



Review papers

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

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ABSTRACT

The ecogroup classification based on the growth-form of plants (Eco-Plant model) is widely used for extant, Cenozoic, Mesozoic, and Paleozoic paleoenvironmental 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, paleoenvironmental and paleoclimate changes in Mesozoic sedimentary records.

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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 paleoenvironmental 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 paleoenvironmental reconstructions. The sporomorph ecogroup model (SEG model) of Abbink et al. (2004b) is also commonly used to reconstruct the paleoenvironment 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 paleoclimate 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.

2. Materials and methods

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 (Fig. 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/sporefamilypgenus.php>) (Zhang et al., 2021).

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 Spora 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, 1962b, 1965a, 1965b; Kremp et al., 1957a, 1957b; Kremp et al., 1958, 1959, 1960a, 1960b; 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 Járαι-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., 2021).

For the analysis of paleoenvironmental and paleoclimate 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.

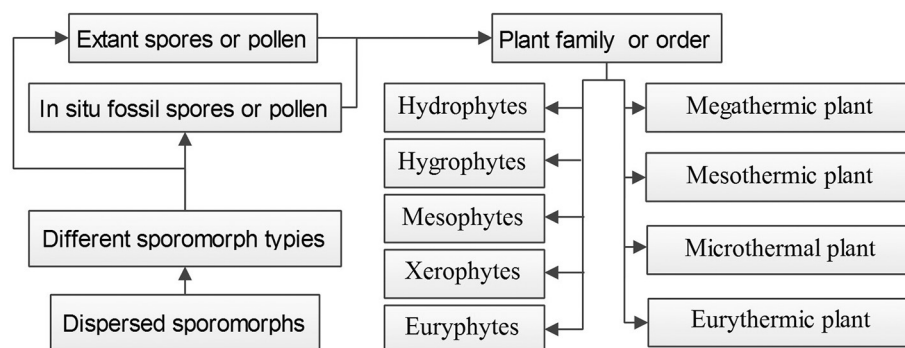


Fig. 1. Flow chart of linking dispersed sporomorphs with plant categories related to Eco-Plant model.

3. Results

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 A) 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 1. The result can be downloaded online (<http://www.sporopollen.com/sporefamilypgenus.php>). Below, dispersed sporomorph genera from the Mesozoic are linked to the different ecogroups:

3.1. Bryophytes

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)

Table 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
	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
	Pteridophytes	Ophioglossaceae	Mesophytes
Osmundales		Hygrophytes	Eurythermic
Polypodiaceae		Mesophytes	Megathermic
Pteridaceae		Euryphytes	Eurythermic
Salviniales		Hydrophytes	Megathermic
Schizaeaceae		Mesophytes	Megathermic
Selaginellaceae		Euryphytes	Eurythermic
Araucariaceae		Hygrophytes	Megathermic
Bennettitales		Hygrophytes	Megathermic
Caytoniaceae		Hygrophytes	Megathermic
Cheirolepidiaceae		Xerophytes	Megathermic
Corystospermales		Mesophytes	Megathermic
Cupressaceae		Euryphytes	Eurythermic
Cycadales		Mesophytes	Megathermic
Czekanowskiales		Mesophytes	Mesothermic
Gymnospermae		Ephedraceae	Xerophytes
	Erdtmanitheceae	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

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).

3.1.2. 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 Járjai-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).

3.1.3. 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).

3.1.4. 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 Járαι-Komlódi, 1975; Zhang et al., 2006). They are hygrophytes and eurythermic plants.

Phaeoceros skottsbergii type isospore

Extant spore: *Notothyas levieri* Schiffner (Chantanaorrapint, 2015; p. 260, figs. 27–28)

Extant spore: *Notothyas 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 10 dispersed isospore genera related to this type are *Annulispora* de Jersey, *Dicyclosporitis* Schulz [S], *Distalanulisporites* Klaus [S], *Disticyclosporitis* Schulz [S], *Guyangspora* Yu et Miao [?], *Neochomotrilites* Reinhardt [S], *Parmulisporitis* Bai [?], *Phaeocerosporites* Nagy, *Polycingulatisporites* Simoncsics et Kedves [?], and *Taurocusporites* Stover [S].

Remarks: *Annulispora* de Jersey is comparable to spores of extant *Notothyas* 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). *Dicyclosporitis* Schulz, *Disticyclosporitis* Schulz, and *Distalanulisporites* Klaus are synonyms of *Annulispora* de Jersey (McKellar, 1974; Potonié, 1966). *Neochomotrilites* 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: *Notothyas 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], *Foraminisporitis* Krutzsch, *Nevesisporites* de Jersey et Paten, *Simeonospora* Balme [S], and *Trisolissporites* Tschudy [S].

Remarks: *Foraminisporitis* Krutzsch and *Nevesisporites* de Jersey et Paten are comparable to spores of extant *Phaeoceros* Proskauer and *Notothyas* 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).

3.1.5. 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 Járαι-Komlódi, 1975; Zhang et al., 2006). They are generally hygrophytes and eurythermic plants.

Riccia frostii type isospore

Extant spore: *Riccia frostii* Austin (Boros and Járαι-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).

3.1.6. 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 Járαι-Komlódi, 1975; p. 84, figs. 1–6)

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

Extant spore: *Sphagnum girsensohnii* 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).

3.2. Pteridophytes

3.2.1. Order: CYATHEALES Frank

The extant order CYATHEALES Frank consists of eight families (Schuettpelez 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 *Cibotioidites* Ross, *Cibotiumidites* (Malyavkina) Potonié, *Cibotiumspora* Chang, *Cibotiumsporites* Rouse, *Crassitudisporites* Hiltmann [?], *Distaltriangulisporites* Singh [?], and *Duplexisporites* (Deák) Playford et Dettmann.

Remarks: *Cibotioidites* 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, figs. 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 12 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 *Zembrasporites* 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 *Zembrasporites* Klaus (Potonié, 1966).

3.2.2. Order: Equisetales de Candolle ex Berchtold & Presl

The extant order Equisetales de Candolle ex Berchtold & Presl (Schuettpelez 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-Stramm and Lugardon, 2009; p. 118, pl. I, fig. 3)

In situ spore: *Equisetostachys verticillata* Grauvogel-Stramm (Grauvogel-Stramm and Lugardon, 2009; p. 118, pl. I, figs. 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).

3.2.3. Order: GLEICHENIALES Schimper

The extant order GLEICHENIALES Schimper consists of three families (Schuettpehl 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) Bernhardt (Tryon and Lugardon, 1991; p. 67, pl. 14, figs. 1–2)

In situ spore: *Dictyophyllum nilssonii* (Brongniart) Goepfert (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 kytotomes (the arcuate folds) on the proximal or distal face. The exospore has three layers.

Dispersed spores: The 16 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 [?], *Gleicheniaceauritulina* (Malyavkina) Potonié, *Gleicheniidites* Ross, *Iraqispora* Singh [?], *Kyrtomisporis* Mädlar [?], *Matonisporites* Couper, *Ornamentifera* Bolchovitina, *Plicifera* Bolchovitina, and *Psilatrilletes* 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 *Gleicheniaceauritulina* (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 *Psilatrilletes* 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.

3.2.4. Order: HYMENOPHYLLALES Frank

The extant order HYMENOPHYLLALES Frank consists of one family HYMENOPHYLLACEAE Martius (Schuettpehl 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).

3.2.5. Order: ISOËTALES Prantl

The order ISOËTALES Prantl (Schuettpehl 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 (Schuettpehl 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 paleolatitudes 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 *Pavlovsporites* 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 *Isoetes* 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 *Isoetes* Linnaeus (Wilde and Hemsley, 2000). *Auriculozonospora* Singh, Srivastava et Roy and *Pavlovsporites* Kozur are synonyms of *Minerisporites* Potonié (Batten and Koppelhus, 1993; Potonié, 1970).

***Annalepis zeileri* type megaspore**

In situ megaspore: *Annalepis zeileri* Fliche (Grauvogel-Stamm and Düringer, 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 10 dispersed megaspore genera related to this type are *Capillisorites* Kozur [?], *Dijkstraisporites* Potonié, *Henrisporites* Potonié [?], *Herbosisorites* Li et Batten [?], *Membranisorites* Delcourt et Sprumont [S], *Nathorstisporites* Jung, *Paxillitriletes* Hall et Nicolson, *Sepisorites* Li et Batten [?], *Tenellisporites* Potonié, and *Thomsonia* Mädlar [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 Düringer, 1983). *Membranisorites* Delcourt et Sprumont and *Thomsonia* Mädlar 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, *Bowenispore* Scott & Playford, and *Maiturisporites* Maheshwari et Banerji.

Remarks: *Bowenispore* 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 *Lundbladispore* 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 *Isoetes* 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 zeileri* type microspore**

In situ spore: *Annalepis zeileri* Fliche (Grauvogel-Stamm and Düringer, 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 zeileri* Fliche (Grauvogel-Stamm and Düringer, 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 *Lundbladispore* Balme.

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

3.2.6. Order: LYCOPODIALES de Candolle ex Berchtold & Presl

The order LYCOPODIALES de Candolle ex Berchtold & Presl (Schuettpezel 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 *Alveolasporea* Zhang [?], *Foveosporites* Krutzsch [S], *Foveolatritriletes* Mädlar [?], *Foveosporites* Balme, *Lycopodiumsporites* (Thiergart) Delcourt et Sprumont, *Microfoveolatisporites* Krutzsch [?], *Reticulitritriletes* Mädlar [?], *Retitritriletes* Pierce [S], and *Selagosporites* Krutzsch.

Remarks: *Lycopodiumsporites* (Thiergart) Delcourt et Sprumont, *Foveosporites* Mädlar, and *Selagosporites* Krutzsch are comparable to spores of extant *Lycopodium* Linnaeus (Kremp and Ames, 1962b; Potonié, 1956, 1960; Song et al., 1999). *Foveosporites* Krutzsch is a synonym of *Foveosporites* Balme (Dettmann, 1963). *Retitritriletes* 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 *Hamulatisporites* Krutzsch, *Ityospora* Zhang [?], *Labrorugaspora* Zhang [?], *Latrobosporites* Harris, *Rugutetraspora* Yu & Zhang [?], and *Tripertina* (Maljavkina) Potonié [?].

Remarks: *Hamulatisporites* 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).

3.2.7. Order: MARATTIALES Link

Species of extant MARATTIALES Link (Schuettpezel 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).

3.2.8. Order: OPHIOGLOSSALES Link

The order OPHIOGLOSSALES Link (Schuettpezel et al., 2016) consists of one extant family OPHIOGLOSSACEAE Martinov including also the former families of BOTRYCHIACEAE Hofaninow and HELMINTHOSACHYACEAE Ching (Smith et al., 2006). Fossils with *in situ* spores of *Lugardonina* 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 to 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 mention 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.

3.2.9. 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 hygrophites 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 Bernhardt 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).

3.2.10. 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 hygrophites 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 11 dispersed isospore genera related to this type are **Cyclophorusporites** Sung et Lee ex Zhang, **Gemmamonoletes** Pierce [S], **Gemmatosporis** Krutzsch [S], **Polypodiaceasporites** 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: **Cyclophorusporites** 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 **Polypodiaceasporites** 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 **Polypodiaceasporites** Thiergart ex Potonié (Potonié, 1956).

Family: PTERIDACEAE Kirchner

Fossils of PTERIDACEAE Kirchner such as **Arctopteris** Samylnina and **Palibiniopteris** Prynada can be found in the Cretaceous from China (Sun et al., 2010). Extant species are essentially worldwide in distribution centered 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 cheilanthis** 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 11 dispersed isospore genera related to this type are *Asseretospora* Schuurman, *Contignisporites* Dettmann [?], *Coronasporites* Zhang [?], *Muricingulisporis* Krutzsch, *Onychiumsporites* Hu, *Pteridaceoisporis* Sun et He, *Pterisporites* 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).

3.2.11. 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 13 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 spongiöse 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: ANEMIAEAE Link

The species of the extant family ANEMIAEAE Link (Schuettelpelz 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) Desvoux (Tryon and Lugardon, 1991; p. 115, pl. 30, figs. 1–3, 7–8)

In situ spore: Ruffordia goepertii (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 neighboring facets can be connected. Some spores have auriculae. The exospore has two layers.

Dispersed spores: The 10 dispersed isospore genera related to this type are *Appendicisporites* Weyland et Krieger, *Cicatricosisporites* Potonié et Gelletich, *Costatoperforosporites* Deák, *Mohriosisporites* 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). *Mohriosisporites* 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 11 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 *Variugosisporites* 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 *Variugosisporites* 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 *Cicatricosisporites* 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). *Cicatricosporites* 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).

3.2.13. Order: SELAGINELLALES Prantl

The extant order SELAGINELLALES Prantl consists of the family SELAGINELLACEAE Willkomm with the single genus *Selaginella* de Beauvois (Schuettpehl 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 eclipses* 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 13 dispersed megaspore genera related to this type are *Aneulettes* Harris, *Bacutritetes* van der Hammen ex Potonié, *Caboconicus* Batten and Ferguson, *Echitritetes* van der Hammen ex Potonié, *Erlansonisporites* Potonié, *Horstisporites* Potonié, *Hughesisporites* Potonié [?], *Istisporites* Potonié, *Kerhartisporites* Knobloch, *Ricinospora* Bergad, *Rugotritetes* van der Hammen ex Potonié, *Thylakosporites* Potonié, and *Verrutritetes* van der Hammen ex Potonié [?].

Remarks: *Aneulettes* Harris, *Bacutritetes* van der Hammen ex Potonié, *Caboconicus* Batten and Ferguson, *Echitritetes* van der Hammen ex Potonié, *Erlansonisporites* Potonié, *Horstisporites* Potonié, *Kerhartisporites* Knobloch, *Ricinospora* Bergad, *Rugotritetes* 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 31 dispersed microspore genera related to this type are *Aequitritadites* Delcourt et Sprumont [S], *Anapiculatisporites* Potonié et Kremp [?], *Anaplanisporites* Jansonius [?], *Anguisporites* Potonié et Klaus [?], *Antulsporites* Archangelsky & Gamero [S], *Bayanhuasporites* Yu [?], *Cadargasporites* de Jersey et Paten [?], *Carnisporites* Mädlar, *Cepulina* Maljavkina [S], *Ceratosporites* Cookson et Dettmann, *Cirratritadites* Wilson et Coe, *Cirratrisporites* Leveine [S], *Clavatisporites* Kedves et Simoncsics, *Dentellisporites* Mädlar [S], *Echinatisporis* Krutzsch, *Heliosporites* Schulz ex Srivastava, *Herkosporites* Stover [?], *Indotritadites* Tiwari [S], *Kraeuselisporites* Leschik, *Liburnisporis* Srivastava [?], *Limbosporites* Nilsson, *Lusatisporis* Krutzsch, *Multinodisporites* Chlonova, *Neoraistrickia* Potonié, *Patellisporites* Ouyang, *Perotritetes* 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, *Patellisporites* 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). *Aequitritadites* Delcourt et Sprumont is a synonym of *Selaginellidites* Krasnova (Potonié, 1966). *Carnisporites* Mädlar and *Cirratritadites* 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 *Cirratritadites* Wilson et Coe, *Cepulina* Maljavkina of *Neoraistrickia* Potonié, *Dentellisporites* Mädlar of *Limbosporites* Nilsson, *Indotritadites* Tiwari of

Kraeuselisporites Leschik, **Antulsporites** Archangelsky & Gambero of **Heliosporites** Schulz ex Srivastava (Potonié, 1966, 1970).

3.3. Gymnospermae

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 **Alkastrobos** 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.

Alkastrobos peltatus type pollen

In situ pollen: **Alkastrobos 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 **Applanopsisipollenites** 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 **Alkastrobos** Del Fueyo et Archangelsky (Del Fueyo and Archangelsky, 2005). **Callialasporites** Sukh Dev is comparable to the *in situ* pollen of **Apterocladus** Archangelsky (Balme, 1995). **Applanopsisipollenites** 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 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: **Acropyle 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 hypophyllum** 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 12 dispersed pollen genera related to this type are **Dacrydiumites** Cookson ex Harris, **Gamerroites** Archangelsky, **Indusiisporites** Leschik, **Lygistepollenites** (Cookson ex Pike) Harris, **Microalattidites** 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, **Microcachrydites** 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 **Microstrobus** Garden & Johnson (Schrank, 2010; Traverse and Ames, 1968). **Trisaccites** Cookson & Pike is comparable to the *in situ* pollen of **Trisacocladius** Archangelsky (Baldoni and Taylor, 1982). **Microcachryditites** 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 **Microstrobus** Garden & Johnson (Specht et al., 1992).

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. 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 sacchi typically show lateral attachment, although in several grains the sacchi 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).

3.3.4. 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 (Stear 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; Stear 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 Gamarro, 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 20 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 Gamarro, 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 **Grebepora** 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 CHEIROLEPIDACEAE 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).

3.3.5. 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 paleotropics during the late Paleozoic 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 paleotropics 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.

3.3.6. 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 kurranniae** Serbet and Stockey (Serbet and Stockey, 1991; p. 74, pl. IV, figs. 1–6)

In situ pollen: **Elatides williamsonii** (Bourguignat) Seward (Kurmman, 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, *Taxodiaceapollenites* 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). *Taxodiaceapollenites* 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 LUERSSSEN

The extant family SCIADOPITYACEAE LUERSSSEN (Christenhusz et al., 2011) consists of 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).

3.3.7. 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 *Androstrombus* Schimper and *Encephalartos* Lehmann can be found in Mesozoic records (Hill, 1990; van Konijnenburg-van Cittert, 1971; Zavalova 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.

Androstrombus balmei type pollen

In situ pollen: *Androstrombus balmei* Hill (Hill, 1990; p. 167, figs. 5–7; p. 169, figs. 9–13)

In situ pollen: *Androstrombus manis* Harris (Zavalova 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.

Androstrombus prisma type pollen

In situ pollen: *Androstrombus prisma* Thomas et Harris (Zavalova 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: *Androstrombus 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: *Androstrombus 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 distinct 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).

3.3.8. 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.

3.3.9. 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], **Gnetaceapollenites** 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). **Gnetaceapollenites** 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 **Gnetaceapollenites** Thiergart (Potonié, 1966).

3.3.10. Order: ERDTMANITHECALES Friis & Pedersen

The Mesozoic fossil family ERDTMANITHECAEAE 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 BENNETTITALEAE 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, **Hadroticolpites** 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). *Pretricolpitenites* Danz -Corsin et Laveine and *Trifossapollenites* Rouse are synonyms of *Eucommiidites* Erdtman ex Potoni  (Potoni , 1966).

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 worldwide, 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 (Potoni , 1960).

3.3.12. Order: PALISSYALES Doweld

The Mesozoic fossil order PALISSYALES Doweld (Pattimore and Rozeffelds, 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 (Potoni , 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; Potoni , 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 least 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.

3.3.13. 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 (Kriings 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* (Zalesky) 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 colovratca* Naugolnykh (Naugolnykh, 2013b; p. 121, pl. 15, figs 1–2, 5–6, 8)

In situ pollen: *Permotheca disparis* (Zalesky) 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* (Zalesky) 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 found in Mesozoic (Balme, 1995) while the *Permotheca disparis* type are mostly 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 39 dispersed pollen genera related to this type are *Accintisporites* Leschik [S], *Citrullisaccites* Zhang [?], *Conovalipollis* Zhang [?], *Costapollenites* Tschudy et Kosanke [?],

Crustaeosporites Leschik [?], **Distriatites** Bharadwaj [S], **Distriomonosaccites** Bharadwaj [?], **Faunipollenites** Bharadwaj [S], **Guttulapollenites** Goubin [?], **Hamiapollenites** Wilson [S], **Hindipollenites** Bharadwaj [S], **Lahirites** Bharadwaj [S], **Lunatisporites** Leschik [S], **Mesostriatites** Mädlar [?], **Mucrosaccus** Wilson [?], **Parataeniaesporites** Liu [?], **Pemphygaletes** Lubner [S], **Protocedrus** Bolchovitina [S], **Protodiploxypinus** Samoiloovitich [S], **Protohaploxypinus** (Samoiloovitich) Hart, **Protosacculina** Maljavkina [S], **Rhizomaspora** Wilson [S], **Striapollenites** Bharadwaj [S], **Striatissaccus** Mädlar [S], **Striatites** Pant [S], **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** Mädlar [S], **Tubantipollenites** Visscher [?], **Verticypollenites** Bharadwaj [S], and **Vittatina** (Luber) Jansonius.

Remarks: **Protohaploxypinus** (Samoiloovitich) 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** (Zalesky) Naugolnykh. **Faunipollenites** Bharadwaj, **Lunatisporites** Leschik, **Pemphygaletes** Lubner, **Protosacculina** Maljavkina, **Striatites** Pant, **Striatopiceites** Sedova, **Striatopinites** Sedova, and **Taeniaesporites** Leschik are synonyms of **Protohaploxypinus** (Samoiloovitich) Hart (Potonié, 1966). **Accinctisporites** Leschik is a synonym of **Lunatisporites** Leschik (Scheuring, 1974). **Hamiapollenites** Wilson, **Protocedrus** Bolchovitina and **Protodiploxypinus** Samoiloovitich are synonyms of **Protohaploxypinus** (Samoiloovitich) Hart (Traverse et al., 1973b). **Hindipollenites** Bharadwaj, **Lahirites** Bharadwaj, **Striatites** Pant, **Striatopodocarpites** (Sedova) Hart, **Strotersporites** Wilson, **Rhizomaspora** Wilson, **Verticypollenites** 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** Mädlar is a synonym of **Striatopinites** Sedova (Traverse and Ames, 1968). In the Paleozoic, **Permotheca** (Zalesky) 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.

3.3.14. 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** Carrière (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 sacchi are often distally attached. The sacchi are generally smaller than the corpus; but in polar view the widths of the sacchi are more or less the same as the width of the corpus. Under SEM the sacchi are generally smooth but under LM reticulate.

Dispersed pollen: The 13 dispersed pollen genera related to this type are **Abiespollenites** Thiergart ex Raatz, **Abietinaepollenites** Potonié (Delcourt & Sprumont), **Cathayapollis** Ziemiańska-Tworzydło, **Cedridites** Maljavkina [?], **Cedripites** Wodehouse, **Erlianpollis** Zhao [?], **Granatrivesiculites** Pierce, **Keteleeriaepollenites** Nagy, **Piceapollenites** (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 **Abietinaepollenites** 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, 1965b; Potonié, 1958). **Piceapollenites** (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 **Piceapollenites** (Potonié) Potonié (Potonié, 1958).

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, **Sertostrobos** Grauvogel-Stamm, and **Willsiostrobos** 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: **Sertostrobos laxus** Grauvogel-Stamm (Taylor and Grauvogel-Stamm, 1995; p. 294, pl. IX, figs. 2–7)

In situ pollen: **Willsiostrobos 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 **Voltziaesporites** Klaus.

Remarks: **Illinites** Kosanke and **Voltziaesporites** Klaus are comparable to the *in situ* pollen of **Willsiostrobos** Grauvogel-Stamm et Schaarschmidt (Balme, 1995; Taylor and Grauvogel-Stamm, 1995). **Triadispora** Klaus is comparable to the *in situ* pollen of **Sertostrobos** 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 10 pollen genera related to this type are **Chordasporites** Klaus [?], **Colpectopollis** Pflug [?], **Infernopolllenites** 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 **Cananoropollis** Potonié et Sah, **Crucisaccites** Lele et Maithy [S], **Dyupetalum** Jansonius et Hills [?], **Gigantospores** Klaus [?], **Nuskosporites** Potonié et Klaus, **Potonieisporites** Bhardwaj, and **Vestigisporites** Balme et Hennelly [S].

Remarks: **Nuskosporites** Potonié et Klaus and **Potonieisporites** Bhardwaj are comparable to the *in situ* pollen of **Otovicia** Florin (Clement-Westerhof, 1984; Kerp et al., 1990). **Cananoropollis** 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 11 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** Bhardwaj.

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** Bhardwaj 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 **Ellipsovelatissporites** Klaus [?], **Enzonalaspores** Leschik, **Patinasporites** Leschik, **Pseudoenzonalaspores** Scheuring, and **Vallasporites** Leschik.

Remarks: **Enzonalasporites** Leschik, **Patinasporites** Leschik, **Pseudoenzonalasporites** Scheuring, and **Vallasporites** Leschik are comparable to the *in situ* pollen of **Patokaia** 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 *Patokaia 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.

3.3.16. 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 16 dispersed pollen genera related to this type are **Alaticolpites** Regali, Uesugui et Santos [?], **Chomsiipites** Smirnova, **Corniculatisporites** Kuvava [S], **Elaterocolpites** Jardiné et Magloire [?], **Elateroplicites** Herngreen [?], **Elateropollenites** Herngreen [?], **Elaterosporites** Jardiné [?], **Galeacornea** Stover [?], **Jugella** Mchedlishvili et Shakhmundes, **Pentapsis** Lammons [?], **Quantonipollenites** 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** Kuvava 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.

4. Discussions

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 **Bayerithea** Kvacek et Pacltová, **Erdtmanithea** Pedersen, Crane et Friis, and **Eucommiithea** Friis et Pedersen (Kvacek and Pacltova, 2001; Mendes et al., 2010), it became apparent that **Eucommiidites** Erdtman ex Potonié is gymnosperm pollen.

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 monoletete 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 monoletete 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 isosporites.

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, ANEMIAEACEAE 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.

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 paleoenvironmental 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.

Declaration of Competing Interest

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

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Appendix A. Supplementary data

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1 Appendix A Uncertain dispersed spores and pollen

2 1. Uncertain Pteridophytes

3 The following 249 dispersed spore genera can not be linked to any specific extant or fossil plants:

4 *Acanthosporis* Mädlér, *Agastospora* Zhang, *Anemiidites* Ross, *Anulatzonites* Mädlér,
5 *Apicrassizonosporites* Kedves & Rákósy, *Apiculatisporis* Potonié & Kremp, *Asbeckiasporites* Brellie,
6 *Auritulina* Malyavkina, *Baculareticulosporis* Singh, Srivastava & Roy, *Baculatitriletes* Brellie,
7 *Baldurnisporites* Delcourt & Sprumont, *Biglobosisporites* Döring, *Bocciaspora* Eem, *Boseisporites*
8 Bharadwaj & Kumar, *Bothriotriletes* Fuglewicz, *Bracteolina* Malyavkina, *Bucculina* Malyavkina,
9 *Bulbella* Malyavkina, *Bullasporis* Krutzsch, *Buttinia* Boltenhagen, *Caliendrina* Malyavkina, *Callispora*
10 (Sukh) Bharadwaj et Kumar, *Camarozonotriletes* Naumova, *Camerozonosporites* Pant ex Potonié,
11 *Cardioangulina* Malyavkina emend. Potonié, *Cardiocolliculina* Malyavkina, *Cardiolina* Malyavkina,
12 *Cardiosectella* Malyavkina, *Catenulasporites* Zhang, *Cingulatisporites* Thomson, *Cingulatzonites*
13 Mädlér, *Cingutritetes* Pierce emend. Dettmann, *Cladophlebites* Malyavkina, *Clavatosporis* Song et
14 Zhang, *Colliculina* Malyavkina, *Compactisporites* Lu & Wang, *Conbaculatisporites* Klaus,
15 *Concavisporites* (Pflug) Delcourt & Sprumont, *Concavitriletes* Krutzsch, *Conipollenites* Cameron,
16 *Converrucosisporites* Potonié & Kremp, *Corculina* Malyavkina, *Corollisporites* Lu & Wang,
17 *Coronatispora* Dettmann, *Cosmosporites* Nilsson, *Crassimonoletes* Singh, Srivastava & Roy,
18 *Craterisporites* de Jersey, *Cyclina* Malyavkina, *Cyclinasporites* Nilsson, *Cyclosporites* Cookson &
19 Dettmann, *Cyclotriletes* Mädlér, *Cycloverrustriletes* Schulz, *Cymbellina* Malyavkina, *Datongsporites* Liu,
20 *Deltoidisporites* Danzé-Corsin & Laveine, *Deltoidospora* (Miner) Potonié, *Didecitriletes* Venkatachala &
21 Kar, *Dipteridaceaeauritulina* Malyavkina, *Distaverrusporites* Muller, *Divaricina* Malyavkina,
22 *Dongbeispora* Pu et Wu, *Dulhuntyispora* (Potonié) Balme et Hennelly, *Duplosporis* Pflug,
23 *Echinatisporites* Krutzsch, *Echizonospora* Bai, *Equisetacites* Malyavkina, *Equisetosporites* (Daugherty)
24 Singh, *Exinella* Malyavkina, *Filtrotriletes* van Hoecken-Klinkenberg, *Flabellisporites* Marcinkiewicz,
25 *Foveoinaperturites* Pierce, *Foveolatisporites* Bharadwaj, *Foveotriletes* Hammen ex Potonié,
26 *Gemmatriletes* (Hammen) Pierce, *Glabrina* Malyavkina, *Globulisporis* Mädlér, *Gradisporites* Döring,
27 *Granulatisporites* (Ibrahim) Potonié & Kremp, *Granulatosporites* (Imgrund) Dybová & Jachowicz,

28 *Grebespora* Jansonius, *Gordonispora* van der Eem, *Guangdongspora* Song, Li et Zhong, *Gushanispora*
29 Li, *Guttatisporites* Visscher, *Gyrina* Malyavkina, *Gyrinella* Malyavkina, *Habrozonosporites* Lu et Wang,
30 *Halosphaeropsis* Mädler, *Hekousporites* Yu, Zhang, Zhao et Song, *Hsuisporites* Zhang, *Hunanispora*
31 Shang, *Hymenoreticulisporites* Döring, *Hystrichosporis* Pacltová, *Ingentosporites* Busnardo et
32 Taugourdeau, *Intertriletes* Anderson, *Interulobites* Phillips, *Intrapunctatosporis* Krutzsch,
33 *Intrapunctosporis* Krutzsch, *Ischyosporites* Balme, *Jerseyiaspora* Kar, Kieser & Jain, *Keuperisporites*
34 Schulz, *Krutzschisporites* Kedves, *Laevigatosporites* Ibrahim, *Laevizonosporites* Döring,
35 *Lapposisporites* Visscher, *Leiotriletes* (Naumova) Potonie & Kremp, *Leschikisporis* Potonié,
36 *Levisporites* Ilina, *Liaoxisporis* Pu et Wu, *Limatulasporites* Helby et Foster, *Lobosporites* Nilsson,
37 *Lunzisporites* Bharadwaj & Singh, *Lygodiumidites* Malyavkina, *Maculatasporites* Tiwari, *Maexisporites*
38 Potonié, *Matthesisporites* Döring, *Medullina* Malyavkina, *Mesozoicisporites* Schulz, *Mitraesporites*
39 Zhang, *Monoleiotriletes* Krutzsch, *Monoletella* Malyavkina, *Monolites* Cookson ex Potonié,
40 *Muerrigerisporis* Krutzsch, *Murospora* Somers, *Narkisporites* Kannegieser & Kozur,
41 *Neotuberculatisporites* Zhang, *Obtusisporis* (Krutzsch) Pocock, *Occultosporites* Khlonova,
42 *Ocultosporites* Chlonova, *Orbella* Malyavkina, *Orbipatella* Malyavkina, *Orientalisporites* Zhang,
43 *Ornatisporites* Nagy, *Otynisporites* Fuglewicz, *Palaeospongisporis* Schulz, *Papillotriletes* Mädler,
44 *Paraconcavisporites* Klaus, *Paradoxisporites* Huang, *Paraklukisporites* Mädler, *Paralundbladispora*
45 Visscher, *Partina* Malyavkina, *Patellisporites* Ouyang, *Perinosporites* Schulz, *Periplecotriletes*
46 Naumova, *Peromonoletes* Couper, *Peromonolites* Couper, *Placulina* Malyavkina, *Polaneuletes*
47 Marcinkiewicz, *Politusella* Malyavkina, *Pollinaria* Malyavkina, *Polypodiaceoisporites* Potonié,
48 *Polypodiacites* Malyavkina, *Polypodiumidites* Malyavkina, *Poroplanites* Pflug, *Prikaspisporites* Kozur,
49 *Propterisispora* Ouyang & Li, *Psilamonoletes* Hammen, *Pterina* Malyavkina, *Pterinella* Malyavkina,
50 *Pterosphaeridia* Mädler, *Punctatosporites* Ibrahim, *Punctatriletes* Pierce, *Pusulosporites* Fuglewicz,
51 *Pyramidella* (Malyavkina) Potonié, *Radialisporis* Krutzsch, *Radorugoisporites* Zhang, *Radisporis* Bai,
52 *Reticuloidisporites* Busnardo et Taugourdeau, *Reticuloidosporites* Pflug, *Retioulatisporites* Brenner,
53 *Retiverrucispora* Liu, *Rogalskaisporites* Danzé-Corsin & Laveine, *Rotinella* Malyavkina,
54 *Rotverrusporites* Döring, *Rugospora* Neves & Owens, *Rugutriletes* (Hammen) Potonié, *Sagittella*

55 Malyavkina, *Santanghusporites* Huang et Xu, *Scabratriletes* Hammen ex Potonié, *Schizoplanites* Pflug,
56 *Scortea* Chlonova, *Seductisporites* Chlonova, *Sellaspora* Eem, *Semisporis* Pflug, *Seritriletes* Zhang,
57 *Sexaneuletes* (Fuglewicz) Marcinkiewicz, *Simozonotriletes* (Naumova) Potonié et Kremp,
58 *Simplicesporites* Leschik, *Skarbysporites* Erve, *Sphaerina* (Malyavkina) Delcourt et Sprumont,
59 *Sphaerinella* Malyavkina, *Spinotriletes* Mädler, *Spongiosisporis* Krutzsch, *Sporopollenites* (Erdtman)
60 Thiergart, *Stellisporites* Alpern, *Stenozonotriletes* Naumova, *Stoverisporites* Norvick & Burger,
61 *Stratexinis* Stach, *Striatisporis* Krutzsch, *Striatisporites* Leschik, *Striatizonites* Mädler, *Striatriletes*
62 Hammen ex Potonié, *Styxisporites* Cookson & Dettmann, *Tabellina* Malyavkina, *Talchirella* Pant &
63 Srivastava, *Tappanispora* Srivastava, *Tenerina* Krutzsch, *Tenuicontactosporites* (Han) Yu et Han,
64 *Thiergartisporis* Mädler, *Thomsonisporites* Leschik, *Thuringiatrilites* Schulz, *Tigrisporites* Klaus,
65 *Toripustulatisporites* Krutzsch, *Trachysporites* Nilsson, *Trachytriletes* Naumova, *Transbaculisporites*
66 Döring, *Triancoraesporites* Schulz, *Triangulina* Malyavkina, *Triaristella* Malyavkina, *Triassisporis*
67 Schulz, *Trichomanidites* Malyavkina, *Triletes* (Erdtman) Potonié, *Trilites* Cookson ex Couper,
68 *Trilobozonosporites* (Pant) Potonié, *Tripartites* (Schemel) Potonié et Kremp, *Triplanosporites* Pflug,
69 *Trizonatisporites* Leschik, *Trizonites* Mädler, *Tuberculatosporites* Imgrund, *Tuberella* Malyavkina,
70 *Tumulispora* Staplin & Jansonius, *Tympanea* Malyavkina, *Umbosporites* Newman, *Undulatisporites*
71 Pflug, *Undulatosporites* Leschik, *Undulipollis* Krutzsch, *Vallizonosporites* Döring, *Velamensporites*
72 Brelié, *Velatisporites* Döring, *Verexinis* Stach, *Verreticulisporis* Krutzsch, *Verrucatotriletes* van
73 Hoeken-Klinkenberg, *Verrucingulatisporites* Kedves, *Verrucosisporites* (Ibrahim) Potonie & Kremp,
74 *Viburamegaspora* Zhang, *Volucellina* Malyavkina, *Waltzisporea* Staplin, *Wulongspora* Yu et Zhang, and
75 *Zlivisporis* Pacltova ex Gupta.

76

77 **2. Uncertain Gymnospermae**

78 **The following 138 dispersed pollen genera can not be linked to any specific extant or fossil plant:**

79 *Abieticedripites* Malyavkina, *Acuminella* Malyavkina, *Aggerella* Malyavkina, *Aggerotsugella*
80 Malyavkina, *Aliferina* Malyavkina, *Alisporites* (Daugherty) Jansonius, *Aumancisporites* Alpern,
81 *Bactrosporites* Chen, *Ballosporites* Mädler, *Bascanisporites* Balme & Hennelly, *Bennettiteapollenites*

82 (Thiergart ex Potonie) Pocock, *Bhardwajispora* Jansonius, *Bialina* Malyavkina, *Brachysaccus* Mädler,
83 *Bullulina* Malyavkina, *Chasmatosporites* (Nilsson) Pocock et Jansonius, *Circellina* Malyavkina,
84 *Conaletes* Reinhardt et Schön, *Concentrisporites* Wall, *Confertisulcites* Anderson, *Confusopollis* Pflug,
85 *Corollaria* Malyavkina, *Crassipollenites* Nilsson, *Cristatisaccus* Mädler, *Curvimonocolpites*
86 Leidelmeyer, *Cycadaceaeplatychila* Malyavkina, *Cycadopites* (Wodehouse) Wilson & Webster,
87 *Cyclosaccus* Mädler, *Dacryrotundina* Malyavkina, *Dilaterella* Malyavkina, *Diplosacculina* Malyavkina,
88 *Dipterella* Malyavkina, *Disaccites* Cookson, *Divisiella* Malyavkina, *Entylissa* (Naumova) Potonié,
89 *Exiguosporites* Leschik, *Extremella* Malyavkina, *Falcina* Malyavkina, *Falcisporites* (Leschik) Klaus,
90 *Ginkgoacites* Malyavkina, *Ginkgoidites* Malyavkina, *Granamegamonocolpites* Jain,
91 *Granamultivesiculites* Pierce, *Granosaccus* Mädler, *Granulatasporites* Leschik, *Guizhoupollis* Shang,
92 *Gynkaletes* Lubert, *Gynkgaletes* Lubert, *Haojiagoupollenites* Huang, *Haploaliferina* Lubert,
93 *Haplosacculina* Malyavkina, *Heliosaccus* Mädler, *Inaperturopollenites* Pflug & Thomson, *Involutella*
94 Malyavkina, *Juniperidites* Malyavkina, *Jurea* Malyavkina, *Klausipollenites* Jansonius,
95 *Laevigatasporites* (Potonié & Gelletich) Ibrahim, *Latosaccus* Mädler, *Limbatella* Malyavkina,
96 *Lorisporites* Leschik, *Megamonoporites* Jain, *Minutosaccus* Mädler, *Monoptycha* Khlonova,
97 *Monosulcites* Cookson ex Couper, *Naumovaspora* Jansonius, *Navisulcites* Anderson, *Oblatinella*
98 Malyavkina, *Orbicularia* Malyavkina, *Pachytella* Malyavkina, *Paleoconiferus* Bolchovitina, *Paleopicea*
99 Bolchovitina, *Panucella* Malyavkina, *Panucellina* Malyavkina, *Paravesicaspora* Klaus, *Perotrilites*
100 (Erdtman) Couper, *Piceidites* Malyavkina, *Piceites* Bolchovitina, *Pinites* Bolchovitina, *Pinojella*
101 Malyavkina, *Pityopollenites* Reissinger, *Pityosporites* (Seward) Manum, *Platychila* Malyavkina,
102 *Platyimbina* Malyavkina, *Podocarpacites* Malyavkina, *Pododipterella* Malyavkina, *Protabies*
103 Bolchovitina, *Protoconifera* Khlonova, *Protopicea* Bolchovitina, *Prototaeniaesporites* Zhang,
104 *Pseudillinites* Mädler, *Pseudopicea* Bolchovitina, *Pseudopinus* Bolchovitina [?], *Pseudoplicatella*
105 Malyavkina, *Pseudopodocarpus* Bolchovitina, *Psilainaperturites* Pierce, *Psophosphaera* Naumova,
106 *Punctabivesiculites* Pierce, *Punctainaperturites* Pierce, *Punctamonocolpites* Pierce,
107 *Punctamultivesiculites* Pierce, *Quadraeculina* Malyavkina, *Rectosulcites* Anderson, *Renopollis* Yu et
108 Miao, *Retectina* Malyavkina, *Retibivesiculites* Pierce, *Rimaesporites* Leschik, *Rotundina* Malyavkina,

109 *Ruginaperturites* Pierce, *Saccopollis* Pflug, *Sacculina* Malyavkina, *Saeptasporites* Leschik,
110 *Samaropollenites* Goubin, *Schismatosporites* Nilsson, *Schizosaccus* Mädler, *Scutrina* Malyavkina,
111 *Shanbeipollenites* Qian et Wu, *Sinuella* Malyavkina, *Spheripollenites* Couper, *Spinainaperturites* Pierce,
112 *Spirellina* Malyavkina, *Sulcusicystis* Bai, *Tenuisaccites* de Jersey, *Tetrasaccus* Pant ex Maithy,
113 *Triangulisaccus* Ouyang et Li, *Trisphaerea* Malyavkina, *Trizonaesporites* Leschik, *Tubermonocolpites*
114 Qu, *Umbrososaccus* Mädler, *Utricellina* Malyavkina, *Velosporites* Hughes & Playford, *Ventosella*
115 Malyavkina, *Verrumonocolpites* Pierce, *Verrumonoporites* Pierce, *Verrusaccus* Schulz, *Walchiites*
116 Bolchovitina, *Wulanpollenites* Li, and *Zonalasporites* Leschik.