

In situ spores of marattialean ferns from the Triassic in Central and Northern Europe

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ABSTRACT

The Middle to Upper Triassic successions of Europe have yielded several rich and well-preserved palaeofloras in which fertile fronds of marattialean ferns with conspicuous sporangia are common components. Here we describe the in situ spores of several marattialean fern species from these floras belonging to the genera *Asterotheca*, *Merianopteris*, *Danaeopsis*, and *Symopteris* with a focus on intra- and interspecific variability. Knowing this spore variability is important for the interpretation of dispersed spores and may provide insights into phylogenetic relationships and ecological influences. The spores of the various *Asterotheca* species are generally similar among each other, but Ladinian specimens are distinct as they have a punctate exine, whereas those from the Carnian are laevigate or microverrucate, rarely verrucate. *Merianopteris augusta*, long regarded as a junior synonym of *A. merianii*, differs markedly in the size and ornamentation of its spores. The spores of the various *Danaeopsis* and *Symopteris* species are generally circular, trilete, smooth-walled or discreetly ornamented, and mostly correspond to *Todisporites* or *Punctatisporites*. However, the rays of the trilete mark are often of unequal length. The various species mostly differ in the average size of the spores, but with notable outliers, potentially pointing to macromorphologically indistinguishable but biologically distinct lineages. In samples with sufficient yield, abnormally small, dense, and often dark spores that we interpret as abortive can be observed. These occur with frequency in every plant, usually in low frequencies, but with considerably high frequencies in a few individuals, which may indicate pathological conditions or natural hybridisation.

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1. Introduction

The Marattiales or marattialean/marattioid ferns belong to the eusporangiate ferns, which are marked by sporangia developing from multiple epidermal cells and with a high output of spores. They are a sister taxon to the leptosporangiate ferns (“true ferns”) and have a rich fossil record starting in the Carboniferous (e.g., Rothwell et al., 2018). They typically have large fronds, and some extinct forms were tree-like. Extant Marattiales are represented by a single family (Marattiaceae Kaulf.) and six currently accepted genera (*Marattia* Sw., *Danaea* Sm., *Angiopteris* Hoffm., *Christensenia* Maxon, *Eupodium* J.Sm., *Ptisana* Murdock; Murdock, 2008a, 2008b). Recent total-evidence phylogenetic analyses recognize Psaroniaceae Unger as a second, extinct family

(Rothwell et al., 2018; Lehtonen et al., 2020). The Psaroniaceae in this sense have a fossil record up to the Cretaceous (Rothwell et al., 2018).

Fossils of Marattiales are especially abundant and diverse in Pennsylvanian to early Permian floras but are also common in the Middle and Late Triassic deposits of Europe. Fertile specimens often have conspicuous sori which made them an early target for the study of in situ spores (Nathorst, 1908). The in situ spores of Palaeozoic Marattiales have been reviewed by Bek (2021) and grouped into seven morphological types based on palynological criteria. Although the in situ spores of many Triassic plant species with sufficiently well-preserved fertile specimens have been studied repeatedly in the past (e.g., Balme, 1995), these investigations were rarely comprehensive. In particular, comparisons with dispersed sporomorph taxa are not always made, and intraspecific morphological variations are not commonly considered. The latter are important, because it is known that the intraspecific variations seen in in situ spores can correspond to differences between various species and even genera among dispersed sporomorphs, whereas conversely,

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different plant macrotaxa may produce similar spores (e.g., Balme, 1995; Taylor et al., 1996; Schweitzer et al., 1997; Nowak et al., 2022).

This work is part of an ongoing effort to reinvestigate the in situ sporomorphs of the European Triassic with a focus on morphological variability. A previous study concerning the in situ spores of leptosporangiate ferns has already been published (Nowak et al., 2022). In this work, we present new findings of in situ spores of marattialean ferns from the Triassic in Central and Northern Europe and discuss their intra- and interspecific variability. Our main goals are to determine the normal range of variability for individual plants and species and to distinguish characters that can serve to identify specific taxa. A secondary goal is to identify patterns in spore morphology that can be linked to different stages of spore maturation and/or environmental stress and to determine the frequency of abnormal spores.

2. Materials and methods

For this study, compression fossils of marattialean ferns with fertile leaves in organic preservation from several palaeofloras of the European Middle–Upper Triassic successions were sampled for in situ spores. This includes the Ladinian palaeoflora of the Erfurt Formation (also known as “Lettenkeuper”) at Thale, Bibersfeld, and Rockhausen in Germany (Kustatscher and Van Konijnenburg-van Cittert, 2011; Kustatscher et al., 2011, 2012a, 2012b; Kelber, 2015), the Carnian palaeofloras of the Lunz Formation from the surroundings of Lunz am See and Gaming, Austria (e.g., Dobruskina, 1998; Pott et al., 2018) and the Klettgau Formation near Basel, Switzerland (Neuwelt, Münchenstein and Moderhalde near Pratteln; e.g., Leschik, 1955; Kräusel and Leschik, 1955, 1959; Kräusel and Schaarschmidt, 1966), and the Rhaetian palaeoflora of the Höganäs Formation at Billesholm, Sweden (e.g., Nathorst, 1878; Lundblad, 1950).

The studied specimens are part of the palaeobotanical collections of the Natural History Museum of Vienna, Austria (NHMW; sample numbers with “NHMW-Geo”), the Geological Survey of Austria (GBA), the Museum für Naturkunde Berlin, Germany (MfN; sample numbers with “MB.Pb.”), the Stuttgart State Museum of Natural History, Germany (SMNS; sample numbers starting with “P”), the Natural History Museum Basel, Switzerland (NMB; sample numbers starting with “B”), and the Swedish Museum of Natural History in Stockholm, Sweden (NRM; sample numbers starting with “S”).

Sporangia were extracted manually from sufficiently well-preserved fertile specimens and treated with a variation of the Schulze method (that was also used in Nowak et al., 2022). This method, i.e., maceration with the Schulze reagent (nitric acid [HNO₃] and potassium chlorate [KClO₃], after Schulze, 1855) is effectively the standard method for the treatment of in situ sporomorphs and cuticles, but the details of the protocol can vary widely. Adjustments are made routinely according to the studied material, but this requires testing and introduces the possibility that differences in the maceration protocol influence the characters that are ultimately observed in the sporomorphs. To prevent such artefacts and to streamline the maceration process for materials from different localities, we tried to find a standard protocol by testing varieties of the Schulze method with subsamples from specific sampling locations on specimens of *Asterotheca merianii*. This species has particularly large sporangia grouped in synangia, providing an abundance of material from the same spot, which can be expected to be as homogenous as possible. Subsamples were treated with different concentrations of nitric acid, with different added amounts of potassium chlorate, and for different durations. Additionally, the effect of different durations of treatment with potassium hydroxide (KOH) was tested.

The protocol that was chosen as standard is a variation of the one proposed by Krings and Kerp (1997) for cuticles. The sample is placed into a glass tube together with a few potassium chlorate crystals

corresponding to little more than the amount of organic matter in the sample. Under a fume hood, 3 ml of nitric acid with a concentration of 30% are added. For the following three days, 1 ml of nitric acid with a concentration of 67.5% is added each day. After an additional day, the acid is decanted, the tube is filled with deionized water, then again decanted and filled with water, to wash out the acid. The water is taken off once more and a few drops of potassium hydroxide (5%) are added. After a couple of seconds, the tube is filled again with deionized water and decanted twice. If the sample reacts fast (the solution turning brown), then a bit of water is added immediately.

Macerated residues were picked under a dissecting microscope, and spores were mounted on glass slides in hot (liquefied) glycerin jelly. Some larger spore masses were drawn apart with a needle to isolate single spores. They were then covered with a cover glass. The slides were examined and photographed via transmitted light microscopy using a Leica DM 2500 LED microscope with a Leica DMC4500 mounted camera. Subsamples were pictured via scanning electron microscopy (SEM) using a ZEISS EVO 40 at the MUSE (Trento, Italy) and a JEOL JSM-6390 at the NHMW. Some of the material used for SEM was acetylated before scanning. Measurements were taken with the software Fiji (ImageJ version 1.53c; Schindelin et al., 2012). Diagrams were made with R (version 4.1.2; R Core Team, 2018) using the packages ggplot2 (version 3.3.5; Wickham, 2016), ggExtra (version 0.9; Attali, 2019), and ggridges (version 0.5.3; Wilke, 2021).

The identification of abortive spores follows the criteria described by Nowak et al. (2022): Spores are considered abortive (not well-developed), if they are significantly smaller, darker, and seemingly compressed (collapsed) from all directions, as opposed to normally compressed spores, which may be flattened, folded, or pinched. Compared to regular specimens, abortive spores are also often strongly wrinkled. Compared to regular specimens, abortive spores are also often strongly wrinkled. Similarly, abortive spores can be identified in recent ferns by having a collapsed exine, blackish colours, and anomalous shapes (Hornych and Ekrt, 2017). It should be noted that abortive spores in hybrids can be larger than regular spores while being opaque. In fossil spores, colours are affected by preservation and maceration. Consequently, we did not find any black spores, but a distinct difference in brightness can be observed. The shapes of the fossil spores are also often obscured due to subsequent compression, which leaves a number of uncertain cases. Hornych and Ekrt (2017) introduced the spore abortive index (SAI) as a metric for the percentage of abortive spores to all examined spores in a sample and determined that an assessment of 1000 spores leads to accurate numbers. We use a similar percentage but found it necessary to provide separate numbers for certain and uncertain cases of spore abortion. The amount of spores per sample that were assessed varies, due to limitations from the size of the samples and the separability of the spores.

As in situ spores were not dispersed prior to burial, they can be considered more or less immature, unless they represent only the sparse remnants after dispersal. Therefore, spores in complete sporangia do not necessarily show the same features as typically mature dispersed spores, but may still be comparable if they were close to being released. Signs of considerable immaturity are: A comparatively thin exine; a lack of or weakly expressed ornamentation; relatively small spore sizes; retention of tetrads or tightly joined spore masses; a triangular amb (if the mature spores are more circular); unequal appearances of spores from different sporangia on the same fossil (e.g., Potonié, 1962; Lugardon, 1990).

3. Systematic palaeobotany

Order: Marattiales Link, 1833

Family: PSARONIACEAE Unger, 1842

Genus: *Asterotheca* Presl ex Corda, 1845

Type species: *Asterotheca sternbergii* (Göppert) Presl, 1845

Remarks: Various authors have placed *Asterotheca* and other Palaeozoic/Mesozoic genera in the families Marattiaceae Berchtold et Presl, 1820, Psaroniaceae Unger, 1842 or Asterothecaceae Sporne, 1962. The relationship of the Asterothecaceae to the Marattiaceae and Psaroniaceae is unclear. Recent phylogenetic analyses have only recognized the latter two families (Rothwell et al., 2018; Lehtonen et al., 2020). *Asterotheca* was not included in these analyses, but representatives of the closely comparable Palaeozoic genus *Acitheca* Schimper in Schimper et Schenk, 1879 (see Zodrow et al., 2006) have been placed in the Psaroniaceae. We, therefore, consider *Asterotheca* to be assignable to the Psaroniaceae as well.

Asterotheca merianii (Brongniart) Stur ex Krasser, 1909

Plate I, 1–4, Plate V, 1–17, Plate VI, 1–7, Plate VII, 4, Plate IX, 1–3, Supplementary Plate I, 1–2

Selected references (for further references see Pott et al., 2018):

1834 *Pecopteris meriani*, Brongniart (in Brongniart, 1828–1837), p. 289, pl. 91, fig. 5

1885 *Asterotheca meriani*, Stur, p. 97, no illustration

1909 *Asterotheca meriani* (Brongniart) Stur, Krasser, p. 17, 18, 20, 32, 43, no illustration

1956 *Asterotheca meriani* (Brongniart) Stur, Bharadwaj and Singh, p. 51, pl. 1, figs. 1–5, pl. 2, figs. 6–25

2018 *Asterotheca merianii* (Brongniart) Stur, Pott et al., p. 7, pls. 2–5, 7, pl. 6, figs. 1–6, non fig. 7, text-fig. 3

Localities: Lunz am See and Gaming, Austria; Moderhalde near Pratteln and Neuwelt, Münchenstein, Switzerland.

Stratigraphic horizons: Lunz Formation, Carnian (Lunz am See and Gaming); Klettgau Formation, Carnian (Moderhalde near Pratteln and Neuwelt, Switzerland).

Studied material: NHMW-Geo: 1845/0051/0013–14, 1845/0052/0003, 1878B/0006/9946, 1882/0013/3056, 1882/0013/3059, 1883/

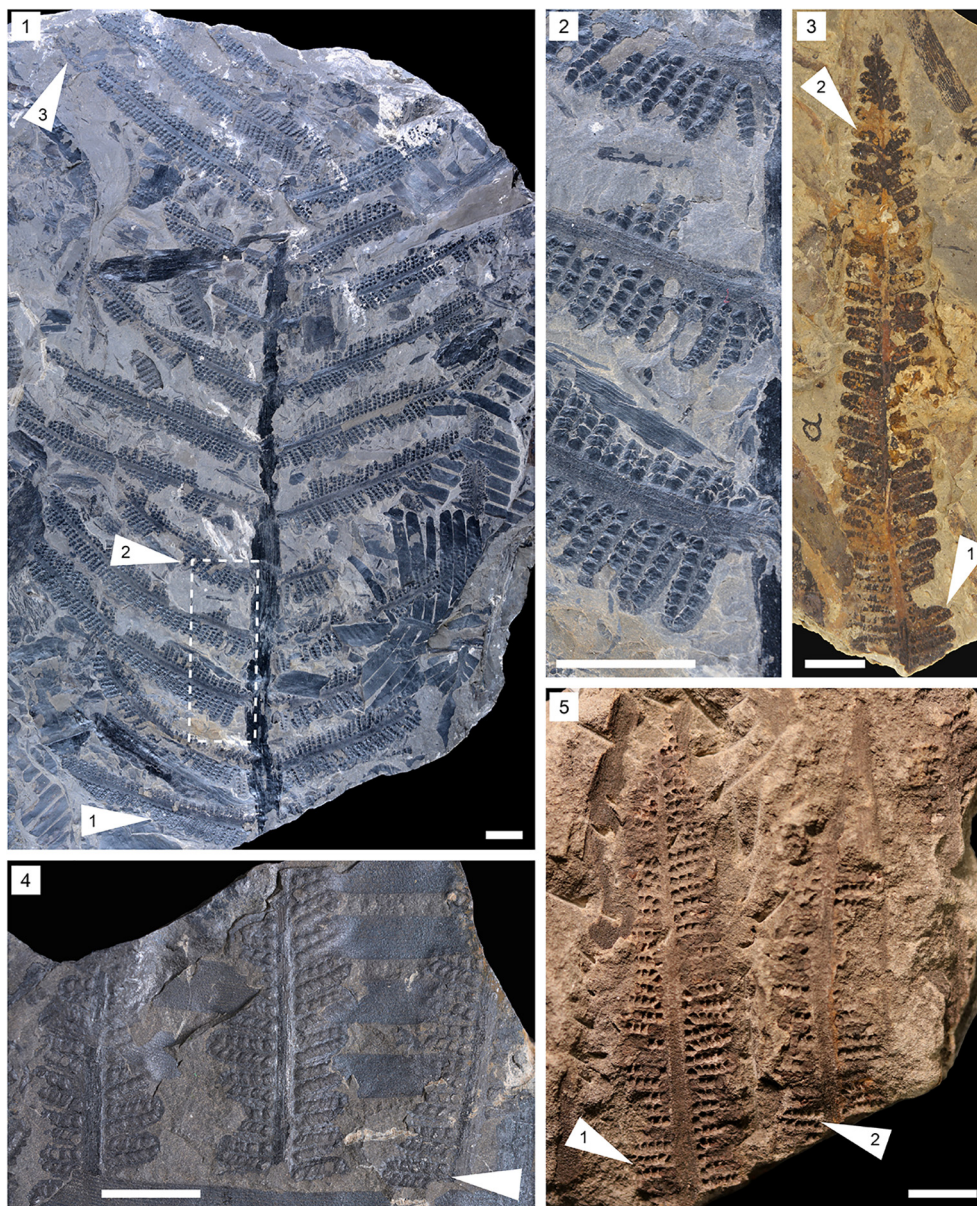


Plate I. Macrofossils of *Asterotheca merianii* from the Carnian of Austria and Switzerland and *Asterotheca* cf. *thalensis* from the Ladinian of Germany. 1–2. NHMW-Geo 1884/0012/1214, Lunz am See, Austria, Carnian. 2. Detail of the specimen in fig. 1 (area indicated by white dashed box) showing the pinnules with conspicuous synangia. 3. B3611, Moderhalde near Pratteln, Switzerland, Carnian. 4. NHMW-Geo 2010/0102/0207, Gaming, Austria, Carnian. 5. *Asterotheca* cf. *thalensis* MB.Pb.2010/83, Thale, Germany, Ladinian. White arrows indicate sampling positions. Scale bars = 10 mm.

0017/5855, 1883/0017/5929, 1884/0012/1209, 1884/0012/1214, 1885/0012/3889, 1885/0012/3930, 1885/0012/3932, 1885/0012/3939, 1885/0012/3954, 1885/0012/3963, 1885/0012/4012, 1885/0012/4069, 1885/0012/4093, 1887/0001/0002, 1887/0001/0022, 2010/0102/0029, 2010/0102/0087, 2010/0102/0168, 2010/0102/0183, 2010/0102/0189, 2010/0102/0196, 2010/0102/0205, 2010/0102/0207, 2019/0185/0002–06.

NMB: B3611, B3614.

MfN: MB.Pb.2003/1099, MB.Pb.2019/281

NRM: S148225-02, S148250, S148530, S148543-02, S148569.

Description of macroremains: The frond fragments are bipinnate, with a strong rachis (up to 25 mm wide) and oppositely to suboppositely inserted pinnae (Plate I, 1). The pinnae are lanceolate to narrow triangular, up to 180 mm long and 15–30 mm wide, and attached at an angle of 50–90°. Pinnules are tongue-shaped (up to 10 × 5 mm) with a rounded apex and attached (almost) perpendicularly, with broad basis to the rachis (Plate I, 2–4). The midrib is distinct with 4–6 pairs of secondary veins arising at an angle of 45–60° (Supplementary Pl. I, 1, 2). Secondary veins bifurcate once in the proximal third of the lamina. Midribs become particularly evident in fertile pinnules (Plate I, 2–4), where the bifurcations of the secondary veins become invisible. In fertile pinnules, several pairs of sori, left and right from the rachis are attached between the veins, and there is one terminal sorus

(Plate I, 2). The sori are 0.9–1.4 mm in diameter and consist of four oval to almost pyramidal sporangia (0.5–0.9 mm in diameter), which are basally connate.

Description of in situ spores: The spores are circular to slightly oval, with a monolete or trilete aperture (Fig. 1A–D) and a diameter of 27–59 µm (mean: 42 µm; length to width ratio up to 1.4:1; Fig. 2). Spores from Lunz have with few exceptions a laevigate or microverrucate, rarely verrucate surface ornamentation. The size and appearance of the aperture varies significantly within and to some degree between individual sporangia (Fig. 3), whereas the ornamentation is rather consistent even across multiple sampling points on a particular frond. The ornamentation does vary between individuals in the Lunz flora, with most samples containing microverrucate and laevigate spores. Spores from specimen NHMW-Geo 1878B/0006/9946 are partly microverrucate and partly verrucate with verrucae measuring 1–1.7 µm in diameter (Plate V, 12–13). A few other samples from Lunz contained spores with a wavy/bumpy surface that could be described as verrucate (Plate V, 15–16; Plate VI, 4), but these appear to be cases of exine thinning and deformation rather than thickening. This pattern is limited to spores on the outer layers of the sporangia and in some cases to only one side of the spores, whereas the rest of the spores show the common laevigate to microverrucate ornamentation. Therefore, this is most

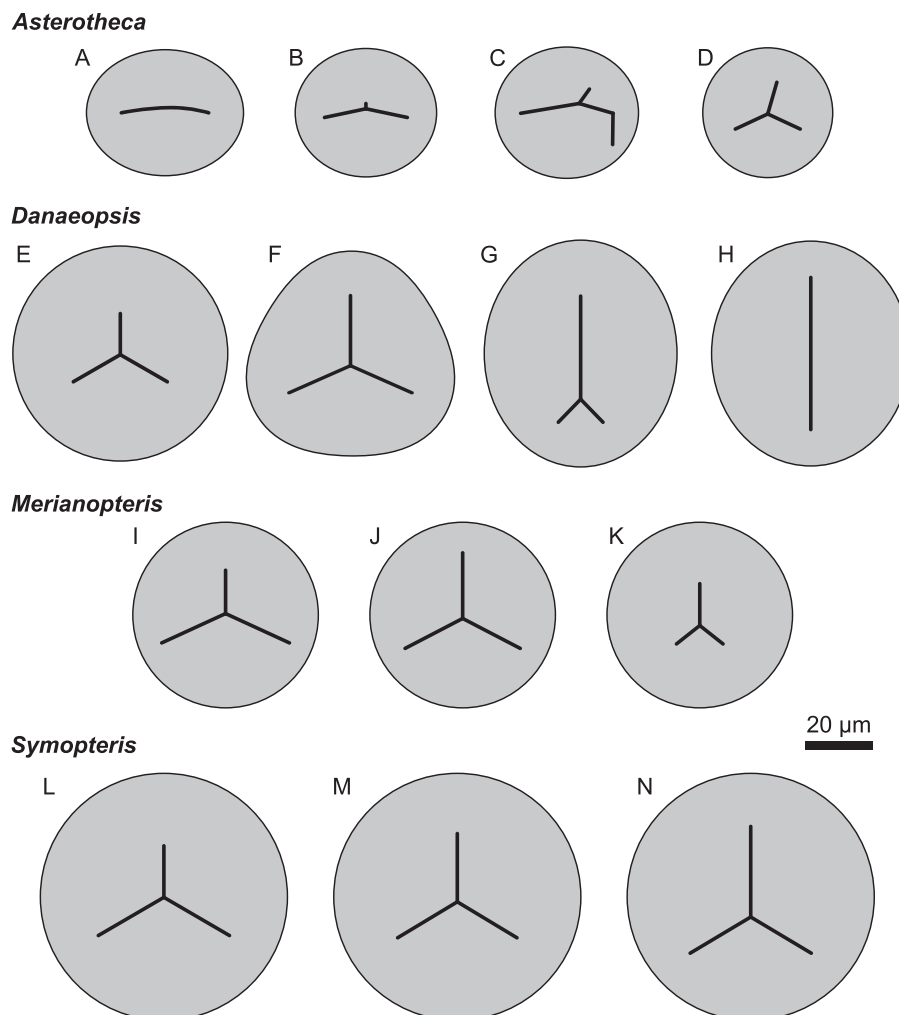


Fig. 1. Examples of basic spore morphologies observed in *Asterotheca*, *Danaeopsis*, *Merianopteris*, and *Symopteris*. A–D. *Asterotheca*. A. Monolete, oval amb. B. Short secondary laesura, slightly oval amb. C. Inclined, eccentric and opposite, terminal secondary laesurae, slightly oval amb. D. Strongly bent primary laesura with long secondary laesura = quasi-trilete, circular amb. E–H. *Danaeopsis*. E. Trilete mark with one reduced ray, circular amb. F. Trilete mark with equal rays, convex rounded triangular amb. G. Trilete mark with two reduced rays and one elongated ray, oval amb. H. Monolete mark, oval amb. I–K. *Merianopteris*. I. Trilete mark with one reduced ray. J. Trilete mark with equal rays. K. Short trilete mark with one relatively longer ray. L–N. *Symopteris*. L. Trilete mark with one reduced ray. M. Trilete mark with equal rays. N. Trilete mark with one elongated ray.

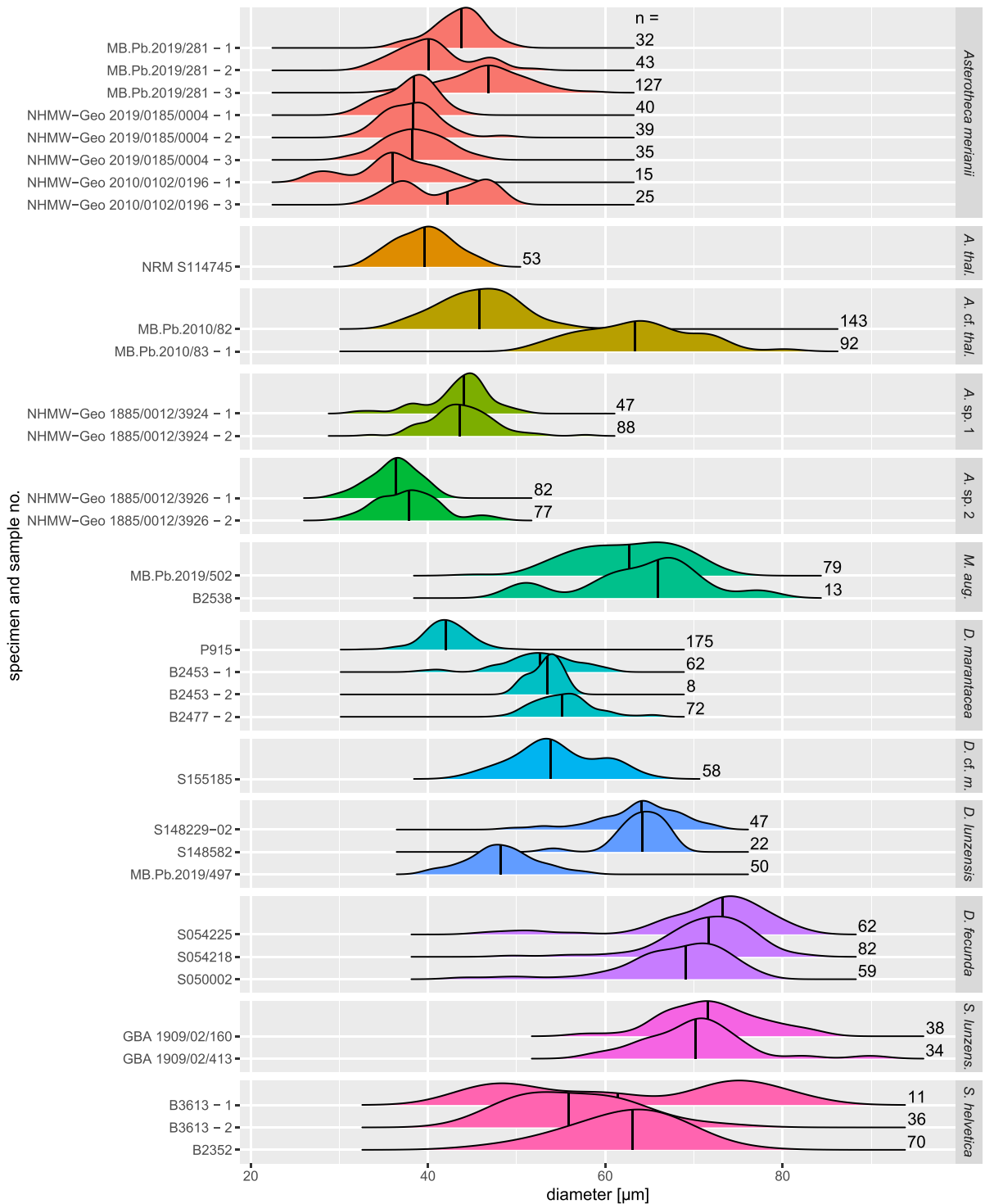


Fig. 2. Size distribution of in situ spore diameters per sample.

likely an effect of alteration. A few samples contained rare spores with a punctate exine. Some of these show punctations across the entire surface (Plate VII, 4), but they are confined to limited areas (sometimes clearly imprints of mineral aggregates; e.g., Plate V, 17) in many cases, again suggesting alteration. Samples from Gaming in Austria (Plate V, 4–5) and Moderhalde near Pratteln in Switzerland (Plate V, 3) yielded only poorly preserved spores that did not show details of the ornamentation or aperture. Abortive spores (Plate XI, 1–3) are present in all specimens and in all but one sample from the Lunz flora, with

frequencies of <1–33% (and up to 16% uncertain cases; Fig. 4). The highest frequencies were observed in three samples from specimen NHMW-Geo 2010/0102/0196.

Discussion: Nathorst (1908) first reported the extraction of spores from *A. merianii* but did not provide many details. Bharadwaj and Singh (1956), and later Pott et al. (2018) studied the spores in more detail and described them similarly to our results (see also Potonié, 1962, 1967; Andrews in Boureau, 1970; Balme, 1995). Bharadwaj and Singh (1964) specified that in situ spores of *A. merianii* correspond to

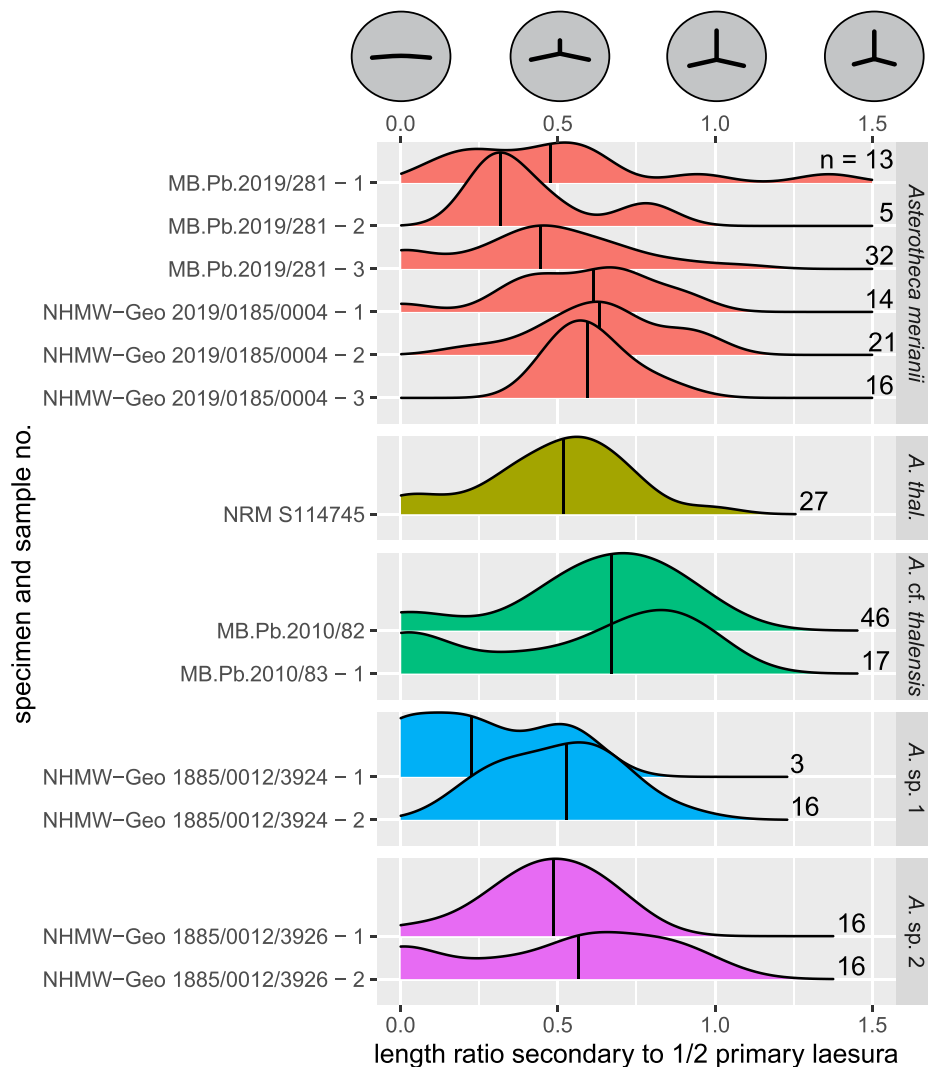


Fig. 3. Comparative ratios of the length of the secondary laesura relative to half the length of the primary laesura in *Asterotheca*. At a ratio of 0, the spore is monolete with only a primary laesura; at a ratio of 1, the spore can appear to be trilete with equal rays. *A.* = *Asterotheca*; *A. thal.* = *Asterotheca thalensis*.

the dispersed taxon *Leschikisporis aduncus* (Leschik) Potonié, 1958 emend. Bharadwaj et Singh, 1964, which was described from Lunz as well.

See also discussion for *Asterotheca thalensis* and *A. cf. thalensis* below.

Asterotheca thalensis Kustatscher et Van Konijnenburg-van Cittert, 2011

Plate VII, 1, 5–8, Plate XI, 7, Supplementary Plate I, 4

References:

2011 *Asterotheca thalensis*, Kustatscher and Van Konijnenburg-van Cittert, p. 214, text-figs. 2A–G, 12B

Localities: Thale, Germany.

Stratigraphic horizons: Erfurt Formation, Ladinian (Thale).

Studied material: NRM: S114745.

Description of macroremains: The frond fragments are bipinnate, with a strong rachis and (sub-)oppositely inserted pinnae (Supplementary Pl. I, 4). The pinnae are lanceolate, up to 40 mm long and 10 mm wide, and attached with an angle of 60–80°. The pinnules are ovate (4–5.5 × 2.5–3 mm) with a rounded apex, attached at an angle of 60–80° and with a broad basis to the rachis. Pinnules are inserted very closely and imbricate slightly. The first basicopic pinnule is slightly larger than the other ones and is sometimes partly attached to the

main rachis. Apically, the pinnules decrease in size and finally fuse at the apex. The midrib is distinct, secondary veins arise from the midrib, curve outwards and fork once. Three to four pairs of closely spaced sori are attached to the lower side of the pinnules, each at the end of a secondary vein. The sori (0.9–1.5 mm in diameter) have a square to slightly roundish outline and are composed of four sporangia. Sporangia are roundish to oval (~0.8 × 1.3 mm) and yielded a large number (>1000) of spores (see Kustatscher and Van Konijnenburg-van Cittert, 2011).

Comparison: *Asterotheca thalensis* resembles *Pecopteris latepinnata* Leuthardt, 1904 from the Carnian Neuwelt flora in the similar gross morphology of its pinnules, although in the latter species they are more loosely spaced, and the secondary veins bifurcate more often. *Pecopteris callipteroides* Hsü et Chu in Hsü et al., 1974 from the Upper Triassic of Yungjen (China) is similar to *Asterotheca thalensis* in having an enlarged basicopic pinnule but differs in having larger pinnules with a denser pecopterid venation. *Asterotheca merianii* (Brongniart) Stur, 1885 differs because the basicopic pinnules are missing in the latter and the pinnules and pinnae are generally inserted perpendicularly. *Asterotheca rigbyana* Herbst, 1977 from the Upper Triassic of Argentina resembles slightly in pinnule shape, although the pinnules are larger, the secondary veins never fork, and each pinnule contains more sori.

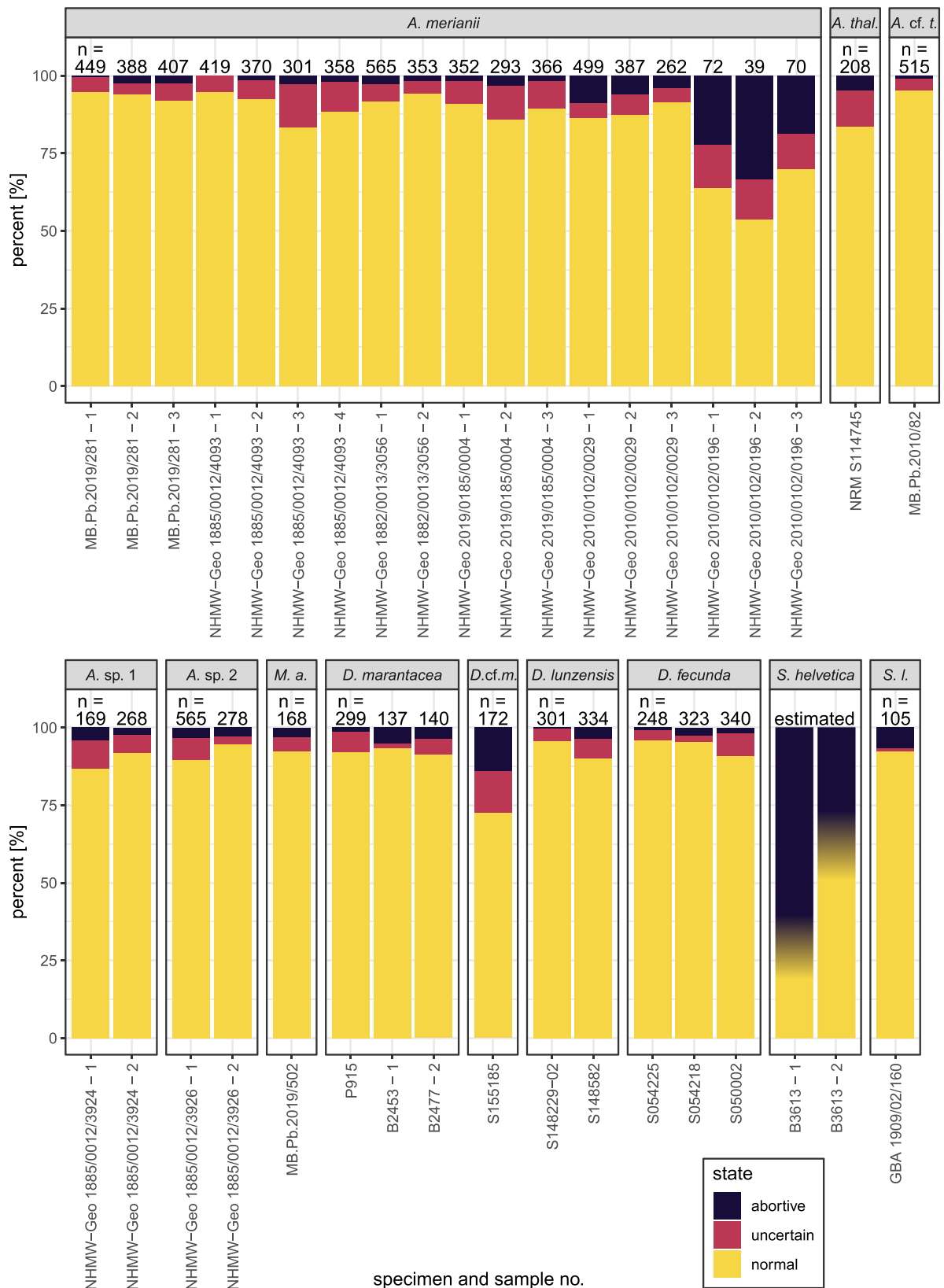


Fig. 4. Percentages of abortive spores per sample. *A.* = *Asterotheca*; *A. thal.* = *Asterotheca thalensis*; *A. cf. t.* = *Asterotheca cf. thalensis*; *M. a.* = *Merianopteris augusta*; *D.* = *Danaeopsis*; *D. cf. m.* = *Danaeopsis cf. marantacea*; *S.* = *Sympteris*; *S. l.* = *Sympteris lunzensis*.

Pecopteris mexicana Newberry, 1876 from the Upper Triassic of Sonora (Mexico) differs from *A. thalensis* in having acute pinnules and the presence of sori in the basal part of the pinnules only although the morphology of the sori is not solved completely.

Description of in situ spores: The spores are oval to approximately circular, with a monolete or triletole aperture (Fig. 1A–D) and a diameter of 33–46 μm (mean: 40 μm ; Fig. 2). The size and appearance of the aperture varies within the sample (Fig. 3). Most of the spores are triletole with a more or less straight main laesura and a secondary slit of up to about half of the length of the former but usually shorter going off approximately perpendicular near the center of the main laesura. The ornamentation is consistently punctate, but the density of the puncta varies between individual spores. Abortive spores (Plate XI, 7) are present with a frequency of at least 5% (12% uncertain; Fig. 4).

Discussion: *Asterotheca thalensis* Kustatscher et Van Konijnenburg-van Cittert, 2011 was described from the Erfurt Formation at Thale and reported to co-occur with *A. merianii* (Kustatscher and Van Konijnenburg-van Cittert, 2011). Pott et al. (2018) interpreted *A. thalensis* and *Merianopteris augusta* (see below) as distal frond portions and, therefore, junior synonyms of *A. merianii*. We did not obtain new in situ samples of specimens fitting in *A. thalensis* but reexamined the old samples studied and figured by Kustatscher and Van Konijnenburg-van Cittert (2011). In that original description, they were described as granulate, but we can now emend that they are punctate. We also found the spores to be larger than originally described (27–36 μm), which may be attributed to swelling due to the mounting medium. See also discussion for *Asterotheca* cf. *thalensis*.

Asterotheca cf. *thalensis* Kustatscher et Van Konijnenburg-van Cittert, 2011

Plate I, 5, Plate VI, 14–17, Plate VII, 9–12, Plate XI, 8, Supplementary Plate I, 6–7

References:

2011 *Asterotheca merianii* (Brongniart) Stur, Kustatscher and Van Konijnenburg-van Cittert, p. 210, text-figs. 1, 12A.

Localities: Thale, Germany.

Stratigraphic horizons: Erfurt Formation, Ladinian.

Studied material: MN: MB.Pb.2000/244, MB.Pb.2000/255a, MB.Pb.2010/478, MB.Pb.2010/82–83.

Description of macroremains: The frond fragments are bipinnate with a strong rachis, decreasing apically, and oppositely to suboppositely inserted pinnae (Plate I, 5; Supplementary Pl. I, 6–7). The pinnae are up to 80 mm long and basally up to 15 mm wide, apically to 5 mm width. The pinna rachis arises almost perpendicularly from the main rachis. The elongated pinnules (4–10 x 3–3.5 mm) with a rounded apex are attached (almost) perpendicularly and with a broad basis to the rachis; there is a single apical pinnule. The midrib is distinct with 4–6 pairs of secondary veins arising at an angle of 45–60°. The secondary veins bifurcate commonly halfway through the lamina (Supplementary Pl. I, 7). The midrib is particularly evident in fertile pinnules, where the bifurcations of the secondary veins disappear (Plate I, 5). The lower surface of the fertile pinnules is covered by 4–5 pairs of sori plus one terminal sorus, attached to the area between the veins. Sori are 0.9–1.5 mm in diameter, consisting of four oval to almost pyramidal sporangia which are basally connate. Sporangia are c. 1 x 1.5 mm in diameter and yielded a large number (> 1000) of spores.

Comparison: The specimens assigned only putatively to *Asterotheca thalensis* differ from those assigned to *Asterotheca thalensis* by the bigger size (at least twice as big compared to *A. thalensis*) and higher angle of attachment of the pinnae and pinnules, the not so evident basiscopic pinnule, the higher number of sori on each pinnule (4–5 against 3–4 pairs in *A. thalensis*) and the slightly bigger sporangia (1 x 1.5 mm against 0.9–1.5 mm in diameter). It resembles noticeably the classical *Asterotheca merianii* as described from Neuwelt and Lunz, to which it has been originally assigned by Kustatscher and Van Konijnenburg-van Cittert (2011), based on the general shape (narrow triangular

and size of the pinnae, as well as wider pinnules (up to 5 mm wide). It differs however from *A. merianii* because of the smaller dimensions of the pinnae (80 x 15 mm against 180 x 15–30 mm in *A. merianii*), the slightly narrower pinnules (4–10 x 3–3.5 mm against 10 x 5 mm), the slightly more distal point of bifurcation of the secondary veins (halfway through the lamina vs. in the proximal third), and the bigger sporangia size (1 x 1.5 mm against 0.5–0.9 mm in diameter in *A. merianii*).

Description of in situ spores: The spores are oval to approximately circular, with a monolete or triletole aperture (Fig. 1A–D) and a diameter of 36–81 μm (mean: 53 μm ; Fig. 2). The size and appearance of the aperture varies within the sample (Fig. 3). Most of the spores are triletole with a more or less straight main laesura and a secondary slit of up to about half of the length of the former but usually shorter, going off approximately perpendicular near the center of the main laesura. The ornamentation is consistently punctate, but the density of the puncta varies between individual spores. Puncta are funnel-shaped, with an outer diameter of up to 0.9 μm and an inner diameter of < 0.1 μm (Plate VI, 16–17). SEM pictures show the presence of layered patches on the surface of the spores that partly cover the puncta (Plate VI, 14–15). The spores are often strongly folded/wrinkled/crumpled and fragile. Although all studied specimens yielded high numbers of *in situ* spores, only those of specimens MB.Pb.2010/82 and MB.Pb.2010/83 were in a condition that allowed the description above. The spores from the latter specimen are considerably larger (51–81 μm , mean: 64 μm) than those from the former (36–60 μm , mean: 46 μm). Abortive spores (Plate XI, 8) are present in both specimens, but due to the majority of spores having a distorted appearance, their frequencies could not be reasonably quantified in MB.Pb.2010/83. In specimen MB.Pb.2010/82, they account for ca. 1 % of the spores, with 4 % uncertain cases (Fig. 4).

Discussion: The *in situ* spores of specimens from Thale assigned to *A. merianii* and *A. thalensis* have been both described by Kustatscher and Van Konijnenburg-van Cittert (2011) as granulate, whereas our new analysis showed them to be punctate. The difference can be explained by the dark optical appearance of the puncta under a transmitted light microscope in most focal planes. A close observation of the spore walls reveals that they are indeed perforations and that the outer surface has no significant protrusions. The negative ornamentation of the *Asterotheca* spores from Thale distinguishes them from nearly all *in situ* spores obtained from *A. merianii* specimens from the Lunz flora, as the latter have a positive (granulate) or neutral (laevigate) relief except in a very few cases that can be attributed to corrosion. This supports that the specimens from Thale may pertain to a biologically distinct species. By contrast, the spores of both *Asterotheca* species from Thale only differ somewhat in size, with those of *A. thalensis* being generally smaller, but with a largely overlapping size range (according to our new measurements, although the original size range given by Kustatscher and Van Konijnenburg-van Cittert, 2011 would leave almost no overlap), and with the limitation that only a single specimen of *A. thalensis* has been studied for *in situ* spores. In consideration of the similarity of the spores of the Thale specimens of all *Asterotheca* material and their differences to those from Lunz, the specimens from Thale formerly assigned to *A. merianii* are here renamed as *A. cf. thalensis*. The species assignment is still in question due to unresolved macromorphological differences. It cannot completely be excluded that those macromorphological differences (dimension and shape of the pinnules, attachment to the rachis, venation pattern, dimension in the basiscopic pinnule, and number and slight dimension of sporangia and sori) could be related to sun and shade leaves and/or different portions of the leaf.

Concerning the differences in the ornamentation between *Asterotheca* spores from Lunz and Thale, it should be noted that spores with negative and positive reliefs are both common in the Marattiales and may appear in closely related species, but not commonly in the same (Balme, 1995). Alternatively, the differences could potentially relate to different environmental conditions influencing the production of

spores, or to preservational effects. Spores from both localities are generally well-preserved, but the presence of a few secondarily punctate spores in Lunz tells us that preservation cannot be ignored. *Leschikisporis aduncus* has been reported as a common element of the palynoassemblage of Thale (Kustatscher et al., 2012b) but no punctate form of *Leschikisporis* Potonié, 1958 emend. Bharadwaj et Singh, 1964 was reported so far. This suggests that either the palynoflora and macroflora have been preserved in different ways, which caused the spores to appear either punctate or non-punctate, or the punctuation has been overlooked during the description of the palynoflora, as it was during the first description of the *in situ* spores. The observation of patches covering the puncta on spores of *A. cf. thalensis* as seen in SEM pictures supports a special preservational effect, as these may represent remnants of an otherwise missing exoexine layer. However, LM images do not show the same patches and it is not clear if they are a common feature of the punctate *Asterotheca* spores from Thale, since only one sample was available for analysis by SEM.

Asterotheca sp. 1

Plate II, 1, 3, Plate VI, 8–9, Plate VII, 13–16, Plate XI, 4

References:

2018 *Asterotheca merianii* (Brongn.) Stur ex Krasser, Pott et al., p. 10 (specimen listed as 1885/0500/3923), non pls. 2–7.

2018 *Mertensides bullatus* (Bunbury) Fontaine, Pott et al., p. 15 (specimen listed as 1885/0500/3924), 17, pl. 10, figs. 1–8, non pls. 8–9.

Locality: Lunz am See, Austria.

Stratigraphic horizon: Lunz Formation, Carnian.

Studied material: NHMW-Geo: 1885/0012/3923–24.

Description of macroremains: The two fragments belong to an at least bipinnate frond with a stout rachis (4.5 mm wide). The fragmentary pinnae are up to 120 mm long and 22 mm wide, with a stout axis (2–3 mm wide). The pinnules are lanceolate with a rounded apex, attached almost perpendicularly, with the broad basis and very closely but without imbricating. The pinnules are up to 9 mm long and 3–3.5 mm wide. Apically the pinnae (e.g., NHMW-Geo 1885/0012/3923) become much smaller with pinnules that are only up to 3 mm long and 1.5 mm wide. Associated sterile pinnae are not known.

Comparison: The specimens are labelled originally as *Oligocarpia robustior*, a species that was assigned by Pott et al. (2018) to *Mertensides bullatus* (Bunbury) Fontaine, 1883. However, already Weber (on label dated 25.9.1991) noted that at least NHMW-Geo 1885/0012/3924 resembled rather *Asterotheca intermedia*. Since the specimens resemble in general shape those of *Asterotheca* and miss the typical enlarged first basicopic pinnule of *Mertensides bullatus*, we assign them to the genus *Asterotheca* in open nomenclature. *Asterotheca* sp. 1 differs from *Asterotheca merianii* because of the long pinnae with slenderer pinnules,

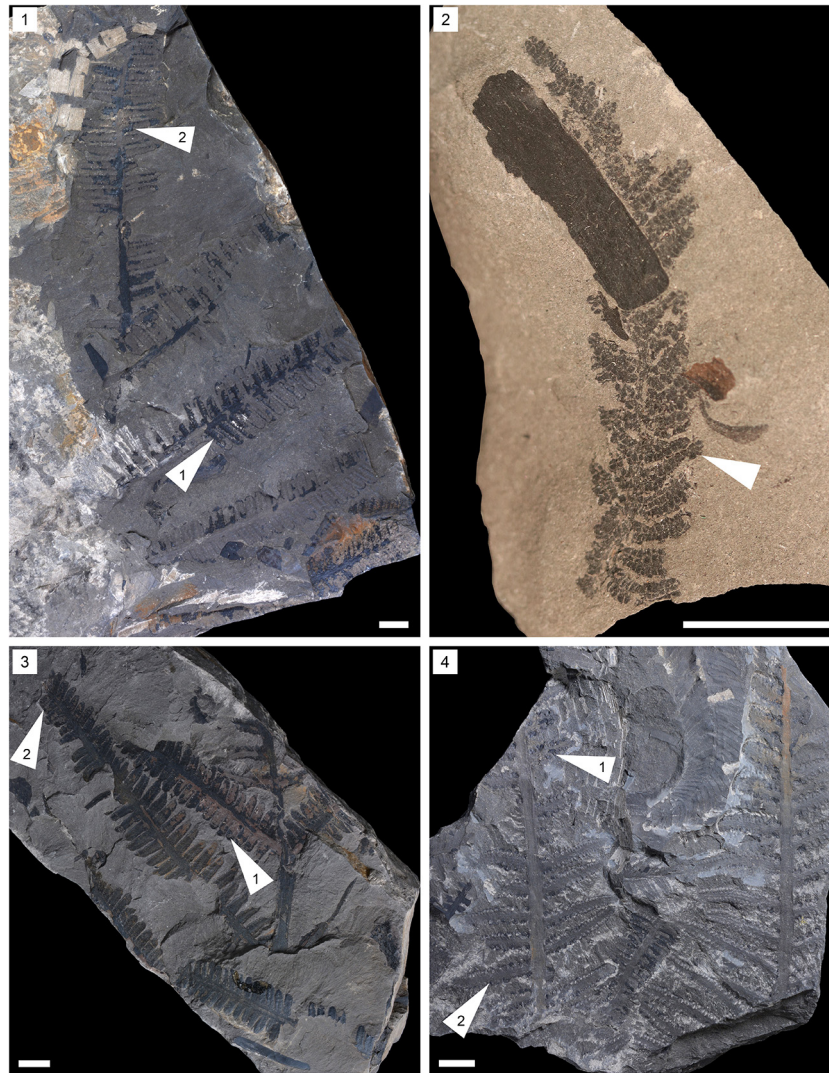


Plate II. Macrofossils of *Merianopteris augusta*, *Asterotheca* sp. 1, and *Asterotheca* sp. 2 from the Carnian of Austria and Switzerland. 1. *Asterotheca* sp. 1, NHMW-Geo 1885/0012/3924, Lunz am See, Austria. 3. *Asterotheca* sp. 1, NHMW-Geo 1885/0012/3923, Lunz am See, Austria. 2. *Merianopteris augusta*, MB.Pb.2019/502, Neuwelt, Münchenstein, Switzerland. 4. *Asterotheca* sp. 2, NHMW-Geo 1885/0012/3926, Lunz am See, Austria. White arrows indicate sampling positions. Scale bars = 10 mm.

a higher number of (smaller) sporangia each fertile pinnule and the not so clear pyramidal structure of the sori. The specimen NHMW-Geo 1885/0012/3923 shows also dimorphic pinnae with long pinnules in the proximal part and small pinnules in the distal part of the frond.

Description of *in situ* spores: The spores are circular to slightly oval, monolet or trilete (Fig. 1A–D), with a diameter of 32–58 µm (mean: 44 µm; Fig. 2) and a microverrucate to microechinate surface ornamentation. Trilete spores have a secondary slit splitting off from the main laesura, which is straight or slightly bent, at approximately the middle, at 90° or often a smaller angle. In some cases, more than one secondary slit is present, which can be at any side and any position along the main laesura, up to its end, resulting in a bend. The secondary slits vary in length and can reach about half the length of the main laesura (Fig. 3). Spores from specimen NHMW-Geo 1885/0012/3924 (Plate VII, 13–16) are similarly strongly to weakly microverrucate, whereas those of NHMW-Geo 1885/0012/3923 are dissimilar in appearance, with sample 1 (see Plate II, 3) containing spores with a strongly pitted (corroded) surface and sample 2 containing weakly microverrucate spores. Abortive spores (Plate XI, 4) are present in low frequencies (2–4%, plus up to 9% uncertain cases; Fig. 4) in each sample.

Discussion: Pott et al. (2018) described the *in situ* spores of NHMW-Geo 1885/0012/3924 (as specimen NHMW 1885/0500/3924 under the name *Mertensides bullatus*) as having a micro-echinate ornamentation and as being comparable to *Leschikisporis*. Our newly extracted samples from these frond remains show an ornamentation that is often more pronounced than in most samples from *Asterotheca merianii* and includes microechinae, but in many cases is comparably microverrucate. At least partly, the spores would fall into the morphological range of *Leschikisporis aduncus* as well.

Asterotheca sp. 2

Plate II, 4, Plate VI, 10–11, Plate VII, 17–20, Plate XI, 5–6

References:

2018 *Asterotheca merianii* (Brongn.) Stur ex Krasser, Pott et al., p. 10 (specimen listed as 2010/0102/0194), pl. 6, fig. 7, non pls. 2–5, 7, pl. 6, figs. 1–6

Locality: Lunz am See, Austria.

Stratigraphic horizons: Lunz Formation, Carnian.

Studied material: NHMW-Geo 1885/0012/3926.

Description of macroremains: The frond fragment (up to 105 mm long and 50 mm wide) is bipinnate, with a strong rachis (up to 4 mm wide) and oppositely to suboppositely inserted pinnae. The pinnae are lanceolate, up to 20–32 mm long and 4–4.5 mm wide and attached at an almost perpendicular angle. The axis is prominent, 1–1.5 mm wide. Pinnules are roundish (1–2 × 1.5–2 mm) with a rounded apex and attached (almost) perpendicularly. Few veins arise from the axis and enter in each pinnae, rarely bifurcating. Each fertile pinnule has a sorus composed of 4–5 sporangia. Associated sterile pinnae are not known.

Comparison: The specimen is labelled as *Asterotheca intermedia* and was interpreted by Pott et al. (2018; shown in their pl. 6, fig. 7 as 2010/0102/1094) as representing a central portion of *Asterotheca merianii*. It differs from *A. merianii* and from *Asterotheca* sp. 1 because of the small size and roundish shape of the pinnules. The pinnae are more narrow and strap-like than those of the previously discussed three species of *Asterotheca*. In type and disposition of the veins the specimen resembles slightly some apical fragments of *Asterotheca thalensis*, but veins are protruding here on all pinnules, not only on apical ones. This specimen has the closest resemblance with distal pinnae of the specimen NHMW-Geo 1885/0012/3923 (*Asterotheca* sp. 1) due to the broad axis with small pinnules attached, but in the former specimen the single pinnules are slender and elongated, whereas in *Asterotheca* sp. 2 the pinnules are rounded and broad.

Description of *in situ* spores: *In situ* spores are circular to oval, monolet or trilete (Fig. 1A–D), with a longest diameter of 30–48 µm (mean: 37 µm; Fig. 2) and a microverrucate exoexine. In trileteoid

spores, a secondary slit splits off from the main laesura, which is straight or slightly bent, at approximately the middle, at 90° or rarely at a smaller angle. The secondary slit varies in length and may almost reach half the length of the main laesura (Fig. 3). Abortive spores (Plate XI, 5–6) are present in moderate frequencies (ca. 3%, up to 7% uncertain cases; Fig. 4) in each sample.

Discussion: The spores resemble closely those of *A. merianii* and *Asterotheca* sp. 1. They tend to have a slightly more pronounced ornamentation than most of the spores of *A. merianii*, similarly to *Asterotheca* sp. 1. The spores are likewise attributable to *Leschikisporis*. In *Asterotheca* sp. 1, the aperture shows some irregular variations that also rarely occur in *A. merianii* but have not been observed in *Asterotheca* sp. 2. However, this could be due to the small sample size.

Genus: *Merianopteris* Heer, 1877

Type species: *Merianopteris augusta* Heer, 1877

Merianopteris augusta Heer, 1877

Plate II, 2, Plate VI, 12–13, Plate X, 1–2, 5–8, Plate XI, 19–20, Supplementary Plate I, 3, 5

Selected references:

1877 *Merianopteris augusta* Heer, p. 88, pl. 24, figs. 7–12, pl. 37, pl. 38, figs. 7–8

1888 *Merianopteris augusta* Heer, Stur, p. 208

1904 *Merianopteris (Pecopteris) augusta* Heer, Leuthardt, p. 127

1909 *Merianopteris augusta* Heer, Krasser, p. 108

Locality: Neuwelt, Münchenstein, Switzerland.

Stratigraphic horizon: Klettgau Formation, Carnian.

Studied material: NMB: B2535, B2538.

MfN: MB.Pb.2019/502.

Description of macroremains: Frond fragments are bi- to tripinnate, with a strong rachis (up to 4 mm wide) and oppositely to suboppositely inserted pinnae (Supplementary Pl. I, 5). The pinnae are lanceolate, over 80 mm long and ca. 15 mm wide, and attached at 70–90°. Pinnules are elongate with a rounded apex and attached at 60–80°, with broad, slightly decurrent basis to the rachis (Supplementary Pl. I, 3, 5). The midrib is distinct with 4–6 pairs of secondary veins arising at an angle of 45–60° (Supplementary Pl. I, 3). Three fertile frond fragments yielded *in situ* spores. The rachis in these fragments is stout, ca. 5 mm wide. The pinnae fragments are up to 40 mm long and 8 mm wide. The pinna axis is 0.5–1 mm wide. The pinnules are 4–7 mm long and 1.5–2 mm wide. In most cases the lamina of the pinnules is badly preserved (Plate II, 2). This enables us to see more in detail the fertile component of the plant. The sporangia are up to 1 mm long and 0.5 mm wide, arranged in groups of at least two but probably in most cases four sporangia that form a roundish structure; they do not seem to be basally adnate.

Comparison: *Merianopteris augusta* has been considered a junior synonym of *Asterotheca merianii* by several authors based on the original description and illustrations (Stur, 1888; Krasser, 1909; Pott et al., 2018). Sporangia resembled macromorphologically closely those of *Asterotheca merianii*, but the number of sori in each pinnule varies and they do not seem to be adnate. However, thanks to pictures sent by Dr. Iwan Stössel of the original material at the ETH in Zürich differences could be observed both on the sterile and the fertile fronds. As pointed out by Heer (1877) and Kustatscher and Van Konijnenburg-van Cittert (2011), the secondary veins on the pinnules are more abundant and arise at a much lower angle than in *Asterotheca merianii*. The lamina of the pinnules is delicate and can get lost during the fossil process and when splitting the rocks, leaving only the rows of sporangia and giving the pinnules an almost pinnate structure. Moreover, the fertile pinnules are smaller than the sterile ones. Heer (1877) indicated that *M. augusta* pinnules were dimorphic with the basal fertile ones being slenderer and more elongate, and the more apically arranged ones being sterile, shorter and broader. This is a real difference with *A. merianii*.

Description of *in situ* spores: The spores are trilete, with an often indistinct mark, approx. circular, with a diameter of 45–77 µm (mean: 63 µm; Fig. 2) and a coarsely verrucate or gemmate ornamentation.

Sculpture elements (1.0–2.5 µm in diameter) are often partly fused to rugulae/vermiculae. The rays of the trilete mark are usually of unequal length, with one ray shorter or longer than the others (Figs. 11–K, 5). The longest rays can be measure < 1/2 radius to almost reaching the equator. Abortive spores (Plate XI, 19–20) were identified with a frequency of 3% (5% uncertain; Fig. 4).

Discussion: Most samples only yielded a few spores, which however showed a rather consistent appearance across samples. The most productive sample came from specimen MB.Pb.2019/502 and contained entire sporangia. In situ spores of *Merianopteris augusta* have not been described before. A synonymy of this species with *Asterotheca merianii* (see comparison above) is contradicted by the clear differences in their spores in terms of size, ornamentation, and in the construction of their trilete mark. The elongate shape of the sporangia is another difference, which can even be observed on macroscale. Furthermore, the coarse, verrucate ornamentation distinguishes the spores of *M. augusta* from those of all other Triassic marattialean ferns from which in situ spores have been reported so far (Table 1). Similar spores are known from the Palaeozoic species *Acitheca polymorpha*

(Brongniart) Schimper, 1879 (Balme, 1995; Bek, 2021, and references therein). The spores are largely comparable to *Verrucosisporites*.

Family: MARATTIACEAE Kaulf., 1824

Genus: *Danaeopsis* Heer ex Schimper, 1869

Type species: *Danaeopsis marantacea* (Presl) Schimper, 1869

Danaeopsis marantacea (Presl) Schimper, 1869

Plate III, 1–2, Plate VIII, 1–2, 4–9, Plate IX, 1–3, Plate XI, 9–10, Supplementary Plate II, 1

Selected references (for further references see Kustatscher et al., 2012a):

1838 *Taeniopteris marantacea* (Jäger), Presl in Sternberg (1838), p. 139

1869 *Danaeopsis marantacea* (Presl) Heer, Schimper, p. 614

2012a *Danaeopsis marantacea* (Presl) Schimper, Kustatscher et al., p. 35, pl. 2, 1–7, pl. 3, fig. 2, text-figs. 1, 2, 2

Locality: Neuwelt, Münchenstein, Switzerland; Bibersfeld, Rockhausen, Germany.

Stratigraphic horizon: Klettgau Formation, Carnian (Neuwelt); Erfurt Formation, Ladinian (Bibersfeld and Rockhausen).

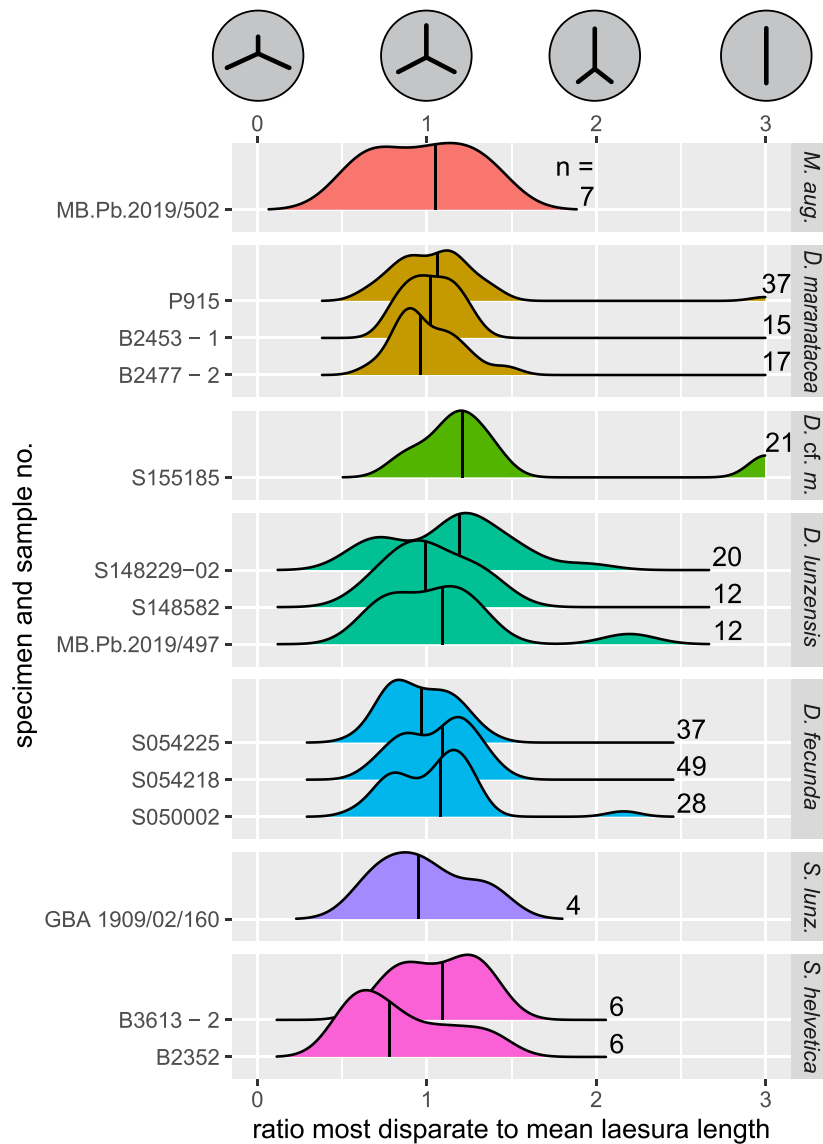


Fig. 5. Length of the most disparate (distance from the mean) ray relative to the mean of all three rays in *Danaeopsis*, *Merianopteris*, and *Symopteris*. At a ratio of 1, the rays are equal; at value 3, the spore is monolete with only one ray present. *M. aug.* = *Merianopteris augusta*; *D.* = *Danaeopsis*; *D. cf. m.* = *Danaeopsis cf. marantacea*; *S.* = *Symopteris*; *S. lunz.* = *Symopteris lunzensis*.

Table 1
Overview of marattialean fern species of the Triassic with reported *in situ* spores.

Species	Aperture	Amb	Diameter	Exine	Comparable dispersed taxa	References
<i>Asterotheca merianii</i> (Brogniart) Stur ex Krasser, 1909	Monolete to asymmetrically trilete	Circular to elliptic	29–(42)–50 µm [1]; 30–53 µm long, polar axis 22–45 µm [2]; 27–(42)–59 µm, length to width ratio up to 1.4:1 [3]	Laevigate to weakly microverrucate, rarely verrucate	<i>Leschikisporis aduncus</i> (Leschik) Potonié, 1958	Nathorst (1908); Bharadwaj and Singh (1956) [1]; Potonié (1962, 1967); Andrews in Boureau (1970); Balme (1995); Pott et al. (2018) [2]; this study [3]
<i>Asterotheca thalensis</i> Kustatscher et Van Konijnenburg-van Cittert, 2011	Monolete to asymmetrically trilete	Circular to elliptic	27–34 µm [1]; 33–(40)–46 µm [2]	Punctate	<i>Leschikisporis</i>	Kustatscher and Van Konijnenburg-van Cittert (2011)[1]; this study [2]
<i>Asterotheca</i> cf. <i>thalensis</i> Kustatscher et Van Konijnenburg-van Cittert, 2011	Monolete to asymmetrically trilete	Circular to elliptic	28–(40)–45 µm [1]; 36–(53)–81 µm [2]	Punctate	<i>Leschikisporis</i>	Kustatscher et al. (2011, as <i>Asterotheca merianii</i>) [1]; this study [2]
<i>Asterotheca</i> sp. 1	Monolete to asymmetrically trilete	Circular to elliptic	35–51 µm long, polar axis 35–45 µm [1]; 32–(44)–58 µm [2]	Weakly to strongly microverrucate or microechinate	<i>Leschikisporis</i>	Pott et al. (2018, as <i>Mertensides bullatus</i>) [1]; this study [2]
<i>Asterotheca</i> sp. 2	Monolete to asymmetrically trilete	Circular to elliptic	30–(37)–48 µm	Weakly to strongly microverrucate	<i>Leschikisporis</i>	This study
<i>Merianopteris augusta</i> Heer, 1977	(Asymmetrically) trilete	Circular	45–(63)–77 µm	Verrucate to gemmate, partly rugulate/vermiculate	<i>Verrucosporites</i>	This study
<i>Danaeopsis marantacea</i> (Presl) Schimper, 1869	(Asymmetrically) trilete	Circular to elliptic or slightly triangular	40–48 µm [1]; 45–60 µm [2]; 33–(47)–66 µm [3]	Laevigate in LM, microreticulate in SEM	<i>Todisporites/Punctatisporites</i> , <i>Laevigatosporites/Latosporites</i>	Kustatscher and Van Konijnenburg-van Cittert (2011) [1]; Kustatscher et al. (2012a) [2]; this study [3]
<i>Danaeopsis</i> cf. <i>marantacea</i> (Presl) Schimper, 1869	(Asymmetrically) trilete	Circular to elliptic or slightly triangular	44–(54)–65 µm	Laevigate or microreticulate	<i>Todisporites/Punctatisporites</i> , <i>Laevigatosporites/Latosporites</i>	This study
<i>Danaeopsis lunzensis</i> Stur ex Kustatscher et al., 2012	(Asymmetrically) trilete	Circular to elliptic or slightly triangular	50–65 µm [1,2,3]; 41–(57)–72 µm [4]	Laevigate in LM, microverrucate to microgemmate in SEM	<i>Todisporites/Punctatisporites</i>	Nathorst (1908) [1]; Potonié (1962, 1967); Balme (1995) [2]; Kustatscher et al. (2012a) [3]; Pott et al. (2018); this study [4]
<i>Danaeopsis fecunda</i> Halle, 1921	(Asymmetrically) trilete	Circular to elliptic or slightly triangular	60–70 µm [1,2]; 44–(70)–82 µm [3]	Laevigate or microreticulate	<i>Todisporites/Punctatisporites</i>	Halle (1921) [1]; Potonié (1962, 1967); Andrews in Boureau (1970); Balme (1995); Taylor et al. (2009); Kustatscher et al. (2012a) [2]; this study [3]
<i>Danaeopsis angustipinnata</i> Brik, 1952	Trilete	Circular	15–(22)–25 µm	Echinate/microechinate (?), 2,3 µm thick		Brik et al. (1955)
<i>Symopteris rumpffii</i> (Schenk) Kustatscher et al., 2011	Trilete, rays 1/2–2/3 of spore radius	Circular	35–38 µm	Slightly punctate, thin	<i>Todisporites/Punctatisporites</i>	Kustatscher et al. (2011)
<i>Symopteris helvetica</i> (Heer) Xu in Xu et al., 1979 emend. Kustatscher et al., 2011	(Asymmetrically) trilete	Circular	45–(60)–81 µm	Laevigate(?)	<i>Todisporites/Punctatisporites</i>	This study
<i>Symopteris lunzensis</i> (Stur ex Krasser 1909a) Xu in Xu et al., 1979	(Asymmetrically) trilete, rays up to 1/2 of radius	Circular	42–48 µm [1]; 58–(71)–90 µm [2]	Laevigate or sparsely microverrucate to verrucate	<i>Todisporites/Punctatisporites</i>	Pott et al. (2018)[1]; this study [2]
<i>Symopteris aktjubensis</i> (Brik) Kustatscher et al., 2011	Trilete, rays > 1/2 of spore radius	Circular?	42–(45)–50 µm	Microechinate(?), 1.5 µm thick		Brik et al. (1955); Kustatscher et al. (2011)
<i>Marattia intermedia</i> (Muenster) Kilpper, 1964	90% monolete, 10% probably trilete	Elliptic or circular	18–(24)–28 µm	Granulate	<i>Punctatosporites/-Cyclogranisporites</i>	Schweitzer et al. (1997)
<i>Marattiopsis crenulatus</i> Lundblad, 1950	Monolete, laesura long	Elliptic; plane-convex in side view	23–(25)–27 µm long, 15–(18)–19 µm wide	Granulate, very thin	<i>Punctatosporites/-Marattisporites scabratus</i> Couper, 1958	Couper (1958); Lundblad (1950); Potonié (1962, 1967); Andrews in Boureau (1970); Balme (1995)
<i>Rhinopteris concinna</i> (Presl) Harris, 1931	Trilete?	Circular	40 µm	Laevigate, thin		Harris (1931); Potonié (1962); Andrews in Boureau (1970)
<i>Scolecopteris antarctica</i> Delevoryas et al., 1992	Alete	Circular	17 µm or 23–31 µm	Thick in larger spores, thin and delicate in small ones		Delevoryas et al. (1992); Balme (1995)

Studied material: NMB: B2453, B2456, B2461, B2474, B2476–77.
 MfN: MB.Pb.2019/261, MB.Pb.2019/485, MB.Pb.2019/489–2.
 NRM: S155192.
 SMNS: P915.

Description of macroremains: Sterile fronds are imparipinnate, with a broad, tapering axis. Pinnae are elongate, up to 200 mm long and 70 mm wide. The margin is entire or slightly undulate, the proximal base is decurrent. Pinna midrib is broad (basally 6–8 mm), secondary veins arise at 60–70° and immediately curve outwards to an angle of almost 90°. Secondary veins fork once near the midrib and anastomose near the pinnule margin (Supplementary Pl. II, 1). The fertile pinnae fragments are 60–110 mm long and 40–50 mm wide (Plate III, 1–2). Originally pinnae were elongate to slightly lanceolate with a gradually tapering apex (e.g., B2477). The midrib is up to 5 mm wide. Secondary veins arise from the midrib at an angle of about 60°, curving immediately outwards to an angle of almost 90°. Each secondary vein forks once near the midrib. Two rows of sporangia are observed between each pair of secondary veins (e.g., B2476). The roundish sporangia are up to 0.5 mm in diameter.

Comparison: The specimens, although fragmentarily preserved, fall well within the general range of *Danaeopsis marantacea* as observed from the Erfurt and the Stuttgart formations of Germany (Kustatscher et al., 2012a). Considering the shape and dimensions of the frond and pinnae of this species (Kustatscher et al., 2012a), the fragments belong probably to some more apical parts of a frond, as shown by the narrower midrib and width of the pinnae. The typical anastomosing of the lateral veins cannot be observed due to the presence of the rows of sporangia and would also be minor in the fertile pinnae.

Description of in situ spores: The spores are approx. circular to oval or convex rounded triangular, trilete or trileteoid, with one ray often being slightly shorter, rarely monolete (Figs. 1E–H, 5), a diameter of 33–66 µm (mean: 47 µm; Fig. 2), and a laevigate/microreticulate exoexine. Microreticulation was only observed in SEM images (Plate IX, 1–3) and is often subdued, while the spores appeared laevigate under LM (e.g., Plate VIII, 6–8). The spores from the Bibersfeld specimen (P915) are generally smaller (33–50 µm, mean: 42 µm) than those from Neuwelt (39–66 µm, means: 53–55 µm) and almost always show a grainy, usually dark spot that may represent cytoplasmic remains

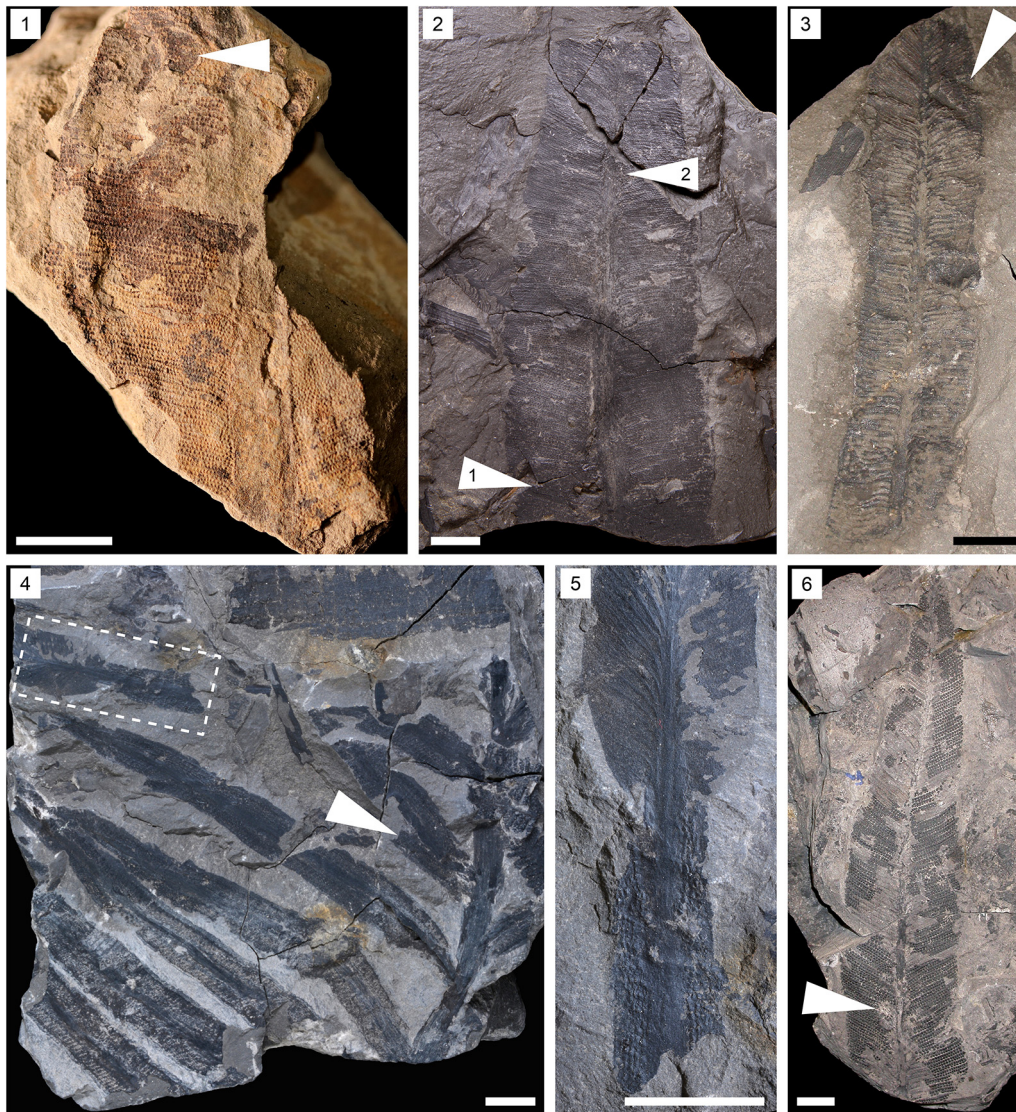


Plate III. Macrofossils of *Danaeopsis* from the Ladinian of Germany, the Carnian of Austria and Switzerland, and the Rhaetian of Sweden. 1–2. *Danaeopsis marantacea*. 1. MB.Pb.2019/489–2, Rockhausen, Germany, Ladinian. 2. B2477, Neuwelt, Münchenstein, Switzerland, Carnian. 3. *Danaeopsis* cf. *marantacea*, S155183–02, Lunz am See, Austria, Carnian. 4–5. *Danaeopsis lunzensis*, 1885/0012/3963, Lunz am See, Austria, Carnian. 5. Detail of the specimen in fig. 4 (area indicated by white dashed box) showing fertile and sterile parts. 6. *Danaeopsis fecunda*, S050002, Billesholm, Sweden, Rhaetian. White arrows indicate sampling positions. Scale bars = 10 mm.

(Plate VIII, 4, 6–8). Abortive spores (Plate XI, 9–10) are present in most samples in low to moderate frequencies (1–5%, up to 6% uncertain; Fig. 4).

Discussion: In situ spores of *Danaeopsis marantacea* have been previously described based on material from the Erfurt Formation at Thale as circular, trilete, and smooth (laevigate), with diameters of 40–48 µm (Kustatscher and Van Konijnenburg-van Cittert, 2011) or 45–60 µm (Kustatscher et al., 2012a). By comparison, we found the spores to be partly larger, not always circular, and having a trilete mark that is often asymmetric or even reduced to a monolete aperture. In addition, while the exoexine appears laevigate in LM, a more or less distinct microreticulate ornamentation can be observed via SEM.

The more circular and trilete spores are comparable to *Todisporites* or *Punctatisporites*, whereas the rare monolete spores could be assigned to *Latosporites* (circular) or *Laevigatosporites* (oval). Several species of *Punctatisporites* have been reported from both Neuwelt (Leschik, 1955) and from the Erfurt Formation (Kustatscher et al., 2012b), with *P. ambiguus* Leschik, 1955 from Neuwelt being explicitly described as having a mark with unequal rays (one being much longer than the other two). *P. ambiguus* was probably produced by *D. marantacea*, although the reported size of the holotype of *P. ambiguus* (43 µm × 38 µm acc. to Leschik, 1955) is small for this species. Larger spores might be accommodated by other species of *Punctatisporites*.

Danaeopsis cf. *marantacea* (Presl) Schimper, 1869

Plate III, 3, Plate VIII, 3, 10–12, Plate XI, 11.

Locality: Moderhalde near Pratteln and Neuwelt, Münchenstein, Switzerland.

Stratigraphic horizon: Klettgau Formation, Carnian.

Studied material: NRM: S155183-02; S155185.

Description of macroremains: The pinna fragments are up to 90 mm long and 20 mm wide, with an up to 3 mm wide midvein. The lateral veins arise at a slightly acute angle (~70–80°) and turn outwards reaching the margin at an almost perpendicular angle. The bifurcation close to the midrib is clearly visible, near the margin the secondary veins again bifurcate and occasionally anastomose. Associated sterile pinnae are not known.

Comparison: The specimens are represented by pinna fragments with not clearly preserved lateral veins. In this case the lateral anastomosing pattern of the veins typical of *Danaeopsis marantacea* is not well developed but the dimension and general shape of the pinna itself is typical for this latter species. Therefore, for now the specimens are assigned only putatively to this species.

Description of in situ spores: The spores are approx. circular to oval or convex rounded triangular, trilete or trileteoid, with one ray often being slightly shorter (Figs. 1E–H, 5), a diameter of 44–65 µm (mean: 54 µm; Fig. 2), and a laevigate or microreticulate exoexine. Abortive spores (Plate XI, 11) are present in relatively high frequencies in S155185 (14%, plus 13% uncertain cases; Fig. 4).

Discussion: The in situ spores of *Danaeopsis* cf. *marantacea* are like those of *D. marantacea* s. str., especially in their size range, but they also show a conspicuous microreticulate ornamentation and occasionally somewhat triangular amb, which are features otherwise seen in *D. fecunda*. However, a triangular amb may occur due to immaturity, while the observation of an (optically) indistinct microreticulation on the spores of *D. marantacea* but not on those of the coeval *D. lunzensis* still supports a close relation to the former species.

Danaeopsis lunzensis Stur ex Kustatscher et al., 2012a

Plate III, 4–5, Plate VIII, 13–16, Plate IX, 4–6, Plate XI, 12–13, Supplementary Plate II, 2

Selected references (for further references see Kustatscher et al., 2012a):

1885 *Danaeopsis lunzensis*, Stur, p. 97, *nomen nudum*

2012a *Danaeopsis lunzensis* Stur ex Kustatscher et al., p. 38, pl. 3, figs. 4–6, pl. 4, figs. 1–8, text-figs. 1, 2.3, 5–6

Locality: Lunz am See, Austria.

Stratigraphic horizon: Lunz Formation, Carnian.

Studied material: NHMW-Geo: 1885/0012/3963.

NRM: S148229-02, S148582.

MFN: MB.Pb.2019/280, MB.Pb.2019/497.

Description of macroremains: The fronds are imparipinnate or paripinnate. The rachis is proximally about 15–20 mm wide and decreases slightly apically. The pinnae are linear to slightly lanceolate with a restricted proximal and distally rounded margin. The pinna shape and attachment to the rachis are variable, from oppositely, suboppositely to alternately, however without imbricating. The pinnae apex is acute, the margin is entire to slightly undulate. The midrib is distinct and up to 2 mm wide, secondary veins arise at an angle of 70–90°, dichotomize once near the midrib and anastomose slightly near the margin (up to the outer half of the width of the lamina in narrow specimens; Supplementary Pl. II, 2). Fertile frond fragments resemble sterile ones but differ in the width of the pinnae, having narrower pinnae. The pinnae arise alternately or oppositely from the thick rachis, have an entire margin and a distinctively pointed apex. The sporangia are elongate and cover the entire lower lamina arranged in two irregular rows, with only a narrow sporangia-free margin. One sample (NHMW-Geo 1885/0012/3936) shows a rare example of apically sterile and basally fertile pinnae of a *Danaeopsis lunzensis* frond.

Comparison: See Kustatscher et al. (2012a).

Description of in situ spores: The spores are approx. circular to oval or convexly rounded triangular, trilete or trileteoid, with one ray often shorter or longer than the other two (Figs. 1E–H, 5), a diameter of 41–72 µm (mean: 57 µm; Fig. 2), and a laevigate or granulate exoexine. The exoexine appears laevigate in LM (Plate VIII, 13–16), but granulate (finely microverrucate to microgemmate) in SEM (Plate IX, 5–6). In cases with one longer and two shorter rays, the appearance may approach that of a monolete spore. Among the samples with quantifiable spore sizes, spores from specimen MB.Pb.2019/497 are comparatively small, with 41–58 µm (mean 48 µm), compared to 50–72 µm (mean: 64 µm) and 54–67 µm (mean: 64 µm) in specimens S148229–02 and S148582, respectively (Fig. 2). Abortive spores (Plate XI, 12–13) are present in every sample, with <1–4% (and up to 6% uncertain cases; Fig. 4) having been counted. They appear to be more frequent in NHMW-Geo 1885/0012/3963, but this specimen did not yield enough material for a reliable count.

Discussion: In situ spores of *D. lunzensis* from Lunz were first described by Nathorst (1908) as trilete and circular to oval, with a diameter of 65 µm. Potonié (1967) specified that they were subcircular to subtriangular, meso- to brevitrilete, quasi-laevigate and punctate. Similarly, Balme (1995) considered them as scabrate/punctate and gave their size as 50–65 µm. Kustatscher et al. (2012a) gave the same size range, measured the length of the trilete rays as up to 2/3 of the radius and suggested that a microreticulate structure may sometimes be present around the trilete mark. Re-evaluating fig. 2.3 in Kustatscher et al. (2012a), the reticulation may have been caused by imprinting crystals. The unequal length of the rays of the trilete mark in many spores has so far not been reported, but it is a frequent occurrence in our samples and can also be seen, e.g., in fig. 2.4 of Kustatscher et al. (2012a). The spores of *D. lunzensis* have been associated by Balme (1995) with the dispersed genus *Punctatisporites*. Similar forms are also frequently assigned to *Todisporites*, which has been reported from the Lunz Formation (Roghi et al., 2010). However, *Punctatisporites* and *Todisporites* refer to purely trilete spores, whereas some of the spores here discussed deviate considerably from the ideal trilete condition.

Danaeopsis fecunda Halle, 1921

Plate III, 6, Plate VIII, 17–20, Plate IX, 7–8, Plate XI, 14–15, Supplementary Plate II, 3–4

Selected references (for further references see Kustatscher et al., 2012a):

1921 *Danaeopsis fecunda* Halle, p. 6, pl. 1, figs. 1–13

2012a *Danaeopsis fecunda* Halle, Kustatscher et al., p. 41, pl. 5, figs. 1–5, text-figs. 1, 2.1, 4

Locality: Billesholm, Scania, Sweden.

Stratigraphic horizon: Höganäs Formation, Rhaetian.

Studied material: NRM: S050002, S054033, S054218, S054225.

Description of macroremains: See mainly Halle (1921). Sterile pinnae are characterized by their venation with secondary veins arising from the strong midrib at an angle of 60–90°, bifurcating once near the midrib, once halfway to the margin, and sometimes anastomosing slightly near the margin (Supplementary Pl. II, 3–4). The fertile pinna used in this study displays an almost 170 mm long pinna fragment with an acute apex (Plate III, 6). The lower side of the lamina (excluding the midrib) is completely covered by double-rows of sporangia, about 0.8–0.9 × 0.65–0.75 mm in size. **Comparison:** See Kustatscher et al. (2012a).

Description of in situ spores: The spores are approx. circular to slightly oval or rounded convex triangular, trilete or trileteoid, with one ray often being shorter or longer than the other two (Figs. 1E–H, 5), a diameter of 44–82 µm (mean: 70 µm; Fig. 2), and a laevigate or microreticulate exoexine ornamentation. In cases with one longer and two shorter rays, the appearance may approach that of a monolete spore. Spores from specimen S054033 are very thin-walled and heavily crumpled/folded. Spores from other specimens are typically thick-walled and less prone to folding. They often show short radial fissures along the equator. Abortive spores (Plate XI, 14–15) are present in all samples in low amounts (1–2%, up to 7% uncertain; Fig. 4).

Discussion: As part of the original description of *Danaeopsis fecunda*, which was based on specimens from Billesholm, Halle (1921) reported the presence of trilete, globular spores with a smooth surface and diameters of usually 60–70 µm, but in many cases smaller. A later description by Kustatscher et al. (2012a), which was based in part on in situ spores from the here restudied specimen S050002, conforms to that of Halle (1921). The length of the laesurae was specified by Potonié (1962) as 1/2 radius or more, by Potonié (1967) as 2/3 in larger spores.

The in situ spores of *D. fecunda* were ascribed by Balme (1995) to *Punctatisporites*, a genus of trilete spores that are also sometimes assigned to *Todisporites*. These two genera do not, however, account for the spores with unequal rays.

Genus: *Symopteris* Xu in Xu et al., 1979

Type species: *Symopteris helvetica* (Heer) Xu in Xu et al., 1979.

Symopteris lunzensis (Stur ex Krasser) Xu in Xu et al., 1979

Plate IV, 1–2, Plate IX, 11–12, Plate X, 4, 13–16, Plate XI, 16, Supplementary Plate II, 5

Selected references (for further references see Kustatscher et al., 2011):

1885 *Bernoullia lunzensis*, Stur, p. 97, *nomen nudum*

1909 *Bernoullia lunzensis* Stur, Krasser, p. 17, 33–34

1979 *Symopteris lunzensis* (Stur), Xu et al., p. 17

Locality: Lunz am See, Austria.

Stratigraphic horizon: Lunz Formation, Carnian.

Studied material: GBA: 1909/2/160, 1909/2/413, 1909/2/460.

Description of macroremains: Only fragmentary specimens of *Symopteris lunzensis* are preserved comprising pinna fragments with pinnules arising at angles of 45–60°. Sterile pinnules have a fasciculate venation with a strong midvein and faint curved secondary veins (Supplementary Plate II, 5). The fertile pinna fragments are up to 100 mm long (Plate IV, 1, 2). They are pinnate with pinnules arising (sub-)alternately at angles of 70–85°. Fertile pinnules are robust and oblong, up to 25 mm long and 8 mm wide. The pinnule lamina is inwardly folded at the margins, partly covering the sporangia that occur on the abaxial surface. Sporangia are not very distinct but could be seen where lamina pieces are lacking. Several rows of small sporangia are arranged parallel to the midvein on the abaxial side of the lamina or follow the pattern of the secondary venation. Sporangia are oval, about 1.6 mm long and 0.5 mm wide.

Comparison: See Kustatscher et al. (2011)

Description of in situ spores: The spores are approx. circular, trilete, with one ray sometimes being slightly shorter or longer (Figs. 1L–N, 5), a diameter of 58–90 µm (mean: 71 µm; Fig. 2), and a laevigate to

(sparsely) microverrucate to verrucate (with elements ~1 µm in diameter; Plate IX, 12) exoexine. The spores are heavily folded and covered in remains of the tapetum. Abortive spores (Plate XI, 16) were counted from specimen GBA 1909/02/160 with a frequency of 7% (1% uncertain; Fig. 4).

Discussion: Kustatscher et al. (2011) and Pott et al. (2018) described the spores of *Symopteris lunzensis* as trilete with a simple, delicate mark and rays of up to ½ of the spore radius, having a punctate exine and a diameter of 42–48 µm. We found significantly larger spores in this species and no punctate cases. The larger size range overlaps well with that of *S. helvetica* (see above), whereas *S. aktjubensis* and *S. rumpffii* are reported to have much smaller spores (Brik et al., 1955; Kustatscher et al., 2011). In a few cases, the spores show clearly differently sized rays in the trilete mark, similar to what can be seen in *Danaeopsis* spp. (see above), although not to the same extent.

Symopteris helvetica (Heer) Xu in Xu et al., 1979 emend. Kustatscher et al., 2011

Plate IV, 3–4, Plate IX, 9–10, Plate X, 3, 9–12, Plate XI, 17–18, Supplementary Plate II, 6

Selected references (for further references see Kustatscher et al., 2011):

1877 *Bernoullia helvetica* Heer, p. 88, pl. 38, figs. 1–6

1979 *Symopteris helvetica* (Heer) Xu in Xu et al., p. 17

2011 *Symopteris helvetica* (Heer) Xu in Xu et al. emend., Kustatscher et al., p. 43, pl. 1, figs. 1–4

Localities: Moderhalde near Pratteln and Neuwelt, Münchenstein, Switzerland.

Stratigraphic horizon: Klettgau Formation, Carnian.

Studied material: NMB: B1966, B2352, B2362, B2368, B2370, B2380, B3613.

Description of macroremains: The bipinnate fronds have a robust rachis, up to 9–10 mm in average width. The pinnae emerge at an angle of 45–60°. Pinna fragments reach up to 18 cm in length and 5–7 cm in width. Pinnae are regularly pinnate, pinnules arise at angles of 60–90°. Sterile (Supplementary Pl. II, 6) and fertile (Plate IV, 3, 4) pinnules occur, oppositely to sub-oppositely attached, on the same pinna or frond, although completely fertile and sterile pinnae may also occur. The margin of sterile pinnules is crenate, lobate or incised, especially in the proximal pinnule portion, although lamina divisions never reach the rachis. The linear to lanceolate pinnules with an apically obtuse to acuminate apex are arranged on a robust rachis. They are basally broadly attached or sessile. The midvein reaches the pinnule tip, bifurcating near the apex. Secondary veins are faint, arise at an angle of c. 45°, curve outwards and have a fasciculate organization.

Fertile pinnules are arranged in the proximal part of the pinnae, elongate to ovate and robust. Sporangia are arranged in rows on the abaxial side of the pinnules, parallel to the midvein, but the marginal portion (2–3 mm) is free of sporangia and curves downwards. This gives the impression that the pinnule margins are folded and partly cover the sporangia. Sporangia are less than 1 mm in diameter and probably oval in outline, which can, however, not be completely seen.

Comparison: See Kustatscher et al. (2011)

Description of in situ spores: Only two specimens (B2352, B3613) yielded reasonably well-preserved spores in high numbers. The spores are approx. circular, trilete, with one ray sometimes being shorter or longer (Figs. 1L–N, 5), a diameter of 45–81 µm (mean: 60 µm; Fig. 2), and a laevigate(?) exoexine. The spores do not separate well from each other and are usually beset with orbicules (presumably remains of the tapetum; Plate IX, 10), which hinders observations. In B3613, abortive spores (Plate XI, 17–18) appear to be more abundant than regular spores, but they do not separate readily, and could therefore not be quantified. In sample 1 from this specimen, they are estimated to account for >2/3 of the spores, in sample 2 for 1/4–1/2 of the spores (Fig. 4).

Discussion: In situ spores had not been described from this species so far. They resemble largely those of *S. lunzensis*, but are typically smaller,

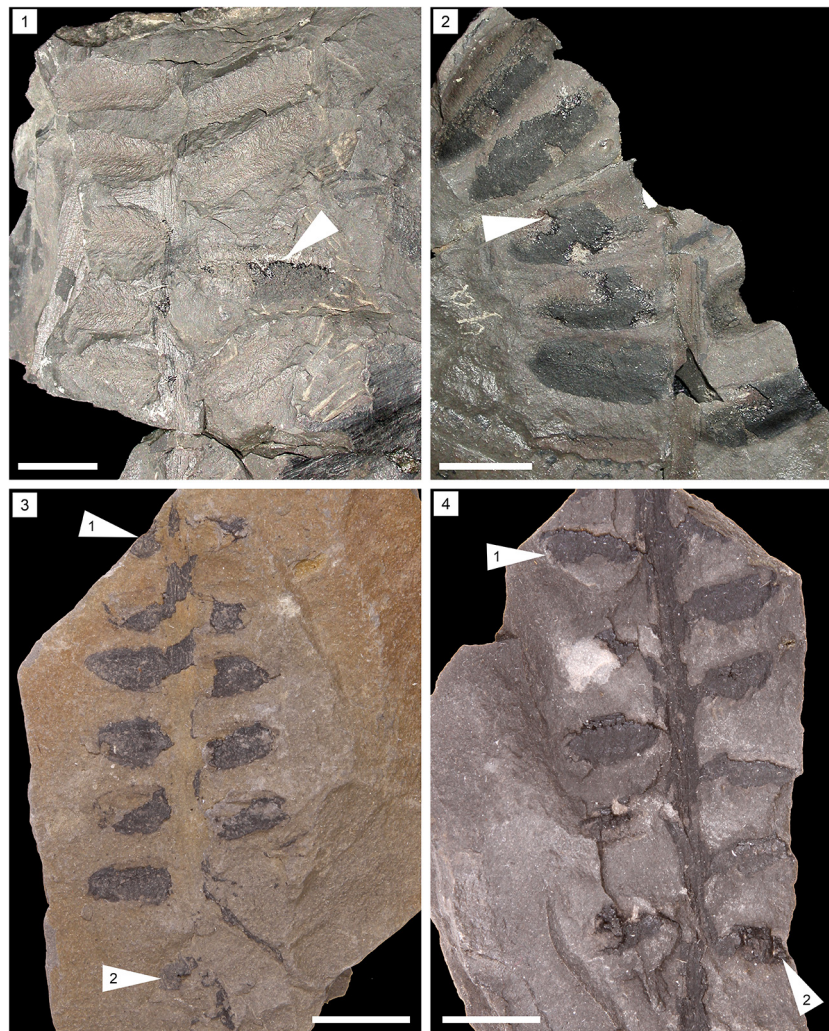


Plate IV. Macrofossils of *Symopteris* from the Carnian of Austria and Switzerland. 1–2. *Symopteris lunzensis*, Lunz am See, Austria. 1. GBA 1909/02/160. 2. GBA 1909/02/413. 3–4. *Symopteris helvetica*. 3. B3613, Moderhalde near Pratteln, Switzerland. 4. B2380, Neuwelt, Münchenstein, Switzerland. White arrows indicate sampling positions. Scale bars = 10 mm.

with a wide overlap in the size ranges. Compared to the spores reported from *S. aktjubensis* and *S. rumpfii* (Brik et al., 1955; Kustatscher et al., 2011), the spores of *S. helvetica* are larger and differ in their lack of ornamentation. Both the lack of a defined ornamentation and the fact that they do not separate easily could be due to immaturity.

4. Discussion

4.1. Spore size variation

While the size ranges of the spores of many of the studied species overlap, the size distribution is more informative (Fig. 2). *Asterotheca* spores are generally similar in size, with the various samples of *Asterotheca merianii* demonstrating that sizes can vary slightly even between samples from the same specimen, but with a wide overlap. The largest spores of *A. merianii* on average and in total came from specimen MB.Pb.2019/281 (mean: 45 μm , maximum: 59 μm), but only a few spores from one sample exceed the largest sizes measured in other samples. Similarly, the spores of *Asterotheca* sp. 1 are slightly larger (32–58 μm , mean: 44 μm) than average for *Asterotheca* in general, but not larger than the largest spores of *A. merianii*. Conversely, *Asterotheca* sp. 2 yielded relatively small spores (30–42, mean: 36 μm) compared to *A. merianii* and *Asterotheca* sp. 1, but the distribution is still comparable to some of the samples of *A. merianii*, and since this species is only

represented by one specimen, the differences cannot be considered diagnostic. The newly measured sizes of the spores of *A. thalensis* (33–46 μm , mean: 40 μm), while being considerably larger than previously reported from the same material (27–36 μm acc. to Kustatscher and Van Konijnenburg-van Cittert, 2011), are quite average for *Asterotheca*, comparable to *A. merianii*. By contrast, the two sampled specimens of *Asterotheca* cf. *thalensis* yielded spores that are in one case partly (MB.Pb.2010/82: 36–60 μm , mean: 46 μm) and in the other case (MB.Pb.2010/83: 51–81 μm , mean: 64 μm) almost consistently larger than what has been observed in other *Asterotheca* specimens. Although the two specimens had previously been assigned to *A. merianii* based on macromorphology, and the spores have an appearance that is very similar to those of *A. thalensis*, the sizes of the spores distinguish them from both species and each other. The spores of *Merianopteris augusta*, a species that was considered to be a junior synonym of *A. merianii* in the past (e.g., Pott et al., 2018.), are likewise distinct in their considerably larger size (45–77 μm , mean: 63 μm), as well as in their ornamentation (see below).

The species of *Danaeopsis* mostly differ from each other in the size distribution of their spores. Although there is some overlap, on average the spores of *D. marantacea* are smaller (47 μm), those of *D. fecunda* larger (70 μm), and those of *D. lunzensis* in the middle (57 μm). Considering that spore size is usually related to genome size, and that *D. marantacea* is the oldest species, as it appears in the Ladinian, with

D. lunzensis appearing in the Carnian and *D. fecunda* being from the Rhaetian, this suggests that the increase in spore size related to an evolutionary trend of increasing ploidy levels. Moreover, even within *D. marantacea*, the smallest spores (mean: 42 µm) came from the oldest (Ladinian) specimen (P915), whereas Carnian specimens were larger (mean: 53–55 µm) and in fact closer to *D. lunzensis*. The spores of *Danaeopsis* cf. *marantacea* show essentially the same distribution (mean: 54 µm) as the Carnian specimens of *D. marantacea*, which supports the species assignment. On the other hand, the average for *D. lunzensis* is affected by a downward outlier in specimen MB.Pb.2019/497, which has spores with a mean diameter of 48 µm, compared to 64 µm in both S148229–02 and S148582. The latter is close to the 65 µm value that had been reported in earlier studies (Nathorst, 1908; Potonié, 1962). Balme (1995) and Kustatscher et al. (2012a) gave a size range of 50–65 µm, which falls within but does not cover the full range observed in our material (41–72 µm). Similarly, the size range we recorded for *D. fecunda* (44–82 µm) is broader than in previous publications (60–70 µm according to Halle, 1921; Balme, 1995; Kustatscher et al., 2012a). Compared to the *Danaeopsis* species studied herein, the in situ spores of *Danaeopsis angustipinnata* Brik, 1952 have been described as unusually small (15–25 µm, mean 22 µm; Brik et al., 1955). Similar sizes are known from other Marattiales, including Triassic representatives of *Marattia*, *Marattiopsis*, and *Scolecopteris* (Table 1), but the spores of *D. angustipinnata* differ not only in size, but also in their reportedly spinate exine ornamentation from other *Danaeopsis* spores, which suggests a biological difference.

Measurements of the spores of *Symopteris lunzensis* and *S. helvetica* were hindered somewhat by the poor separability of the spores, but they appear to have widely overlapping size ranges, with the spores of *S. lunzensis* being larger on average (71 µm compared to 60 µm). Previously, Pott et al. (2018) reported much smaller spore sizes for *S. lunzensis* (42–48 µm). However, we found consistently larger spores in samples from two separate specimens, which suggests that the material studied by Pott et al. (2018) may have been an outlier, like what we observed in *D. marantacea* and *D. lunzensis*. It is noteworthy that in situ spores of *Symopteris aktjubensis* (Brik) Kustatscher et al., 2011 from the Upper Triassic of Kazakhstan have also been described with much smaller sizes (42–50 µm, mean: 45 µm; Brik et al., 1955; see Table 1), confirming that the total size range for *Symopteris* spores is rather broad.

Variations in the mean sizes of spores from samples representing different sampling positions on the same specimen can probably mostly be attributed to different maturation stages. A similar pattern has been observed in Triassic leptosporangiate ferns (Nowak et al., 2022). The spread around the mean should in part be due to natural variation and in part due to distortions from compaction (although heavily folded or damaged spores were not measured). In addition, some samples demonstrate a bimodal distribution, with a usually minor peak below the median. This is most conspicuous in samples with a high amount of abortive spores (from specimens NHMW – Geo 2010/0102/0196 and B3613; Figs. 2, 4). Although the same samples allowed only relatively few measurements to be taken, the presence of a high number of unusually small but otherwise seemingly well-developed spores alongside clearly abortive ones is notable, and it stands to reason that both had the same cause, although is not testable whether or which of the diminutive spores were unviable.

4.2. Aperture

The in situ spores of *Asterotheca merianii* as well as *Asterotheca* sp. 1 and *Asterotheca* sp. 2 described from the Lunz flora and *Asterotheca thalensis* along with *A. cf. thalensis* from the Thale flora are all monolete to trileteoid, as has been reported previously (see Table 1, Figs. 1A–D, 3). To this we can add that trileteoid apertures in *Asterotheca* can in rare cases be accompanied by other secondary laesurae (Fig. 1C; Plate V, 14, Plate VII, 12, 15–16). The secondary

laesurae may fork off from the primary monolete aperture perpendicularly or at a lower angle, and they may be positioned along the entire length of the primary aperture. When the primary aperture has a curve, then a secondary slit usually connects to the corner of the curve. The primary aperture can also have a slight curve without a secondary slit, or it can be straight with or without a secondary slit. These variations occur across the various species of *Asterotheca* without diagnostic differences. Individual samples may display a tendency towards shorter or longer secondary laesurae, but it should be noted that reliable measurements were only possible in relatively few spores (Fig. 3).

Spores of the genera *Danaeopsis* and *Symopteris* have been regarded as simply trilete so far (e.g., Brik et al., 1955; Kustatscher et al., 2012a), but we found them to frequently demonstrate asymmetrical trilete marks, wherein one ray is shorter or longer than the others (Figs. 1E–H, L–N, 5). Cases with an elongated ray can be regarded as an intermediate stage between trilete and monolete, and very few spores appear to be completely monolete. Spores from individual specimens can have a tendency towards either one shorter or longer ray, but more commonly, the distribution is more or less balanced, and there does not appear to be a significant difference between species in this regard (Fig. 5).

Cases of trilete and monolete spores occurring together in situ along with transitional forms are known from some Palaeozoic and Jurassic Marattiales (Van Konijnenburg-van Cittert, 1975, 1999; Pšenička et al., 2003). Apart from *Asterotheca* and the Late Triassic to Middle Jurassic species *Marattia intermedia* (Muenster) Kilpper, 1964 (see Schweitzer et al., 1997), this pattern has so far not been reported from the Triassic (see Table 1) but considering our findings it could be a rather common yet overlooked trait of the group during this time. It can also be seen in the spores of *Merianopteris augusta*, but with so far very few examples, as the aperture is often inconspicuous in this species (Figs. 1I–K, 5). Even when the aperture is clearly visible, the transitional forms are not always obvious, and would be even less so in dispersed assemblages without the context of in situ spores. An asymmetric trilete mark could in most cases easily be mistaken for the result of diagenetic distortion or a malformation. Only cases with an extreme reduction of one or two rays and in a favorable position are evident by themselves. A modified trilete mark (among other characteristics) can also appear in otherwise purely trilete spores due to environmental disturbances (Lindström et al., 2019). This feature can therefore provide valuable information, but to distinguish the different possible causes, it is necessary to consider the breadth of variations that are present within a population. The presence of an asymmetric trilete mark or the co-occurrence of monolete and trilete cases can help to differentiate spores of Marattiales and Osmundales, which can have similar appearances – such as spores that fall into the range of *Todisporites* (see Nowak et al., 2022). However, in dispersed assemblages, it is necessary to investigate the whole population and to link the obvious specimens to the less obvious to see similar patterns.

There are a few examples for the recognition of such features in dispersed assemblages: A trilete mark with unequal rays is a diagnostic feature of, e.g., *Polymorphisporites* Alpern, 1958, *Punctatisporites ambiguus* Leschik, 1955, and *Scabratisporites scabratus* Visscher, 1966. *Leschikisporis* was originally described as trilete with an asymmetric mark (Potonié, 1958), but was emended later to include monolete spores (Bharadwaj and Singh, 1964). The inclusion of both monolete and seemingly trilete spores was based on the co-occurrence of these forms in situ in *Asterotheca merianii*, and *Leschikisporis* has since been regarded as monolete in principal, with the apparent third ray that is observable in a part of the spores being recognized as a secondary crack (Bharadwaj and Singh, 1956, 1964). *Thymospora canaliculata* Schuurman, 1977 from the Late Triassic of France has been described as generally monolete, but occasionally trilete (Schuurman, 1977). Spores corresponding to this species are not known in situ, but monolete spores corresponding to the genus *Thymospora* Wilson et

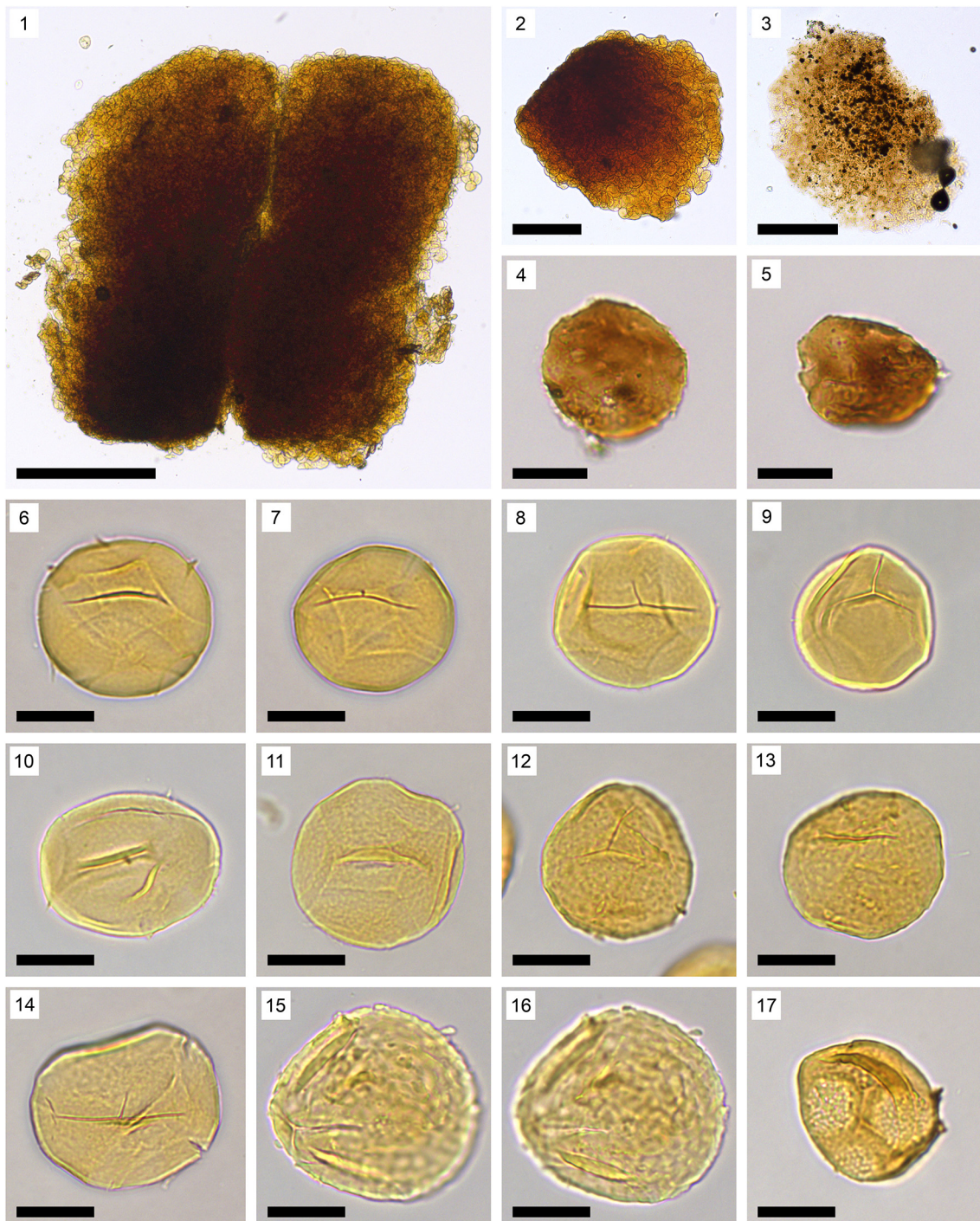


Plate V. In situ spores of *Asterotheca merianii*. 1–2, Sporangia, Lunz am See, Austria. 1. Sorus with four sporangia, MB.Pb.2019/281, sample 3. 2. Single sporangium, NHMW-Geo 1885/0012/3939, sample 1. 3. Sporangium with very light and delicate spores, Moderhalde, Switzerland, B3614, sample 1. 4–5. Poorly preserved spores, Gaming, Austria, NHMW-Geo 1845/0051/0014, sample 2. 6–17. Single spores, Lunz am See, Austria. 6. Monolete spore, MB.Pb.2019/281, sample 3. 7. Monolete aperture with very short secondary laesura, MB.Pb.2019/281, sample 3. 8. Monolete aperture with an inclined secondary laesura of intermediate length, MB.Pb.2019/281, sample 1. 9. Quasi-trilete aperture, NHMW-Geo 2019/0185/0004, sample 1. 10. Spore with a long monolete aperture and elliptic outline in oblique view, MB.Pb.2019/281, sample 1. 11. Spore with a circular amb and pronounced microverrucate ornamentation, NHMW-Geo 1884/0012/1214, sample 2. 12–13. Spores with verrucate ornamentation, NHMW-Geo 1878B/0006/9946. 12. Quasi-trilete spore. 13. Monolete spore. 14. Relatively large spore with an elliptic amb and two secondary laesurae in a central and terminal position on the primary laesura, MB.Pb.2019/281, sample 3. 15–16. Relatively large spore with partially verrucate exine, presumably due to alteration, NHMW-Geo 1885/0012/3889. 17. Spore with three imprints from mineral aggregates, which have punctured the exine in these areas, NHMW-Geo 2019/0185/0002. Scale bars: Fig. 1: 500 μ m, Figs. 2–3: 200 μ m, all others: 20 μ m.

Venkatachala, 1963 are known from Carboniferous and Permian Marattiales (*Lesnikowska and Willard, 1997; He et al., 2006*). It stands to reason that *T. canaliculata* also belongs to this group and represents yet another transitional case. Similarly, spores corresponding

to *Torisporea* Balme, 1952 (at times suspected to be sporangial wall cells) are known from Palaeozoic Marattiales and have been described as encompassing monolete and trilete or trileteoid forms (e.g., *Lesnikowska and Willard, 1997; Bek, 2021*).

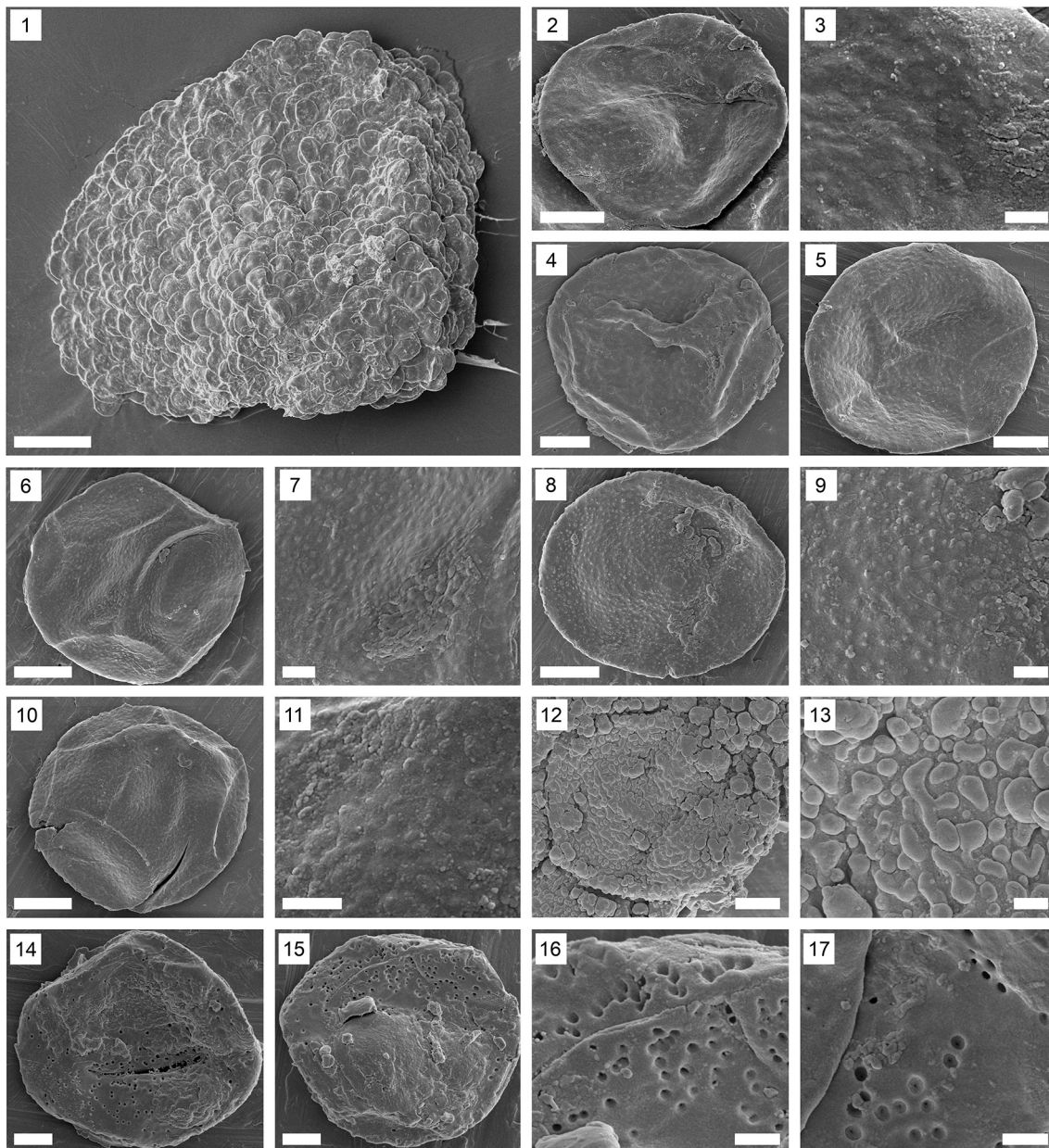


Plate VI. SEM pictures of in situ spores of *Asterotheca* spp. and *Merianopteris augusta*. 1–7. Spores of *Asterotheca merianii*, Lunz am See, Austria. 1. Sporangium, NHMW-Geo 1885/0012/3939, sample 1. 2–3. Spore with a monolet aperture and reduced, essentially laevigate ornamentation. 3. Detail of the specimen in fig. 2 showing the mark and reduced ornamentation, MB.Pb.2019/281, sample 1. 4. Spore with a verrucate/deformed(?) surface, NHMW-Geo 2010/0102/0183, sample 3. 5–7. Spores with dense and well-defined microverrucate ornamentation. 5. S148569. 6–7. S148250. 7. Detail of the specimen in fig. 6 showing the well-defined microverrucate ornamentation, 8–9. Spore of *Asterotheca* sp. 1, NHMW-Geo 1885/0012/3924, sample 2. 9. Detail of the specimen in fig. 8 showing the microverrucate to microechinate ornamentation, 10–11. Spore of *Asterotheca* sp. 2, NHMW-Geo 1885/0012/3926. 11. Detail of the specimen in fig. 10 showing the relatively coarse and dense microverrucate ornamentation, 12–13. Spore of *Merianopteris augusta*, Neuwelt, Münchenstein, Switzerland, MB. Pb.2019/502, acetolyzed. 13. Detail of the specimen in fig. 12 showing the trilete verrucate to rugulate/vermiculate ornamentation, 14–17. Spores of *Asterotheca* cf. *thalensis*, Thale, Germany, MB.Pb.2010/82. 14–16. Spores showing the concentration of puncta around the aperture. 16. Detail of the specimen in fig. 15 showing the puncta around the aperture, 17. Detail of some puncta showing the funnel shape. Scale bars: Fig. 1: 100 μm ; Figs. 2,4–6,8,10,12: 10 μm ; Figs. 3,7,9,11,13,16–17: 2 μm ; Figs. 14–15: 5 μm .

4.3. Ornamentation

Spore wall ornamentation among the studied marattialean species is shown to be relatively consistent for individual specimens, apart from some differences that can be attributed to corrosion, primarily on the outer layers of the sporangia. However, individuals can differ in this regard, as evidenced by specimens of *Asterotheca merianii* yielding spores with a more pronounced (verrucate) or more reduced (laevigate) ornamentation. For the most part, these differences probably represent different stages of maturation, but preservational and/or other effects may play a role as well. The occurrence of spores with relatively larger

verrucae in one particular specimen on the other hand cannot be explained in this way and may represent a mutation. Leptosporangiate fern spores have been shown to vary strongly in terms of ornamentation within single sporangia (Nowak et al., 2022). This is mostly due to the occasional reduction of otherwise prominent sculptural elements. By contrast, most of the marattialean spores studied here only have a weak ornamentation in any case, which means that missing or underdeveloped elements have little effect on the overall appearance of the spores. Only the spores of *Merianopteris augusta* have a considerable and characteristic ornamentation, but the latter is also consistent, with so far no observed examples of spores with reduced or missing sculpture elements.

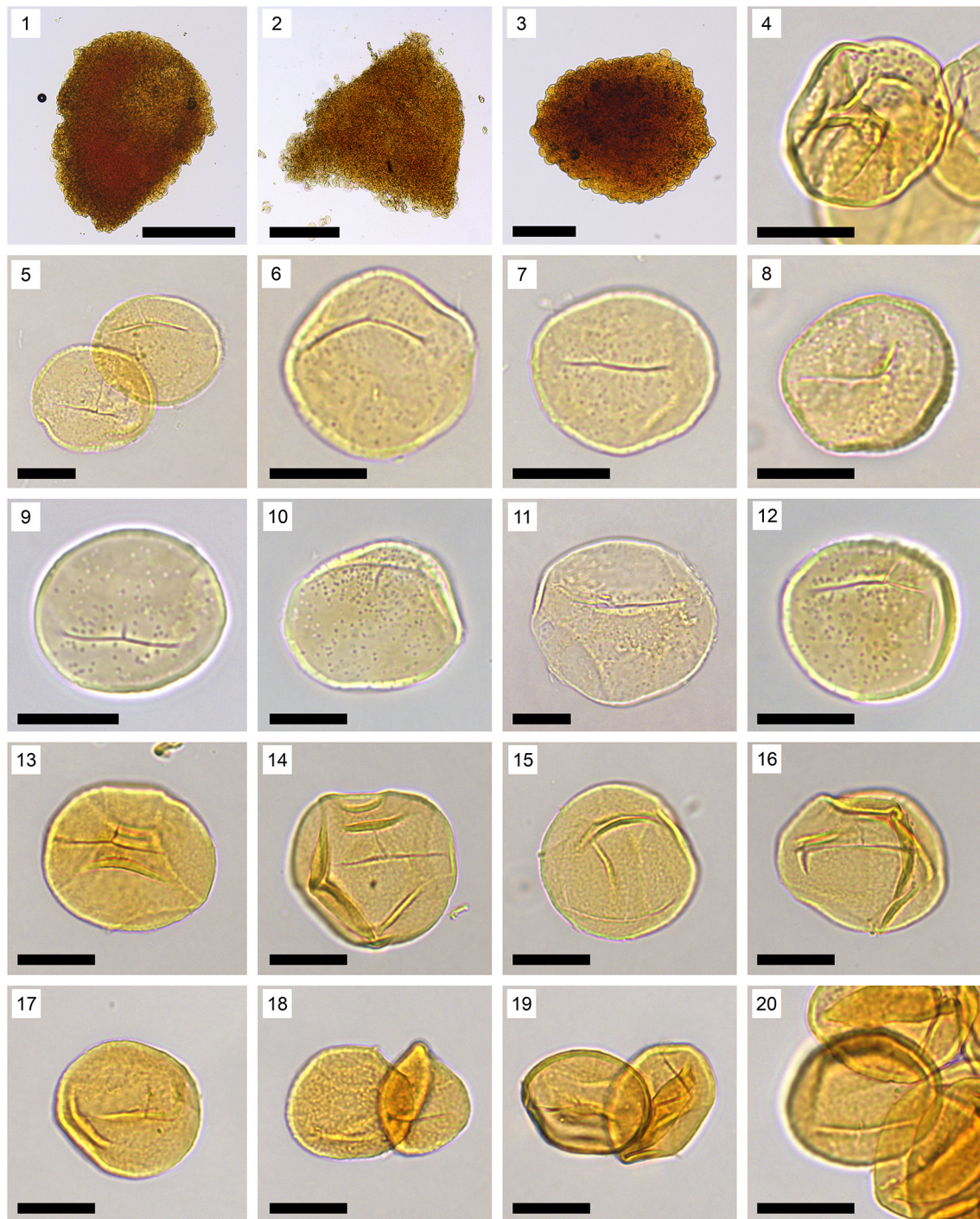


Plate VII. In situ spores of *Asterotheca* spp. 1. Sporangium of *Asterotheca thalensis*, Thale, Germany, NRM S114745. 2. Sporangium of *Asterotheca* cf. *thalensis*, Thale, Germany, MB.Pb.2010/83, sample 1. 3. Sporangium of *Asterotheca* sp. 1, Lunz am See, Austria, NHMW-Geo 1885/0012/3923, sample 2. 4. Spore of *Asterotheca merianii* with a punctate, presumably corroded, exine, Lunz am See, Austria, NHMW-Geo 2019/0185/0005. 5–8. Punctate spores of *Asterotheca thalensis*, Thale, Germany, NRM S114745. 5. Two spores with a straight primary aperture and long, perpendicular secondary laesurae. 6. Spore in oblique view showing higher density of pores near the aperture. 7. Essentially monolete spore with only a faint trace of a secondary laesura. 8. Essentially monolete spore with a secondary laesura at the right-hand end of the primary laesura, resulting in a bend. 9–12. Punctate spores of *Asterotheca* cf. *thalensis*, Thale, Germany. 9. Typical spore with a slightly elliptic amb and a monolete aperture with a short secondary laesura, MB.Pb.2010/82. 10. Spore in oblique view showing higher density of pores near the aperture, MB.Pb.2010/82. 11. Large monolete spore, MB.Pb.2010/83, sample 1. 12. Spore with two opposing secondary laesurae in excentric positions, MB.Pb.2010/82. 13–16. Granulate spores of *Asterotheca* sp. 1, Lunz am See, Austria. 13. Typical spore with an elliptic amb and a short secondary laesura, NHMW-Geo 1885/0012/3924, sample 1. 14. Spore with a circular amb and a long secondary laesura, NHMW-Geo 1885/0012/3924, sample 2. 15. Spore with a circular amb and two faint and equidirectional secondary laesurae; one approximately central on the primary laesura, the other on the left-hand end, NHMW-Geo 1885/0012/3924, sample 2. 16. Spore with an elliptic amb and two opposing secondary laesurae, NHMW-Geo 1885/0012/3924, sample 2. 17–20. Spores of *Asterotheca* sp. 2, Lunz am See, Austria, NHMW-Geo 1885/0012/3926, sample 1. 17. Typical spore with a monolete aperture with a secondary laesura. 18. Two spores with pronounced granulate ornamentation. 19. Two spores with laevigate exines. 20. Spore with two short and opposing, closely positioned secondary laesurae. Scale bars: Figs. 1–2: 500 μ m, Fig. 3: 200 μ m, all others: 20 μ m.

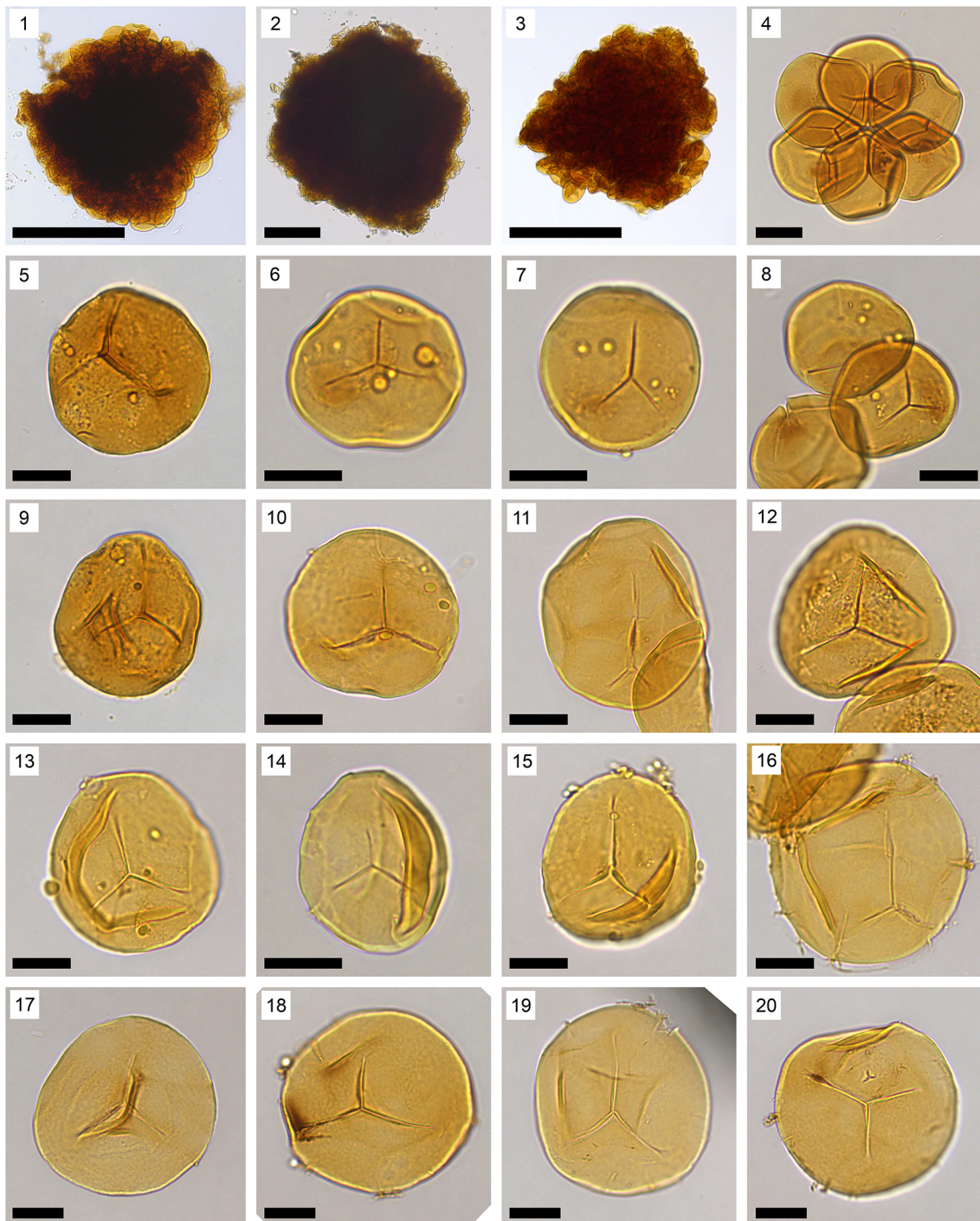


Plate VIII. In situ spores of *Danaeopsis* spp. 1–2. Sporangia of *Danaeopsis marantacea*. 1. Specimen from the Carnian Klettgau Formation at Neuwelt, Münchenstein, Switzerland, B2477, sample 1. 2. Specimen from the Ladinian Erfurt Formation at Bibersfeld, Germany, P915. 3. Sporangium of *Danaeopsis* cf. *marantacea*, S155185. 4–9. Spores of *Danaeopsis marantacea*; 4, 6–8: Bibersfeld, Germany, P915; 5–6: Neuwelt, Münchenstein, Switzerland, B2477. 4. Cluster of spores showing unaligned positions of trilete marks. 5. Circular spore, trilete mark with approximately equal rays. 6. Elliptic spore, trilete mark with one reduced ray. 7. Elliptic spore, trilete mark with two reduced rays/one elongated ray. 8. Rounded triangular spore on the right; apparently monolete spore on the upper left. 9. Spore with a trilete mark having one slightly longer ray. 10–12. Spores of *Danaeopsis* cf. *marantacea*, Neuwelt, Münchenstein, Switzerland, S155185. 10. Circular spore, trilete mark with one reduced ray. 11. Elliptic spore, trilete mark with two strongly reduced rays. 12. Rounded triangular spore, trilete mark with approximately equal rays. 13–16. Spores of *Danaeopsis lunzensis*, Lunz am See, Austria. 13. Spore with probably rounded triangular amb (but distorted due to pinching/folding), trilete mark with approximately equal rays, S148582. 14. Folded spore, trilete mark with one reduced ray, MB.Pb.2019/497. 15. Elliptic spore, trilete mark with one elongated ray, S148582. 16. Relatively large, circular spore, trilete mark with two reduced rays/one elongated ray, S148229–02. 17–20. Spores of *Danaeopsis fecunda*, Billesholm, Sweden. 17. Spore with a subcircular, slightly triangular amb, trilete mark with approximately equal rays, S054225. 18. Spore with a slightly elliptic amb, trilete mark with one reduced ray, S054225. 19. Spore with elliptic amb, trilete mark with two reduced rays/one elongated ray, S054033. 20. Spore showing a small secondary trilete aperture, probably related to abortive spores, S054033. Scale bars: Figs. 1–3: 200 μ m, all others: 20 μ m.

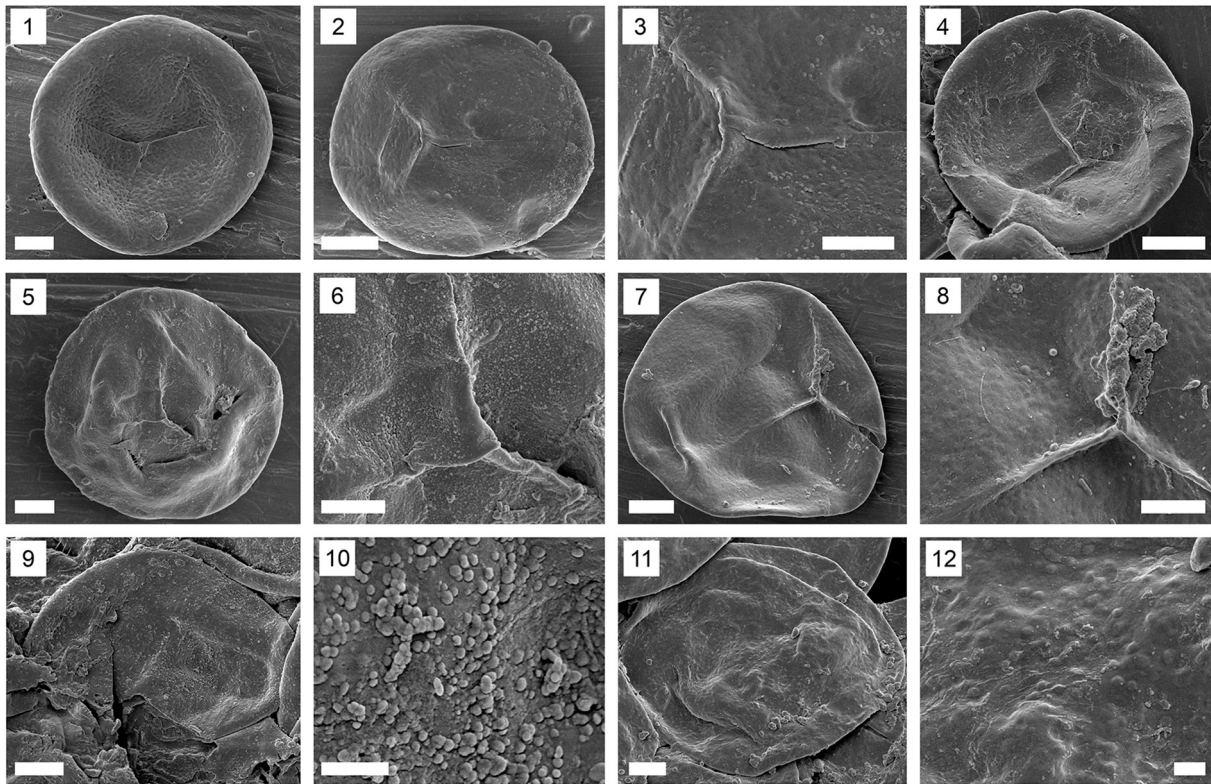


Plate IX. SEM pictures of in situ spores of *Danaeopsis* spp. and *Symopteris* spp. 1–3. Spores of *Danaeopsis marantacea*. 1. Spore with a trilete mark with one reduced ray and microreticulate ornamentation, Bibersfeld, Germany, P915. 2–3. Spore with a trilete mark with two reduced rays/one elongated ray and low-relief microreticulate ornamentation, B2474, sample 2, acetolyzed. 3. Detail of the specimen in fig. 2 showing the trilete mark and ornamentation, 4–6. Spores of *Danaeopsis lunzensis*. Lunz am See, Austria, 4. MB.Pb.2019/497. 5–6. S148582. 6. Detail of the specimen in fig. 5 showing the trilete mark and granulate ornamentation, 7–8. Spore of *Danaeopsis fecunda*, Billesholm, Sweden, S054225. 8. Detail of the specimen in fig. 7 showing the trilete mark and microreticulate ornamentation. 9–10. Spore of *Symopteris helvetica*, Neuwelt, Münchenstein, Switzerland, B2352, acetolyzed. 10. Detail of the specimen in fig. 9 showing the surface beset with orbicules that are interpreted as remains of the tapetum, 11–12. Spore of *Symopteris lunzensis*, Lunz am See, Austria, GBA 1909/02/160, acetolyzed. 12. Detail of the specimen in fig. 11 showing the sparse microverrucate to verrucate ornamentation, Scale bars: Figs. 1,3,6,8: 5 μ m; Figs. 2,4,5,7,9,11: 10 μ m; Figs. 10,12: 2 μ m.

The spores of *A. thalensis* and *A. cf. thalensis* differ from the Lunz specimens of *Asterotheca* spp. in having a negative instead of a positive relief, which suggests that the two populations, which are also of different ages, represent biologically distinct lineages, ecological variants, or are affected by diagenetic effects.

Although in the past, *Merianopteris augusta* has been considered a synonym of *A. merianii*, its spores differ significantly from those of the latter in terms of size, ornamentation, and appearance of the aperture. All these differences support a taxonomic distinction. In fact, the coarse and partly fused verrucae and gemmae seen in the spores of *M. augusta* distinguish them from the in situ spores known from any other Triassic marattialean fern. They are, however, comparable to the spores of some Palaeozoic Marattiales (Bek, 2021).

The spores of *Danaeopsis* spp. are generally similar to each other, with a laevigate, granulate or microreticulate surface. In the current material, a microreticulate ornamentation has only been seen in *D. fecunda*, *D. marantacea*, and *D. cf. marantacea*, but was also reported from *D. lunzensis* by Kustatscher et al. (2012a). The latter may have been a preservational artefact from the imprint of crystals. We found the spores of *D. lunzensis* to be finely granulate. In general, the presence of these structures can only be observed reliably in SEM. Due to the dimensions of the sculpture elements, especially their often very low relief, they are not always visible in LM. More or less conspicuous cases occur within samples, which could relate to slight differences in the maturity of the spores – with the ornamentation not having properly formed in less mature ones –, or even in the maceration process, but could also be a result of natural variation.

The exines of spores from *Symopteris lunzensis* and *S. helvetica* were observed to be generally laevigate or sparsely (micro-)verrucate, but

much of the studied material was obscured by remains of the tapetum and/or other spores. It is possible that the few observed specimens were too immature to show the fully-formed sculpture elements. Other kinds of ornamentation are possible for *Symopteris*, as the spores of *S. lunzensis* as well as those of *S. rumpfii* have been described by Kustatscher et al. (2011) as slightly punctate, whereas Brik et al. (1955) reported spines on the spores of “*Bernoullia*” (= *Symopteris*) *aktjubensis*. However, the previously reported punctate state of the exine in *S. lunzensis* was not as consistent and conspicuous as in *S. rumpfii* (comp. Plate VII, figs. 1–4 and 5–8 in Kustatscher et al., 2011) and may have been a preservational artefact, as we could not confirm it.

4.4. Abortive spores

Abortive spores are present in small numbers in nearly all samples representing entire sporangia, and sometimes in samples yielding only a few spores (Fig. 5). Only one sporangium of *Asterotheca merianii* (NHMW-Geo 1885/0012/4093, sample 1) yielded no abortive spores (out of more than 400 examined spores). In other samples, only one or two abortive spores may be present, but commonly, they occur with frequencies of 1–5%. They can, therefore, be regarded as a normal occurrence. However, some samples contain abortive spores with significantly elevated frequencies (up to >66%). This has been observed previously in Triassic leptosporangiate ferns as well (Nowak et al., 2022), although to a lesser degree (up to 12.6%). High amounts of abortive spores are also known from extant ferns and usually regarded as a result of hybridisation or genetic defects from other causes (Barrington et al., 1989). As these spores are unable to

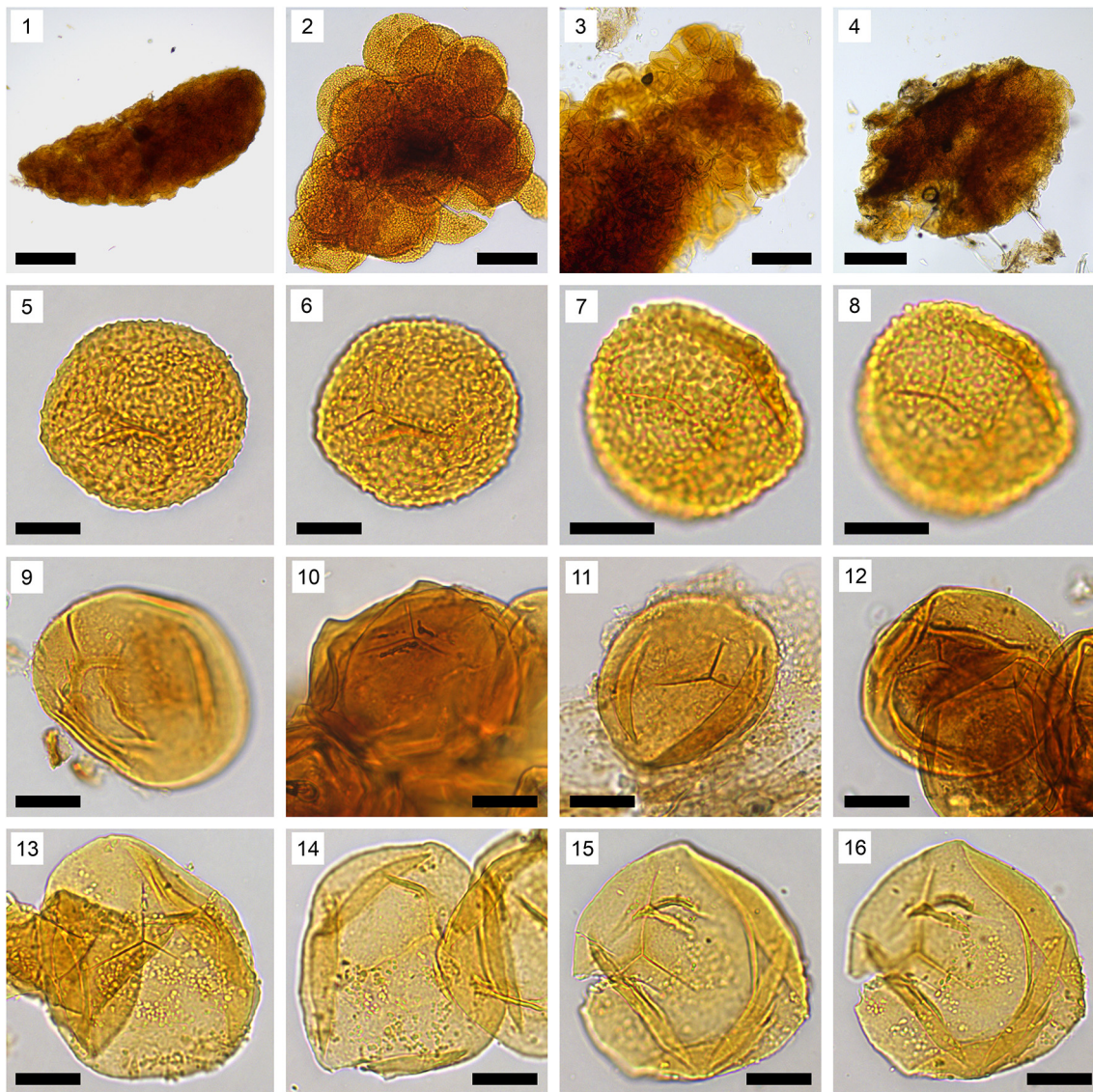


Plate X. In situ spores of *Merianopteris augusta*, *Symopteris helvetica*, and *S. lunzensis*. 1–2. *Merianopteris augusta*, Neuwelt, Münchenstein, Switzerland, MB.Pb.2019/502. 1. Sporangium. 2. Cluster of spores. 3. Sporangial fragment of *Symopteris helvetica*, B2352. 4. (Incomplete?) sporangium of *Symopteris lunzensis*, Lunz am See, Austria, GBA 1909/2/413. 5–8. Spores of *Merianopteris augusta*, Neuwelt, Münchenstein, Switzerland, MB.Pb.2019/502. 5–6. Spore with verrucate ornamentation, trilete mark with long rays, possibly one elongated ray. 7–8. Spore with verrucate/gemmate ornamentation, trilete mark with short rays and asymmetric. 9–12. Spores of *Symopteris helvetica*, Neuwelt, Münchenstein, Switzerland. 9. Spore with faint trilete mark, B2352. 10. Overlapping spores in a sporangium, B2352. 11. Trilete mark with at least one relatively shorter ray, B3613, sample 2. 12. Trilete mark with at least one relatively shorter ray, B2352. 13–16. Spores of *Symopteris lunzensis*, Lunz am See, Austria, GBA 1909/2/160. 13. Trilete mark with one slightly shorter ray. 14. Spore with faint trilete mark. 15–16. Trilete mark with at least one relatively shorter ray. Scale bars: Figs. 1, 4: 200 μ m, Fig. 2: 50 μ m, Fig. 3: 100 μ m, all others: 20 μ m.

germinate, they indicate lower reproductive fitness (in non-apomictic plants). Most likely, many spores that appear well-developed based on the preserved exine were also unviable – or would have been after maturation. As such, our percentage of abortive spores can only be considered a lower bound for the inverse germination rate.

Significantly high amounts of abortive spores were found in some specimens of *Symopteris helvetica*, *A. merianii*, and *Danaeopsis* cf. *marantacea* (Fig. 5). However, it was observed that abortive spores, when they are highly frequent, form tight clusters that were not easily divided. Consequently, the highest frequencies could not be quantified. Nevertheless, in at least one case in *S. helvetica* (B3613, sample 1), the number of abortive spores is clearly higher (> 66%) than the amount of regular spores. A second sample from the same specimen also showed unusually high but still much lower numbers of abortive spores, with an estimate of 25–50%.

The abundance of in situ material from *Asterotheca merianii* makes this species ideal to study patterns in the distribution of abortive spores. Significantly elevated frequencies are observed in two specimens (NHMW – Geo 2010/0102/0196 and 2010/0102/0029), in both cases across three separate samples (Fig. 5). This confirms the hypothesis that the main cause is a systemic defect of the parent plant. However, the various samples also show considerable variation, with some uncertainty due to a high number of compacted spores that may or may not be abortive. A similar variation in the frequency of abortive spores between samples from the same frond has been observed in extant leptosporangiate ferns (Hornych and Ekrt, 2017).

The abortive spores can have a variety of appearances, with some observable patterns. A common occurrence are heavily distorted and compacted spores (Plate XI, 13, 20), which are not always clearly distinguishable from diagenetically distorted ones. However, other abortive spores retain some features of the regular spores, while being

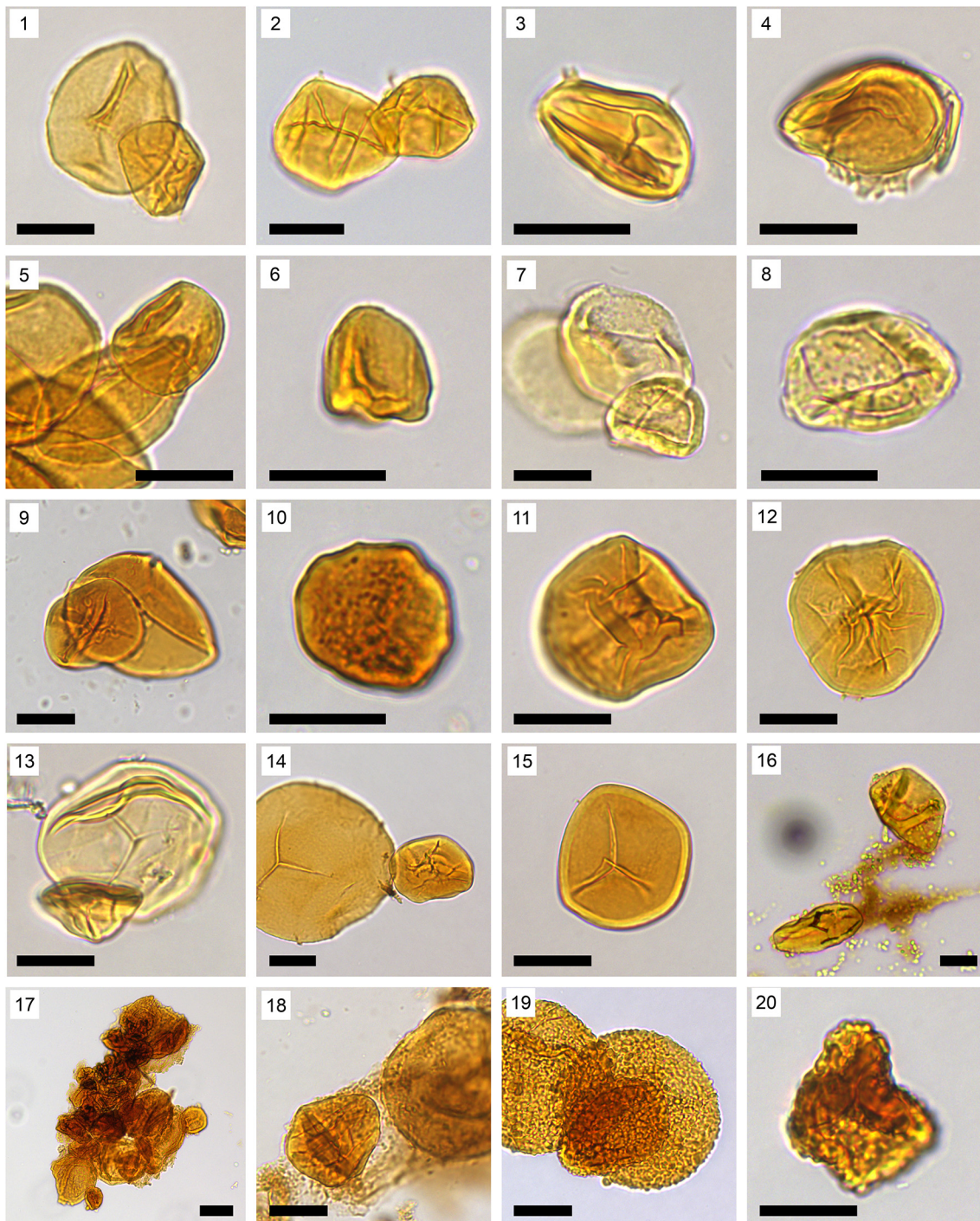


Plate XI. Abortive spores. 1–3. *Asterotheca merianii*. 1. Abortive spore with irregular furrows next to a regular spore, NHMW-Geo 1884/0012/1214, sample 2. 2. Two abortive spores showing parallel furrows perpendicular to the main laesura, NHMW-Geo 1883/0017/5925, sample 1. 3. Abortive spore showing longitudinal furrows, NHMW-Geo 1882/0013/3056, sample 1. 4. *Asterotheca* sp. 1, NHMW-Geo 1885/0012/3924, sample 2. 5–6. *Asterotheca* sp. 2, 1885/0012/3926, sample 1. 5. Diminutive, probably abortive spore next to regular spores. 6. Very small abortive spore. 7. *Asterotheca thalensis*, abortive spore next to regular spores, NRM S114745. 8. *Asterotheca* cf. *thalensis*, MB.Pb.2010/82.9–10. *Danaeopsis marantacea*. 9. Abortive spore with irregular furrows next to regular, folded spore, B2453, sample 1. 10. Especially dense abortive spore, B2477, sample 2. 11. *Danaeopsis* cf. *marantacea*, abortive spore with irregular furrows, S155185. 12–13. *Danaeopsis lunzensis*. 12. Abortive spore with irregular furrows, S148582. 13. Abortive spore next to regular spore, MB.Pb.2019/497. 14–15. *Danaeopsis fecunda*. 14. Abortive spore with irregular furrows next to regular spore, S050002. 15. Diminutive and dark, probably abortive but undistorted spore, S054225. 16. *Symopteris lunzensis*, two abortive spores, GBA 1909/2/413. 17–18. *Symopteris helvetica*. 17. Cluster of numerous abortive spores and a few regular spores, stuck on a piece of cuticle, B3613, sample 1. 18. Abortive spore next to a regular spore, B3613, sample 2. 19–20. *Merianopteris augusta*, MB.Pb.2019/502. 19. Probable abortive spore on top of two regular spores. 20. Strongly distorted abortive spore. Scale bars: Fig. 17: 50 μ m, all others: 20 μ m.

conspicuously smaller and darker. The aperture is often at least faintly visible. Many abortive spores have furrows, which may be irregularly meandering (e.g., Plate XI, 11–12) or relatively straight (Plate XI, 2–3, 7–8). In the abortive spores of *Asterotheca merianii*, straight furrows

tend to run either perpendicular (Plate XI, 2) or parallel (Plate XI, 3) to the main aperture. In rare cases where these furrows are missing (Plate XI, 5, 15, 17, 19), it is not entirely clear if the spores in question are abortive spores of the same kind as the others, or if a different

process caused abnormally small but potentially viable spores to be produced.

5. Conclusions

The in situ spores of the studied marattialean ferns from the Triassic of Europe show many common features and can be grouped into three types (*Leschikisporis*, *Punctatisporites/Todisporites*, *Verrucosisporites*) based mainly on their ornamentation and the general appearance of their mark. More detailed distinctions between the species in the genus *Danaeopsis* can be made by comparing their size distribution. Some outliers with consistently differently sized spores potentially point to genetically distinct lineages. However, such details are easily overlooked, and the observed natural variability requires an assessment of multiple specimens. In dispersed assemblages, the differences may not be obvious but can potentially be found by statistically analyzing a population.

The observation that almost all the studied in situ spores do not conform to a well-defined trilete state but are strictly speaking trileteoid, with rays of unequal length, suggests that this feature may in fact be typical for the group. The effect is often slight and not consistent, as well as often obscured by deformation, which would explain why it was not reported earlier in publications on the in situ spores of *Danaeopsis* and *Symopteris*. Future studies will hopefully show its pervasiveness in the Marattiales.

Last but not least, the study of in situ spores permits to distinguish different fossil taxa that macromorphologically would not be distinguishable at all. In particular, specimens from Thale and Neuwelt that have previously been assigned to *Asterotheca merianii* have been found to show considerable differences from those of Lunz in the exine ornamentation and partly in the size of their spores. Among other things, our results confirm the taxonomic independence of *Asterotheca thalensis* and *Merianopteris augusta*. This proves how important the quantitative and qualitative analysis of the in situ spores has become also for the assessment of land plant biodiversity in the Triassic. In addition, this study has revealed that the original description of *Merianopteris augusta* requires an emendation, which is in preparation.

Data availability

Data will be made available on request.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Hendrik Nowak reports financial support and travel were provided by SYNTHESYS. Two of the authors are guest editors for the special issue - HN, EK.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2022.104785>.

References

- Attali, D., 2019. ggExtra – add marginal histograms to ggplot2, and more ggplot2 enhancements. <https://cran.r-project.org/package=ggExtra>.
- Balme, B.E., 1995. Fossil in situ spores and pollen grains: an annotated catalogue. *Rev. Palaeobot. Palynol.* 87, 81–323. [https://doi.org/10.1016/0034-6667\(95\)93235-X](https://doi.org/10.1016/0034-6667(95)93235-X).
- Barrington, D.S., Haufler, C.H., Werth, C.R., 1989. Hybridization, reticulation, and species concepts in the ferns. *Am. Fern J.* 79, 55–64. <https://doi.org/10.2307/1547160>.
- Bek, J., 2021. Palynological grouping of Paleozoic marattialean miospores. *Rev. Palaeobot. Palynol.* 284, 104341. <https://doi.org/10.1016/j.revpalbo.2020.104341>.
- Bharadwaj, D.C., Singh, H.P., 1956. *Asterotheca merianii* (Brogniart) Stur and its spores from the Upper Triassic of Lunz (Austria). *The Paleobotanist* 5, 51–55.
- Bharadwaj, D.C., Singh, H.P., 1964. An Upper Triassic miospore assemblage from the coals of Lunz, Austria. *Paleobotanist* 12, 28–44.
- Boureau, É. (Ed.), 1970. *Traité de paléobotanique, IV (1): Filicophyta*. Masson, Paris.
- Brik, M.I., Kopytova, Z.A., Tiritanova-Ketova, A.I., 1955. Nekotorye mezozojskie paprotniki Yugo-Zapadnogo Priural'va i ih spory. In: Glazunova, A.E. (Ed.), *Materijal po geologii i poleznym iskopaemym*, Moscow, pp. 131–177.
- Brongniart, A., 1828–1837. *Histoire des végétaux fossiles ou recherches botaniques et géologiques sur les végétaux refermés dans les diverses couches du globe*. Tome Premier. G. Dufour et Ed. d'Ocagne, Paris.
- Couper, R.A., 1958. British Mesozoic microspores and pollen grains. A systematic and stratigraphic study. *Palaeontogr. Abt. B* 103, 75–179.
- Delevoryas, T., Taylor, T.N., Taylor, E.L., 1992. A marattialean fern from the Triassic of Antarctica. *Rev. Palaeobot. Palynol.* 74, 101–107. [https://doi.org/10.1016/0034-6667\(92\)90140-C](https://doi.org/10.1016/0034-6667(92)90140-C).
- Dobruskina, I.A., 1998. Lunz flora in the Austrian Alps – a standard for Carnian floras. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 143, 307–345. [https://doi.org/10.1016/S0031-0182\(98\)00116-3](https://doi.org/10.1016/S0031-0182(98)00116-3).
- Halle, T.G., 1921. On the sporangia of some Mesozoic ferns. *Arkiv. för Botanik* 17, 1–28.
- Harris, T.M., 1931. The fossil flora of Scoresby Sound East Greenland – part 1: Cryptogams (exclusive of Lycopodiales). *Medd. Grønland* 85, 1–102.
- He, X.-Y., Wang, S.-J., Hilton, J., Zhou, Y.-L., 2006. A new species of the marattialean fern *Scoleopteris* (Zenker) Millay from the uppermost Permian of Guizhou Province, south-western China. *Bot. J. Linn. Soc.* 151, 279–288. <https://doi.org/10.1111/j.1095-8339.2006.00536.x>.
- Heer, O., 1877. *Flora fossilis Helveticae. 1. Lieferung. Die Steinkohlenflora*. Verlag von J. Wurster & Comp, Zürich.
- Hornych, O., Ekrt, L., 2017. Spore abortion index (SAI) as a promising tool of evaluation of spore fitness in ferns: an insight into sexual and apomictic species. *Plant Syst. Evol.* 303, 497–507. <https://doi.org/10.1007/s00606-016-1386-3>.
- Kelber, K.-P., 2015. Die Makroflora des Lettenkeupers. In: Hagdorn, H., Schoch, R., Schweigert, G. (Eds.), *Der Lettenkeuper - Ein Fenster in Die Zeit Vor Den Dinosauriern - Palaeodiversity Supplement*. Staatliches Museum für Naturkunde, Stuttgart, pp. 51–100.
- Krasser, F., 1909. Die Diagnosen der von Dionysius Stur in der obertriadischen Flora der Lunzerschichten als Marattiaceenarten unterschiedenen Farne. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Wien, Math Naturw. Kl., Abt. I* 118, 13–43.
- Kräusel, R., Leschik, G., 1955. Die Keuperflora von Neuwelt bei Basel – I. Koniferen und andere Gymnospermen. *Schweizer Paläontol. Abh.* 71, 1–27.
- Kräusel, R., Leschik, G., 1959. Die Keuperflora von Neuwelt bei Basel – III. Equisetaceen. *Schweizer Paläontol. Abh.* 77, 5–19.
- Kräusel, R., Schaarschmidt, F., 1966. Die Keuperflora von Neuwelt bei Basel – IV. Pterophyllen und Taeniopteriden. *Schweizer Paläontol. Abh.* 84, 5–79.
- Krings, M., Kerp, H., 1997. An improved method for obtaining large pteridosperm cuticles. *Rev. Palaeobot. Palynol.* 96, 453–456. [https://doi.org/10.1016/S0034-6667\(96\)00059-0](https://doi.org/10.1016/S0034-6667(96)00059-0).
- Kustatscher, E., Van Konijnenburg-van Cittert, J.H.A., 2011. The ferns of the Middle Triassic flora from Thale (Germany). *N. Jb. Geol. Paläontol. Abh.* 261, 209–248. <https://doi.org/10.1127/0077-7749/2011/0174>.
- Kustatscher, E., Pott, C., Van Konijnenburg-van Cittert, J.H.A., 2011. A contribution to the knowledge of the Triassic fern genus *Symopteris*. *Rev. Palaeobot. Palynol.* 165, 41–60. <https://doi.org/10.1016/j.revpalbo.2011.02.006>.
- Kustatscher, E., Kelber, K.-P., Van Konijnenburg-van Cittert, J.H.A., 2012a. *Danaeopsis* Heer ex Schimper 1869 and its European Triassic species. *Rev. Palaeobot. Palynol.* 183, 32–49. <https://doi.org/10.1016/j.revpalbo.2012.06.011>.
- Kustatscher, E., Heunisch, C., Van Konijnenburg-van Cittert, J.H.A., 2012b. Taphonomical implications of the Ladinian megaflora and palynoflora of Thale (Germany). *PALAIOS* 27, 753–764. <https://doi.org/10.2110/palo.2011.p11-090r>.
- Lehtonen, S., Poczai, P., Sablok, G., Hyvönen, J., Karger, D.N., Flores, J., 2020. Exploring the phylogeny of the marattialean ferns. *Cladistics* cl.12419. <https://doi.org/10.1111/cl.12419>.

- Leschik, G., 1955. Die Keuperflora von Neuwelt bei Basel – II. Die Iso- und Microsporen. *Schweizer Paläontol. Abh.* 72, 1–70.
- Lesnikowska, A.D., Willard, D.A., 1997. Two new species of *Scolecoperis* (Marattiales), sources of *Torispora securis* Balme and *Thymospora thiesseii* (Kosanke) Wilson et Venkatachala. *Rev. Palaeobot. Palynol., Euramerican Carboniferous Paleobotany and Coal Geology* 95, 211–225. [https://doi.org/10.1016/S0034-6667\(96\)00035-8](https://doi.org/10.1016/S0034-6667(96)00035-8).
- Leuthardt, F., 1904. Die Keuperflora Neuwelt bei Basel. II Teil. Kryptogamen. *Abhandlungen der schweizerischen paläontologischen Gesellschaft* 31, 25–46.
- Lindström, S., Sanei, H., van de Schootbrugge, B., Pedersen, G.K., Leshner, C.E., Tegner, C., Heunisch, C., Dybkjær, K., Outridge, P.M., 2019. Volcanic mercury and mutagenesis in land plants during the end-Triassic mass extinction. *Sci. Adv.* 5, eaaw4018. <https://doi.org/10.1126/sciadv.aaw4018>.
- Lugardon, B., 1990. Pteridophyte sporogenesis: A survey of spore wall ontogeny and fine structure in a polyphyletic plant group. In: Blackmore, S., Knox, R.B. (Eds.), *Microspores: Evolution and Ontogeny*. Academic Press Limited, pp. 95–120.
- Lundblad, B., 1950. Studies in the Rhaeto-Liassic Floras of Sweden: I. 1 Pteridophyta, Pteridospermae, and Cycadophyta from the mining district of NW Scania. *Kungliga Svenska Vetenskapsakademiens Handlingar*, ser. 4 1, 5–82.
- Murdock, A.G., 2008a. Phylogeny of marattioid ferns (Marattiaceae): inferring a root in the absence of a closely related outgroup. *Am. J. Bot.* 95, 626–641. <https://doi.org/10.3732/ajb.2007308>.
- Murdock, A.G., 2008b. A taxonomic revision of the eusporangiate fern family Marattiaceae, with description of a new genus *Ptisana*. *Taxon* 57, 737–755. <https://doi.org/10.1002/tax.573007>.
- Nathorst, A.G., 1878. Bidrag till Sveriges fossila flora. Floran vid Höganäs och Helsingborg. *Kungliga Svenska Vetenskapsakademiens för Handlingar* 16, 1–53.
- Nathorst, A.G., 1908. Paläobotanische Mitteilungen 4–6. *Kungl. Svenska Vetenskapsakademiens Handlingar* 43, 1–33.
- Nowak, H., Kustatscher, E., Roghi, G., Van Konijnenburg-van Cittert, J.H.A., 2022. Variability of in situ spores in some leptosporangiate ferns from the Triassic in Italy and Austria. *Rev. Palaeobot. Palynol.* 296, 104544. <https://doi.org/10.1016/j.revpalbo.2021.104544>.
- Potonié, R., 1958. Synopsis der Gattungen der Sporae dispersae. II. Sporites (Nachträge), Saccites, Aletes, Praecolpates, Polyplicates, Monocolpates, Beiheft des Geologischen Jahrbuchs. Amt für Bodenforschung, Hannover.
- Potonié, R., 1962. Synopsis der Sporae in situ. Die Sporen der fossilen Fruktifikationen (Thallophyta bis Gymnospermophyta) im natürlichen System und im Vergleich mit den Sporae dispersae, Beihefte zum Geologischen Jahrbuch. Bundesanstalt für Bodenforschung, Hannover.
- Potonié, R., 1967. Versuch der Einordnung der fossilen Sporae dispersae in das phylogenetische System der Pflanzenfamilien. Westdeutscher Verlag, Köln, Opladen, *Forschungsberichte des Landes Nordrhein-Westfalen*.
- Pott, C., Bouchal, J.M., Choo, T.Y.S., Yousif, R., Bomfleur, B., 2018. Ferns and fern allies from the Carnian (Upper Triassic) of Lunz am See, Lower Austria: a melting pot of Mesozoic fern vegetation. *Palaeontogr. Abt. B* 297, 1–101. <https://doi.org/10.1127/palb/2018/0059>.
- Pšenička, J., Bek, J., Zodrow, E.L., Cleal, C.J., Hemsley, A.R., 2003. A new late Westphalian fossil marattialean fern from Nova Scotia. *Bot. J. Linn. Soc.* 142, 199–212. <https://doi.org/10.1046/j.1095-8339.2003.00169.x>.
- R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>.
- Roghi, G., Gianolla, P., Minarelli, L., Pilati, C., Preto, N., 2010. Palynological correlation of Carnian humid pulses throughout western Tethys. *Palaeogeography, Palaeoclimatology, Palaeoecology, Triassic climates* 290, 89–106. <https://doi.org/10.1016/j.palaeo.2009.11.006>.
- Rothwell, G.W., Millay, M.A., Stockey, R.A., 2018. Resolving the overall pattern of marattialean fern phylogeny. *Am. J. Bot.* 105, 1304–1314. <https://doi.org/10.1002/ajb.21115>.
- Schimper, W.P., 1869. *Traité de Paléontologie végétale ou la flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel*. Tome premier. Baillière J.B. et Fils, Paris.
- Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B., Tinevez, J.-Y., White, D.J., Hartenstein, V., Eliceiri, K., Tomancsek, P., Cardona, A., 2012. Fiji: an open-source platform for biological-image analysis. *Nat. Methods* 9, 676–682. <https://doi.org/10.1038/nmeth.2019>.
- Schulze, F., 1855. Über das Vorkommen wohlhaltener Cellulose in Braunkohle und Steinkohle. *Ber. K. Akad. Wiss.* 21, 676–678.
- Schuurman, W.M.L., 1977. Aspects of late Triassic palynology. 2. Palynology of the “Grès et Schiste à *Avicula contorta*” and “Argiles de Levallois” (Rhaetian) of northeastern France and Southern Luxembourg. *Rev. Palaeobot. Palynol.* 23, 159–253. [https://doi.org/10.1016/0034-6667\(77\)90007-0](https://doi.org/10.1016/0034-6667(77)90007-0).
- Schweitzer, H.-J., van Konijnenburg van Cittert, J.H.A., van der Burgh, J., 1997. Die rhätojurassischen Floren des Iran und Afghanistans. 10. Bryophyta, Lycophyta, Sphenophyta, Pterophyta-Eusporangiatae & Protolptosporangiatae. *Palaeontogr. Abt. B* 243, 103–192.
- Sternberg, K., 1838. Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt. Gottlieb Haase Söhne, Prague.
- Stur, D.R.J., 1885. Die obertriadische Flora der Lunzer-Schichten und des bituminösen Schiefers von Raibl. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften*, 1. Abth. 111, 93–103.
- Stur, D.R.J., 1888. Die Lunzer- (Lettenkohlen-) Flora in den “older Mesozoic beds of the Coal-Field of Eastern Virginia”. *Verhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt* 10, 203–217.
- Taylor, T.N., Osborn, J.M., Taylor, E.L., 1996. Chapter 14C – the importance of in situ pollen and spores in understanding the biology and evolution of fossil plants. *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, pp. 427–441.
- Taylor, T.N., Taylor, E.L., Krings, M., 2009. *Paleobotany: the Biology and Evolution of Fossil Plants*. 2. ed. Elsevier/Acad. Press, Amsterdam.
- Van Konijnenburg-van Cittert, J.H.A., 1975. Some notes on *Marattia anglica* from the Jurassic of Yorkshire. *Rev. Palaeobot. Palynol.* 20, 205–214. [https://doi.org/10.1016/0034-6667\(75\)90021-4](https://doi.org/10.1016/0034-6667(75)90021-4).
- Van Konijnenburg-van Cittert, J.H.A., 1999. On the evolution of fern spore architecture. In: Kurmann, M.H., Hemsley, A.R. (Eds.), *The Evolution of Plant Architecture*. Royal Botanic Gardens, Kew, pp. 279–287.
- Wickham, H., 2016. *Ggplot2: Elegant Graphics for Data Analysis*. 2. ed. Springer Verlag, Cham. <https://cran.r-project.org/package=ggplot2>.
- Wilke, C.O., 2021. Introduction to ggrridges. <https://cran.r-project.org/package=ggrridges>.
- Xu, R., Zhu, J.-N., Chen, Y., Duan, S.-Y., Hu, Y.-F., Zhu, W.-Q., 1979. *Chinese Late Triassic Plants from Baoding*. Science Press, Beijing.
- Zodrow, E.L., Šimůnek, Z., Cleal, C.J., Bek, J., Pšenička, J., 2006. Taxonomic revision of the Palaeozoic marattialean fern *Acitheca* Schimper. *Rev. Palaeobot. Palynol.* 138, 239–280. <https://doi.org/10.1016/j.revpalbo.2006.01.007>.