Aggerotsugella*** Malyavkina, ***Aliferina*** Malyavkina, ***Alisporites*** (Daugherty) Jansonius, ***Aumancisporites*** Alpern, ***Bactrosporites*** Chen, ***Ballosporites*** Mädler, ***Bascanisporites*** Balme & Hennelly, ***Bennettiteaepollenites*** (Thiergart ex Potonie) Pocock, ***Bhardwajispora*** Jansonius, ***Bialina*** Malyavkina, ***Brachysaccus*** Mädler, ***Bullulina*** Malyavkina, ***Chasmatosporites*** (Nilsson) Pocock et Jansonius, ***Circellina*** Malyavkina, ***Conaletes*** Reinhardt et Schön, ***Concentrisporites*** Wall, ***Confertisulcites*** Anderson, ***Confusopollis*** Pflug, ***Corollaria*** Malyavkina, ***Crassipollenites*** Nilsson, ***Cristatisaccus*** Mädler, ***Curvimonocolpites*** Leidelmeyer, ***Cycadaceaeplatychila*** Malyavkina, ***Cycadopites*** (Wodehouse) Wilson & Webster, ***Cyclosaccus*** Mädler, ***Dacryrotundina*** Malyavkina, ***Dilaterella*** Malyavkina, ***Diplosacculina*** Malyavkina, ***Dipterella*** Malyavkina, ***Disaccites*** Cookson, ***Divisiella*** Malyavkina, ***Entylissa*** (Naumova) Potonié, ***Exiguisporites*** Leschik, ***Extremella*** Malyavkina, ***Falcina*** Malyavkina, ***Falcisporites*** (Leschik) Klaus, ***Ginkgoacites*** Malyavkina, ***Ginkgoidites*** Malyavkina, ***Granamegamonocolpites*** Jain, ***Granamultivesiculites*** Pierce, ***Granosaccus*** Mädler, ***Granulatasporites*** Leschik, ***Guizhoupollis*** Shang, ***Gynkaletes*** Luber, ***Gynkgaletes*** Luber, ***Haojiagoupollenites*** Huang, ***Haploaliferina*** Luber, ***Haplosacculina*** Malyavkina, ***Heliosaccus*** Mädler, ***Inaperturopollenites*** Pflug & Thomson, ***Involutella*** Malyavkina, ***Juniperidites*** Malyavkina, ***Jurea*** Malyavkina, ***Klausipollenites*** Jansonius, ***Laevigatasporites*** (Potonié & Gelletich) Ibrahim, ***Latosaccus*** Mädler, ***Limbatella*** Malyavkina, ***Lorisporites*** Leschik, ***Megamonoporites*** Jain, ***Minutosaccus*** Mädler, ***Monoptycha*** Khlonova, ***Monosulcites*** Cookson ex Couper, ***Naumovaspora*** Jansonius, ***Navisulcites*** Anderson, ***Oblatinella*** Malyavkina, ***Orbicularia*** Malyavkina, ***Pachytella*** Malyavkina, ***Paleoconiferus*** Bolkhovitina, ***Paleopicea*** Bolkhovitina, ***Panucella*** Malyavkina, ***Panucellina*** Malyavkina, ***Paravesicaspora*** Klaus, ***Perotrilites*** (Erdtman) Couper, ***Piceidites*** Malyavkina, ***Piceites*** Bolchovitina, ***Pinites*** Bolchovitina, ***Pinojella*** Malyavkina, ***Pityopollenites*** Reissinger, ***Pityosporites*** (Seward) Manum, ***Platychila*** Malyavkina, ***Platylimbina*** Malyavkina, ***Podocarpacites*** Malyavkina, ***Pododipterella*** Malyavkina, ***Protabies*** Bolchovitina, ***Protoconifera*** Khlonova, ***Protopicea*** Bolchovitina, ***Prototaeniaesporites*** Zhang, ***Pseudillinites*** Mädler, ***Pseudopicea*** Bolchovitina, ***Pseudopinus*** Bolchovitina [?], ***Pseudoplicatella*** Malyavkina, ***Pseudopodocarpus*** Bolchovitina, ***Psilainaperturites*** Pierce, ***Psophosphaera*** Naumova, ***Punctabivesiculites*** Pierce, ***Punctainaperturites*** Pierce, ***Punctamonocolpites*** Pierce, ***Punctamultivesiculites*** Pierce, ***Quadraeculina*** Maljavkina, ***Rectosulcites*** Anderson, ***Renopollis*** Yu et Miao, ***Retectina*** Malyavkina, ***Retibivesiculites*** Pierce, ***Rimaesporites***

Leschik, ***Rotundina*** Malyavkina, ***Ruguinaperturites*** Pierce, ***Saccopollis*** Pflug, ***Sacculina*** Malyavkina, ***Saeptasporites*** Leschik, ***Samaropollenites*** Goubin, ***Schismatosporites*** Nilsson, ***Schizosaccus*** Mädler, ***Scutrina*** Malyavkina, ***Shanbeipollenites*** Qian et Wu, ***Sinuella*** Malyavkina, ***Spheripollenites*** Couper, ***Spinainaperturites*** Pierce, ***Spirellina*** Malyavkina, ***Sulcusicystis*** Bai, ***Tenuisaccites*** de Jersey, ***Tetrasaccus*** Pant ex Maithy, ***Triangulisaccus*** Ouyang et Li, ***Trisphaerea*** Malyavkina, ***Trizonaesporites*** Leschik, ***Tubermonocolpites*** Qu, ***Umbrososaccus*** Mädler, ***Utricellina*** Malyavkina, ***Velosporites*** Hughes & Playford, ***Ventosella*** Malyavkina, ***Verrumonocolpites*** Pierce, ***Verrumonoporites*** Pierce, ***Verrusaccus*** Schulz, ***Walchiites*** Bolchovitina, ***Wulanpollenites*** Li, and ***Zonalasporites*** Leschik.

Appendix 4-1 The PHP code for the user interface

```
/*
This part includes the PHP code for the user interface.
All the explanations are in orange. All the functional codes are in black.
*/

$URL="TheProcessAddress";//This is the website address where the processing code is stored.
echo("<form id='drawplot' lang='en' target='_blank' name='drawplot' method='post' action='$URL'>");
echo("<input id='speciescombinationlist' name='speciescombinationlist' type='file' lang='en'
value='open'></input>");
echo("  <select id='enenvironmenttype' name='enenvironmenttype'>");
          echo("<option value='plant_family'>Vegetation Family</option>");
          echo("<option value='plant_order'>Vegetation Order</option>");
          echo("<option value='plant_phylum'>Vegetation Phylum</option>");
          echo("<option value='humidity'>Eco-Plant EPH</option>");
          echo("<option value='temperature'>Eco-Plant EPT</option>");
          echo("<option value='plant_family_pdf'>Vegetation Family PDF</option>");
          echo("<option value='plant_order_pdf'>Vegetation Order PDF</option>");
          echo("<option value='plant_phylum_pdf'>Vegetation Phylum PDF</option>");
          echo("<option value='humidity_pdf'>Eco-Plant EPH PDF</option>");
          echo("<option value='temperature_pdf'>Eco-Plant EPT PDF</option>");
          echo("<option value='drawcurve_pdf'>Draw Curve PDF</option>");
echo("</select>");
echo(" <input type='submit' value='Submit'></input>");
echo("</form>");
```

Appendix 4-2 The PHP and MySQL codes for different modes processing the uploaded dataset.

```
/*
This part includes the main functions of linking the user uploaded dataset with the datasets in this database and
giving the result in a dataset or diagram.
All the explanations are in orange. All the functional codes are in black.
As this database is designed for both Chinese and English users, some Chinese characters are shown in the
codes.
*/
//Open MySQL database
$_DB=F_NetConnect();
if ($_DB==false){
  return(false);
}
$outcropname=addslashes(trim($_POST["outcropname"]));
$enenvironmenttype=addslashes(trim($_POST["enenvironmenttype"]));
//Read the user-uploaded dataset
$fileobjectname="speciescombinationlist";
$ifwith0=false;
if ($enenvironmenttype=="drawcurve_pdf"){
  $tablename=loadtcsvfile($fileobjectname,"","",true);
```

```
}else{
  $tablename=loadtcsvfile($fileobjectname,"abundance,genus,sample","",true);
}
//If reading the uploaded dataset is false, exit
if ($tablename==false){
        exit();
}
if($enenvironmenttype!="drawcurve_pdf"){
  //Delete data that is not necessary
  $query="delete from $tablename where genus is null or sample is null or genus=" or sample="";
  $result=mysql_query($query);
  $query="delete from $tablename where  abundance is null or abundance=0 or abundance="";
  $result=mysql_query($query);
  $query="select genus from $tablename";
  $result=mysql_query($query);
  $num=mysql_num_rows($result);
  if ($num==0){
          echo("<br>错误! 您输入的数据表中没有有效的数据!!");
          echo("<br>Error! There is no useful data in your uploaded dataset!!<br>");
  }
  //Transfer the uploaded numbers in to percentage.
                           //Count the number of samples
  $query="select sample,sum(abundance) from $tablename group by sample order by sample";
  $result=mysql_query($query);
  $line=mysql_fetch_row($result);
  $numlist="";
  while ($line!=false){
                  if ($numlist==""){
                          $numlist="$line[1]";
                          $lastSample="$line[0]";
                  }else{
                          $numlist=$numlist.",$line[1]";
                  }
                 //next
                 $line=mysql_fetch_row($result);
  }
  $arrNum=explode(",",$numlist);
                           //Transfer percentage
  $query2="select sample,genus,sum(abundance) from $tablename group by sample,genus order by
sample,genus";
  $result2=mysql_query($query2);
  $num2=mysql_num_rows($result2);
  $valuelist="";
  if ($num2>0){
          $line2=mysql_fetch_row($result2);
          $n=0;
          $kk=1;
          while ($line2!=false){
                          if ($lastSample!=$line2[0]){
                                  $lastSample=$line2[0];
                                  $n=$n+1;
                          }
                           if ($arrNum[$n]=="0"){
                                   $abundance=0;
                           }else{
```

```
                                        $abundance=round((1000*$line2[2]) / $arrNum[$n])/10;
                                }
                                if ($valuelist==""){
                                        $valuelist="('$line2[0]','$line2[1]','$abundance')";
                                }else{
                                        $valuelist=$valuelist.",('$line2[0]','$line2[1]','$abundance')";
                                }
                                //next
                                $line2=mysql_fetch_row($result2);
                                $kk=$kk+1;
                }
  }
  $query2="delete from $tablename";
  $result2=mysql_query($query2);
  $tablenameK=$tablename;
  $tablename=randletter().$tablename;
  $tablename=strtolower($tablename);
  createtemptable($tablename,$querystring="",$idfield="PID",$noneidfieldlist="sample,genus,abundance");
  $query2="insert into $tablename(sample,genus,abundance) values $valuelist";
  $result2=mysql_query($query2);
  //Calculate percentage
  $sumtablename="sum".$tablename;
  createtemptable($sumtablename,$querystring="select sample,genus,sum(abundance) as sumabundance from
$tablename group by sample,genus order by sample,genus",$idfield="",$noneidfieldlist="");
  //create genera list
  $allgenustablename="allgenus".$tablename;
  createtemptable($allgenustablename,$querystring="select distinct genus from $tablename order by
genus",$idfield="",$noneidfieldlist="");
}
//Certify analysis mode
if (empty($enenvironmenttype)==true){
 //exit if without useful data
 echo("<script type='text/javascript'>window.location.href='../index.php';</script>" );
 exit();
}
if (stripos($enenvironmenttype,"_pdf")>0){
  $ifdrawPDF=true;
}else{
  $ifdrawPDF=false;
}
if ($enenvironmenttype=="plant_family" or $enenvironmenttype=="plant_family_pdf"){
  if (stripos($enenvironmenttype,"_pdf")==0){
            echo("Vegetation Family 植被科<br>");
  }
  $datatablename=$sumtablename;
  $proxytable="taxonomy";
  $proxycolumn="family";
  $withoutgenustablename="withoutg".$tablename;
  $usefulgenustablename="useg".$tablename;
  $resulttablename="result".$tablename;
reconstructsegs($datatablename,$proxytable,$proxycolumn,$withoutgenustablename,$usefulgenustablename,$r
esulttablename,$allgenustablename,$ifdrawPDF);
}else if ($enenvironmenttype=="plant_order" or $enenvironmenttype=="plant_order_pdf"){
  if (stripos($enenvironmenttype,"_pdf")==0){
           echo("Vegetation Order 植被目<br>");
```

```
  }
  $datatablename=$sumtablename;
  $proxytable="taxonomy";
  $proxycolumn="orders";
  $withoutgenustablename="withoutg".$tablename;
  $usefulgenustablename="useg".$tablename;
  $resulttablename="result".$tablename;
reconstructsegs($datatablename,$proxytable,$proxycolumn,$withoutgenustablename,$usefulgenustablename,$resulttablename,$allgenustablename,$ifdrawPDF);
}else if ($enenvironmenttype=="plant_phylum" or $enenvironmenttype=="plant_phylum_pdf"){
  if (stripos($enenvironmenttype,"_pdf")==0){
          echo("Vegetation Phylum 植被门<br>");
  }
  $datatablename=$sumtablename;
  $proxytable="taxonomy";
  $proxycolumn="phylum";
  $withoutgenustablename="withoutg".$tablename;
  $usefulgenustablename="useg".$tablename;
  $resulttablename="result".$tablename;
reconstructsegs($datatablename,$proxytable,$proxycolumn,$withoutgenustablename,$usefulgenustablename,$resulttablename,$allgenustablename,$ifdrawPDF);
}else if ($enenvironmenttype=="humidity" or $enenvironmenttype=="humidity_pdf"){
  if (stripos($enenvironmenttype,"_pdf")==0){
          echo("Eco-Plant EPH 湿度<br>");
  }
  $datatablename=$sumtablename;
  $proxytable="humidity";
  $proxycolumn="humidity";
  $proxytable="taxonomy";
  $proxycolumn="ephs";
  $withoutgenustablename="withoutg".$tablename;
  $usefulgenustablename="useg".$tablename;
  $resulttablename="result".$tablename;
reconstructsegs($datatablename,$proxytable,$proxycolumn,$withoutgenustablename,$usefulgenustablename,$resulttablename,$allgenustablename,$ifdrawPDF);
}else if ($enenvironmenttype=="temperature" or $enenvironmenttype=="temperature_pdf"){
  if (stripos($enenvironmenttype,"_pdf")==0){
          echo("Eco-Plant EPT 温度<br>");
  }
  $datatablename=$sumtablename;
  $proxytable="temperature";
  $proxycolumn="temperature";
  $proxytable="taxonomy";
  $proxycolumn="ept";
  $withoutgenustablename="withoutg".$tablename;
  $usefulgenustablename="useg".$tablename;
  $resulttablename="result".$tablename;

reconstructsegs($datatablename,$proxytable,$proxycolumn,$withoutgenustablename,$usefulgenustablename,$resulttablename,$allgenustablename,$ifdrawPDF);
}else if ($enenvironmenttype=="sealevel"){
  if (stripos($enenvironmenttype,"_pdf")==0){
          echo("Sea level 海平面<br>");
  }
  $datatablename=$sumtablename;
```

```
  $proxytable="ecogroup";
  $proxycolumn="ecogroup";
  $withoutgenustablename="withoutg".$tablename;
  $usefulgenustablename="useg".$tablename;
  $resulttablename="result".$tablename;
reconstructsegs($datatablename,$proxytable,$proxycolumn,$withoutgenustablename,$usefulgenustablename,$r
esulttablename,$allgenustablename,$ifdrawPDF);
}else if ($enenvironmenttype=="plant_type"){
  if (stripos($enenvironmenttype,"_pdf")==0){
          echo("Vegetation Type 植被类型<br>");
  }
  $datatablename=$sumtablename;
  $proxytable="genusplanttype";
  $proxycolumn="planttype";
  $withoutgenustablename="withoutg".$tablename;
  $usefulgenustablename="useg".$tablename;
  $resulttablename="result".$tablename;
reconstructsegs($datatablename,$proxytable,$proxycolumn,$withoutgenustablename,$usefulgenustablename,$r
esulttablename,$allgenustablename,$ifdrawPDF);
}else if ($enenvironmenttype=="drawcurve_pdf"){
  $samplefieldname="sample";
  if (table_fieldindex($tablename,$samplefieldname)<0){
          $samplefieldname="Sample";
          if (table_fieldindex($tablename,$samplefieldname)<0){
                  echo("<br>The Sample field is missing!<br>Sample 列缺失!");
          }
  }
  $DepthFieldName="depth";
  if (table_fieldindex($tablename,$DepthFieldName)<0){
          $DepthFieldName="Depth";
          if (table_fieldindex($tablename,$DepthFieldName)<0){
                  $DepthFieldName="ID";
                  if (table_fieldindex($tablename,$DepthFieldName)<0){
                          $DepthFieldName="id";
                  }
          }
  }
  DrawPollenCollumnPDF($tablename,$samplefieldname,$DepthFieldName);
}
function F_NetConnect($_说明_联接不成功返回 false 成功返回数据库联接标签=""){
                 //This function is to connect the MySQL database;
                 $_netConnect = mysql_connect(C_NI, C_NU, C_NP) ;
                 if ($_netConnect ==false) {
                         return($_netConnect);
                 }
                 // Connect database
                 $_DBConnect =mysql_select_db(C_ND) ;
                 if ($_DBConnect ==false) {
                         mysql_close($_netConnect);
                         return($_DBConnect);
                 }
                 //设置数据库字体这一步非常重要,否则会出现乱码
                 mysql_query("set names utf8");
                 //返回值
                 return($_netConnect);
```

```
}
function loadtcsvfile($csvobjectname,$fieldmustinclude="", $newtablename="",$iftemptable=false){
            //说明 $csvobjectname 被上传文件在表单中的名称
            //说明 $fieldmustinclude 被上传文中必须包含的列加逗号分隔,如果为空说明所有类型都可以, 如
果被上传文件不满足要求则返回 false 函数结束
            //说明 $newtablename 被上传文件被上传后的表名称,如果为空则为: 随机数组+IP+随机字母+时
间 构成
            //说明 $iftemptable 文件上传后是否形成临时文件, 是值为 true,不是值为 false,默认值为 false.
            //说明 函数调用不成功返回 false,调用成功返回新生成表名.
            //打开数据库
            $_DB=F_NetConnect();
            if ($_DB==false){
                     if (Language=="简体中文"){
                               echo("信息:数据库无法打开!!!");
                     }else{
                               echo("信息:database can not be open!!!");
                     }
                     exit();
            }
                    set_time_limit(0);
              // 导入 CSV 文件必须有 Genus 列
                    //将生成临时表,如果不成功返回 false 成功返回生成表名
                    //fieldmustinclude 为一定要包含的列列表逗号分隔
                    //newtablename 空为随机名称
                    //iftemptable=true 为新建临时表
                    //有错退出
                    if($_FILES["error"] != 0){
                      return(false);
                    }
                    if(empty($_FILES[$csvobjectname]["tmp_name"])==true){
        return(false);
                    }
                    //确保文件格式正确
                               //提取文件后缀
                    $pos=strrpos($_FILES[$csvobjectname]["name"],".");
                    if ($pos==0 or $pos==false){
                              return(false);
                    }
                    $suffix=substr($_FILES[$csvobjectname]["name"],$pos);
                    $suffix=trim($suffix);
                               //文件后缀不是 csv 退出
                    if ($suffix!=".csv" ){//只允许上传 csv 格式文件
                      return(false);
                    }
                    //提取首列
                    $file=fopen($_FILES[$csvobjectname]["tmp_name"],"r");//打开文件
                    fseek($file,0);//移到文件首
                    $line=fgetcsv($file);//获取第一行各列数组
                    $line[0]=iconv('gb2312','utf-8',$line[0]);//将所行数据转换为通用代码
                    $mm=count($line);//总列数
                    $ifbreackbycomma=true;
                    if ($mm==1 and stripos($line[0],";")>0){//某些文件分号分行必须重新分行
```

```
                $line=explode(";",$line[0]);
                $mm=count($line);
                $ifbreackbycomma=false;
        }
        //获致所有列列表
        $nn=0;
        $allfieldlist=",";
        while($nn<$mm){
                if ($nn!=0 and $ifbreackbycomma=true){
                  $line[$nn]=iconv('gb2312','utf-8',$line[$nn]);
                }
                $line[$nn]=trim($line[$nn]);
                $line[$nn]=strtolower($line[$nn]);
                $allfieldlist=$allfieldlist.$line[$nn].",";
                //下一步
                $nn=$nn+1;
        }
        $allfieldlist=",".$allfieldlist.",";
        //确定必有列存在
        $mustfieldlist=$fieldmustinclude;
        $mustfieldlist=str_replace(" ","",$mustfieldlist);
        if (empty($mustfieldlist)==false){
                        $field=explode(",",$mustfieldlist);
                        $n=0;
                        $m=count($field);
                        while ($n<$m){
                                $k=stripos($allfieldlist,",".$field[$n].",");
                                if ($k==false or $k<1){
                                        echo("<br>错误!!数据输入表缺少 $field[$n] 列 !!<br>
Error!!Uploaded dataset must includes conlumn $field[$n] !!");
                                        return(false);
                                }
                          $n=$n+1;
                        }
        }
        //恢复所有列列表
        $allfieldlist=str_replace(",,",",",$allfieldlist);
        //新建表
                      //确定文件名
        $tablename=trim($newtablename);
        if (empty($tablename)==true){
          $tablename=randletter().$_SERVER['REMOTE_ADDR'].randletter().date("YmdHis");
          $tablename=str_replace(".","",$tablename);
        }
                      //新建表
        if ($iftemptable==true){

    createtemptable($tablename,$querystring="",$idfield="ID",$noneidfieldlist=$allfieldlist);
        }else{
           createtable($tablename,$querystring="",$idfield="ID",$noneidfieldlist=$allfieldlist);
        }
        //填充数据
        $line=fgetcsv($file);
        while ($line!=false){
```

```
            //数据处理
            $line[0]=iconv('gb2312','utf-8',$line[0]);
            $mm=count($line);//总列数
            $ifbreackbycomma=true;
            if ($mm==1 and stripos($line[0],";")>0){
                $line=explode(";",$line[0]);
                $mm=count($line);
                $ifbreackbycomma=false;
            }
            //提取数据
            $nn=0;
            $value="";
            while ($nn<$mm){
                    if ($nn!=0 and $ifbreackbycomma=true){
                     $line[$nn]=iconv('gb2312','utf-8',$line[$nn]);
                    }
                    $line[$nn]=trim($line[$nn]);
                    if ($value==""){
                      $value="'".$line[$nn]."'";
                    }else{
                      $value=$value.",'".$line[$nn]."'";
                    }
                    //下一步
                    $nn=$nn+1;
            }
            //导入数据表
            $query="insert into ".$tablename."(".$allfieldlist.") values(".$value.")";
            mysql_query($query);
                //下一步
            $line=fgetcsv($file);
        }
          //返回临时表名
        return($tablename);
}
function randletter(){//返回随机大写字母
    $num=mt_rand(65,90);
    $str=chr($num);
    return($str);
}
function createtemptable($tablename,$querystring="",$idfield="",$noneidfieldlist=""){
       //$query 为空时 id 列,普通列都必须存在 $query 不为空时时 id 列,普通列无效
        //新建临时表
                //打开数据库
        $_DB=F_NetConnect();
        if ($_DB==false){
            return(false);
        }
                //数据处理
                        //表名
        $str=trim($tablename);
        if (empty($str)==true){
            return(false);
        }
        $query= "create temporary table ".$str."(";
```

```
                        //查询字符串
        $str=trim($querystring);
        if (empty($str)==false){
            $query=$query.$str.")";
            $result = mysql_query($query);
                    //返回是否调用成功
            if ($result==true){
                $r=true;
                return($r);
            }else{
                $r=false;
                return($r);
            }
        }
                        //ID 列名
        $str=trim($idfield);
        if (empty($str)==true){
            return(false);
        }
        $query= $query.$str." bigint AUTO_INCREMENT";
                        //普通列
        $str=trim($noneidfieldlist);
        if (empty($str)==true){
            return(false);
        }
        $arr=explode(",",$str);
        $m=count($arr);
        $n=0;
        while ($n<$m){
              $query=$query.",".$arr[$n]." text CHARACTER SET utf8 COLLATE
utf8_unicode_ci";
              $n=$n+1;
        }
                        //key ID 列名
        $str=trim($idfield);
        if (empty($str)==true){
            return(false);
        }
        $query= $query.",PRIMARY KEY (".$str."))";
                //建立表格
        $result = mysql_query($query);
                //返回是否调用成功
        if ($result==true){
            $r=true;
            return($r);
        }else{
            $r=false;
            return($r);
        }
}
function reconstructsegs ($datatablename, $proxytable, $proxycolumn, $withoutgenustablename,
$usefulgenustablename, $resulttablename, $allgenustablename, $ifdrawPDF=false){
    //说明 $datatablename 被分析数据表必需同时包含 genus, abundance, sample 三列
    //说明 $proxytable 存放媒介表比如 humidity
```

```
    //说明 $proxycolumn 存和媒介列比如 humit
    //说明 $withoutgenustablename 生成无内容属表名
    //说明 $usefulgenustablename 生成有内容属表名
    //说明 $resulttablename 生成结果表名
    //生成有用属表
    $querystring="select distinct ".$proxytable.".".$proxycolumn.",".$proxytable.".genus from ".$proxytable." inner join ".$allgenustablename." on ".$proxytable.".genus=".$allgenustablename.".genus order by ".$proxycolumn;
    createtemptable($usefulgenustablename,$querystring,$idfield="",$noneidfieldlist="");
    //生成无用属表
    $querystring="select distinct ".$allgenustablename.".genus from ".$allgenustablename." left join ".$usefulgenustablename." on ".$usefulgenustablename.".genus=".$allgenustablename.".genus where ".$usefulgenustablename.".genus is null";
    createtemptable($withoutgenustablename,$querystring,$idfield="",$noneidfieldlist="");
    //生成未交叉结果表
    $resulttablename0="zz".$resulttablename;
    $querystring="select ".$datatablename.".sample,".$usefulgenustablename.".".$proxycolumn.",sum(".$datatablename.".sumabundance) as abundance from ".$datatablename." left join ".$usefulgenustablename." on ".$datatablename.".genus=".$usefulgenustablename.".genus group by ".$datatablename.".sample,".$usefulgenustablename.".".$proxycolumn."";
    createtemptable($resulttablename0,$querystring,$idfield="",$noneidfieldlist="");
    $querystring="update ".$resulttablename0." set ".$proxycolumn."='Uncertain' where ".$proxycolumn." is null or ".$proxycolumn."="";
    $result=mysql_query($querystring);
    //生成交叉结果表
    transformtable($resulttablename0,$groupfieldlist="sample",$pivotfield=$proxycolumn,$valuefield='abundance',$resulttablename,$iftemp=true,$wherewithoutwhere="",$calculate="sum",$nulldefault="0");
    //显示结果
    if ($ifdrawPDF==true){
        DrawPollenCollumnPDF($resulttablename,"sample","id");
    }else{
        echo("<br>Result 分析结果<br>");
        showtablealldata($resulttablename);
        echo("<br>This Result is based on the following genera collected in this database.<br>");
        echo("本分析结果根据本数据库已收集到的如下指示化石得出.<br>");
        showtablealldata($usefulgenustablename);
        $query="select genus from ".$withoutgenustablename." ";
        $result=mysql_query($query);
        $num=mysql_num_rows($result);
        if ($num==1){
          echo("<br>As the environmental significance of following genus is not clear, its abundance is under the column uncertain.<br>");
          echo("以下属的环境意义尚不表楚,其丰度值位于结果的 uncertain 列<br>");
          showtablealldata($withoutgenustablename);
        }else if ($num>1){
          echo("<br>As the environmental significances of following genera are not clear, their total abundance is under the column uncertain.<br>");
          echo("以下属的环境意义尚不表楚,其丰度值位于结果的 uncertain 列<br>");
          showtablealldata($withoutgenustablename);
        }
    }
}
```

```
function
DrawPollenCollumnPDF($TableWithAbundance,$SampleFieldName,$DepthFieldName,$AverageColumnWidt
hMm=10,$NotShowFieldList=""){
                $HeightEachRowMm=4;
                $GapEachColumnMm=1;
                $MarginMm=20;
                $pix_mm=360/127;;
                //没有深度列则 id 列为深度
                $SampleFieldName=str_replace(",","",$SampleFieldName);
                $NotShowFieldList=str_replace(",","",$NotShowFieldList);
                //提取内容
                $querystring="select * from $TableWithAbundance";
                $result=mysql_query($querystring);
          $num=mysql_num_rows($result);
                $FieldNum=mysql_num_fields($result);
                if ($num==0){
                        return(-1);
                }
                $DrawHeightMm=$num*$HeightEachRowMm;
                //提取所有列 数值列
                $n=0;
                $AllFiledList="";
                $ValueFieldlist="";
                $MaxValueFieldlist="";
                $DepthFieldIndex=-1;
                while ($n<$FieldNum){
                    $FieldName=mysql_field_name($result,$n);
                          if ($FieldName==$DepthFieldName){
                                  $DepthFieldIndex=$n;
                          }
                          if ($AllFiledList==""){
                                  $AllFiledList=$FieldName;
                          }else{
                                  $AllFiledList=$AllFiledList.",".$FieldName;
                          }
                          if
(stripos(",,".$DepthFieldName.",".$SampleFieldName.",".$NotShowFieldList,",".$FieldName.",")==0){
                                  if ($ValueFieldlist==""){
                                          $ValueFieldlist=$FieldName;
                                          $MaxValueFieldlist="max(CONVERT(".$FieldName.",
DECIMAL(10,2)))";
                                  }else{
                                          $ValueFieldlist=$ValueFieldlist.",".$FieldName;

$MaxValueFieldlist=$MaxValueFieldlist.",max(CONVERT(".$FieldName.", DECIMAL(10,2)))";
                                  }
                          }
                          $n=$n+1;
                }
                if ($DepthFieldIndex==-1){
                        return(-1);
                }
                //计算数值列总宽度
                $querystring="select $MaxValueFieldlist from $TableWithAbundance";
                $MaxResult=mysql_query($querystring);
```

```
        $numValueField=mysql_num_fields($MaxResult);
        $AllValueSum=0;
        $MaxValue=0;
        $MinValue=0;
        $AllValueList="";
        $MaxLine=mysql_fetch_row($MaxResult);
        $n=0;
        while ($n<$numValueField){
                $AllValueSum=$AllValueSum+$MaxLine[$n];
                if ($AllValueList==""){
                  $AllValueList=$MaxLine[$n];
                }else{
                  $AllValueList=$AllValueList.",".$MaxLine[$n];
                }
                if ($MaxLine[$n]>$MaxValue){
                        $MaxValue=$MaxLine[$n];
                }
                if ($MinValue==0){
                        $MinValue=$MaxLine[$n];
                }else if ($MinValue>$MaxLine[$n]){
                        $MinValue=$MaxLine[$n];
                }
                //next
                $n=$n+1;
        }
        $MeanValue=$AllValueSum/$numValueField;
        //计算绘图列总宽度
        $n=0;
$DrawAllValueSum=0;
        while ($n<$numValueField){
    if ($MaxLine[$n]<$MeanValue/2){
                        $CurrDrawValue=$MeanValue/2;
                }else{
                        $CurrDrawValue=$MaxLine[$n]+$MeanValue/10;
                }
                $DrawAllValueSum=$DrawAllValueSum+$CurrDrawValue;
                //next
                $n=$n+1;
        }
        //计算标本列总宽度
        $index=query_fieldindex($result,$SampleFieldName);
        mysql_data_seek($result, 0);
        $line=mysql_fetch_row($result);
        $MaxSampleNameMm=0;
        $fonttype="./fonts/arialuni.ttf";
        if (file_exists($fonttype)==false){
              if (file_exists("../fonts/arialuni.ttf")==true){
               $fonttype = "../fonts/arialuni.ttf";
              }else{
               $fonttype = "./fonts/arialuni.ttf";
              }
        }
        $fontsize=8;
        while ($line!=false){
                $str=$line[$index];
```

```
             $alltextpixsize=imagettfbbox($fontsize,0,$fonttype,$str);
             $strPixSize=$alltextpixsize[2]-$alltextpixsize[0];
             $strPixSize=$strPixSize/$pix_mm;
             if ($MaxSampleNameMm<$strPixSize){
                 $MaxSampleNameMm=$strPixSize;
             }
             //next
          $line=mysql_fetch_row($result);
        }

    $DrawWeidthMm=$MaxSampleNameMm+$DrawAllValueSum*$AverageColumnWidthMm/$MeanV
alue+$GapEachColumnMm*($numValueField+1);
        $PdfWeidthMm=$DrawWeidthMm+3*$MarginMm;
        $PdfHeightMm=$DrawHeightMm+3*$MarginMm;

        //新建 PDF
  $pdf=new PDF_Extend();
        if ($PdfHeightMm>$PdfWeidthMm){
            $pdf->__construct("P","mm",array($PdfWeidthMm,$PdfHeightMm));
        }else{
            $pdf->__construct("L","mm",array($PdfWeidthMm,$PdfHeightMm));
        }
        $pdf->AddPage();
        $pdf->SetFont('Arial',",10);
        /* 参数
        $TextString=$ValueFieldlist;
        //$pdf->Write(10,$MaxValueFieldlist);
        $pdf->Write(10,$AllValueList);
        $pdf->Write(10,chr(10)."$numValueField All Values: $AllValueSum");
        $pdf->Write(10,chr(10)."DrawAllValueSum: $DrawAllValueSum");
        $pdf->Write(10,chr(10)."MaxSampleNameMm: $MaxSampleNameMm");
        $pdf->Write(10,chr(10)."Min Value: $MinValue");
        $pdf->Write(10,chr(10)."Max Value: $MaxValue");
        $pdf->Write(10,chr(10)."Mean Value: $MeanValue");
        $pdf-
>RotateText($TextString,$WordX=10,$WordY=140,$WordSize=10,$WordAngle=0,$WordColorR=0,$WordC
olorG=0,$WordColerB=0,$WordFamily="Arial",$WordStyle="");
        //输出 PDF
        */
        //标出标本
        mysql_data_seek($result, 0);
        $line=mysql_fetch_row($result);
        $n=1;
        while ($line!=false){
             $str=$line[$index];
             $alltextpixsize=imagettfbbox($fontsize,0,$fonttype,$str);
             $strPixSizeY=$alltextpixsize[1]-$alltextpixsize[7];
             $strSizeYMm=$strPixSizeY/$pix_mm;
             $CurrY=2*$MarginMm+$DrawHeightMm-
$n*$HeightEachRowMm+$HeightEachRowMm/2+$strSizeYMm/2;
          $pdf-
>RotateText($str,$WordX=$MarginMm,$WordY=$CurrY,$fontsize,$WordAngle=0,$WordColorR=0,$WordC
olorG=0,$WordColerB=0,$WordFamily="Arial",$WordStyle="");
             //next
          $line=mysql_fetch_row($result);
```

```
                    $n=$n+1;
            }
    //标出标本线
            $n=1;
    $SampleScaleStyle = array('width' => 0.2, 'cap' => 'butt', 'join' => 'miter', 'dash' => '0', 'phase' => 10,'color'
=> array(232, 232, 232));
            $SampleXL=$MarginMm+$MaxSampleNameMm;
            $SampleXR=$MarginMm+$DrawWeidthMm;
            while ($n<=$num){
        $SampleY=2*$MarginMm+$DrawHeightMm-$n*$HeightEachRowMm+$HeightEachRowMm/2;
                    $pdf->Line($SampleXL, $SampleY, $SampleXR, $SampleY, $SampleScaleStyle);
                    //next
                    $n=$n+1;
            }
    //标出方格
            $n=0;
    $DrawAllValueSum=0;
            $LastXmm=$MarginMm+$MaxSampleNameMm;
            $TopYMm=2*$MarginMm;
            $BottomYMm=$TopYMm+$DrawHeightMm;
    $ValueFieldNameArr=explode(",",$ValueFieldlist);
    $BoxLineStyle = array('width' => 0.2, 'cap' => 'butt', 'join' => 'miter', 'dash' => '0', 'phase' => 10,'color' =>
array(0, 0, 0));
            while ($n<$numValueField){
        //计算当前列宽
                    if ($MaxLine[$n]<$MeanValue/2){
                            $CurrDrawValue=$MeanValue/2;
                    }else{
                            $CurrDrawValue=$MaxLine[$n]+$MeanValue/10;
                    }
                    $CurrDrawWidthMm=$AverageColumnWidthMm*$CurrDrawValue/$MeanValue;
                    $CurrXMm=$GapEachColumnMm+$LastXmm+$CurrDrawWidthMm;
                    //标出列名
                    $pdf-
>RotateText($ValueFieldNameArr[$n],$WordX=2*$GapEachColumnMm+$LastXmm,$WordY=$TopYMm-
$GapEachColumnMm,$WordSize=10,$WordAngle=30,$WordColorR=0,$WordColorG=0,$WordColerB=0,$
WordFamily="Arial",$WordStyle="");

                    //画左线
                    $pdf->Line($GapEachColumnMm+$LastXmm, $TopYMm,
$GapEachColumnMm+$LastXmm, $BottomYMm, $BoxLineStyle);
                    //画右线
                    $pdf->Line($CurrXMm, $TopYMm, $CurrXMm, $BottomYMm, $BoxLineStyle);
                    //画上线
                    $pdf->Line($GapEachColumnMm+$LastXmm, $TopYMm, $CurrXMm, $TopYMm,
$BoxLineStyle);
                    //画下线
                        $pdf->Line($GapEachColumnMm+$LastXmm, $BottomYMm, $CurrXMm,
$BottomYMm, $BoxLineStyle);
                    //设置刻度
                    $imagepixrange=$CurrDrawWidthMm*$pix_mm;
                    $reallength=$CurrDrawValue;
                    $realsmallscale=calculatesmallscale($imagepixrange,$reallength);
                    $realbigscale=5*$realsmallscale;
```

```
                        $donotshowrealbigscale="-10";
                        $axiszonerealXleft=0;
                        $axiszonerealXright=$CurrDrawValue;
                        $axiszonerealYright=0.5;
                        $axiszonerealYleft=0.5;
                        $axisrealY=0.5;
                        $drawzonelefttoppixX=($GapEachColumnMm+$LastXmm)*$pix_mm;
                        $drawzonelefttoppixY=$TopYMm*$pix_mm;
                        $drawzonerightbottompixX=$CurrXMm*$pix_mm;
                        $drawzonerightbottompixY=$BottomYMm*$pix_mm;
                        $drawzonelefttoprealX=0;
                        $drawzonerightbottomrealX=$CurrDrawValue;
                        $drawzonelefttoprealY=$num+0.5;
                        $drawzonerightbottomrealY=0.5;

PdfDrawScaleX($pdf,$realsmallscale,$realbigscale,$donotshowrealbigscale,$axisrealY,$axiszonerealXleft,$axi
szonerealYleft,$axiszonerealXright,$axiszonerealYright,$drawzonelefttoppixX,$drawzonelefttoppixY,$drawzo
nerightbottompixX,$drawzonerightbottompixY,$drawzonelefttoprealX,$drawzonelefttoprealY,$drawzonerightb
ottomrealX,$drawzonerightbottomrealY,$ifisupscale=true,$ifdrawbigscale=true,$startcaption="",$endcaption="
");
                        //画多边形
                            //提取多边形坐标
                        mysql_data_seek($result, 0);
                        $line=mysql_fetch_row($result);
                        $nn=1;
                        $ValueFieldInext=query_fieldindex($result,$ValueFieldNameArr[$n]);
                        $DXMm=$GapEachColumnMm+$LastXmm;
        $SampleY=2*$MarginMm+$DrawHeightMm-$nn*$HeightEachRowMm+$HeightEachRowMm/2;
                        $ArrStr=$DXMm.",".$SampleY;
                        while ($line!=false){
                                        $CurrAbundance=$line[$ValueFieldInext];

$CurrPolyLineWidthMm=$AverageColumnWidthMm*$CurrAbundance/$MeanValue;
            $SampleY=2*$MarginMm+$DrawHeightMm-
$nn*$HeightEachRowMm+$HeightEachRowMm/2;
$DXMm=$GapEachColumnMm+$LastXmm+$CurrPolyLineWidthMm;
                                        $ArrStr=$ArrStr.",".$DXMm.",".$SampleY;
                                        //next
                                        $line=mysql_fetch_row($result);
                                        $nn=$nn+1;
                        }
                        $DXMm=$GapEachColumnMm+$LastXmm;
                        $ArrStr=$ArrStr.",".$DXMm.",".$SampleY;
                        $PolyArr=explode(",",$ArrStr);
                            //绘制多边形
                        $pdf->Polygon($PolyArr, 'F',array('all' => $BoxLineStyle),array(0,0,0));
                        //next
                        $n=$n+1;
                        $LastXmm=$CurrXMm;
                }
    $pdf->Output();
                return(-1);
}
```