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Variability of *in situ* spores in some leptosporangiate ferns from the Triassic in Italy and Austria

Hendrik Nowak [a],*, Evelyn Kustatscher [a,b,c], Guido Roghi [d], Johanna H.A. Van Konijnenburg-van Cittert [e,f]

[a] *Museum of Nature South Tyrol, Bozen/Bolzano, Italy*
[b] *Department für Geo- und Umweltwissenschaften, Paläontologie und Geobiologie, Ludwig-Maximilians-Universität, München, Germany*
[c] *Bayerische Staatssammlung für Paläontologie und Geobiologie, München, Germany*
[d] *Institute of Geosciences and Earth Resources (CNR), Padova, Italy*
[e] *Naturalis Biodiversity Center, PO Box 9517, 2300 RA Leiden, the Netherlands*
[f] *Laboratory of Palaeobotany and Palynology, Vening Meinesz Building A, Princetonlaan 8A, 3584 CB Utrecht, the Netherlands*

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ABSTRACT

Spores or pollen from a single species or even an individual plant or sporangium may vary in morphology and size to a point that equivalent forms found dispersed in the sediment have been described as different species or even genera. In addition, not all these organs were mature at the moment of burial, and therefore they do not always contain completely developed microspores. To understand these variations better, we studied the intraspecific and interspecific morphological variability of *in situ* spores of leptosporangiate ferns (belonging to the Osmundales, possible Osmundales, and Gleicheniales) from the Triassic of Europe. The material comes from the Anisian Kühwiesenkopf/Monte Prà della Vacca flora of Italy and the Carnian Lunz flora of Austria. Our analysis is aimed at distinguishing the normal range of variability, differentiating developmental stages, and determining the frequency of abnormal spores. Results show significant variation in both size and surface ornamentation of spores from the same sporangia, as well as between sporangia and individuals, which may have various causes. Abortive spores are usually rare but occur with higher frequency in different samples from some specimens, suggesting that they can serve to identify systemic defects in the plants.

1. Introduction

Based on the sporangial development, ferns are divided into the informal eusporangiate (large sporangia developed from many initial cells and producing hundreds of spores, *e.g.*, Marattiales) and leptosporangiate (small sporangia developed from a single cell, producing a small number of spores) groups. The leptosporangiate ferns comprise today more than 300 genera and some 11,000 species, widely distributed in the tropics and temperate regions (Taylor et al., 2009). They are commonly characterized by (several times) pinnate fronds but can also have dichotomously branched fronds or simple leaves. The sporangia can be single or arranged in sori, attached at the margin or on the abaxial surface of the frond. Spores are typically monolete or trilete. Most leptosporangiate ferns are homosporous, but the aquatic forms are heterosporous. Extant leptosporangiate ferns (Polypodiidae) comprise the orders Osmundales (osmundaceous ferns), Gleicheniales (gleichenioid ferns), Schizaeales (schizaeaoid ferns), Hymenophyllales (filmy ferns), Cyatheales (extant tree ferns and allies), Polypodiales (polypods), and Salviniales (water ferns or heterosporous ferns).

The group was subjected to three evolutionary radiations, respectively in the Mississippian–Pennsylvanian, Permian–Jurassic and Cretaceous, due to opportunistic evolution within the rapidly increasing complexity of the plant communities (Rothwell and Stokey, 2008). The oldest evidence for leptosporangiate ferns consists of small annulate sporangia with trilete spores from the Mississippian of France (Galtier, 1981; Rothwell and Stokey, 2008). Several of the Paleozoic leptosporangiate fern families appearing in the Carboniferous, such as the Anachoropteridaceae, Kaplanopteridaceae, Psalixochlaenaceae, Sermayaceae, Tedeleaceae, went extinct during the Permian. The second radiation during the Permian–Jurassic gave origin to all basal orders of living leptosporangiate ferns, including Osmundales, Gleicheniales, Schizaeales, and Hymenophyllales (Rothwell and Stokey, 2008; Taylor et al., 2009). The Osmundales are the most ancient extant lineage of leptosporangiate ferns and have the richest fossil record of any extant group of ferns, with compression fossils of fronds and trunks as well as permineralized rhizomes (Tidwell and Ash, 1994; Cantrill, 1997; Stockey and Smith, 2000). Their oldest record comes from the Permian (Bomfleur et al., 2017). As the most basal group of leptosporangiate

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* Corresponding author.
E-mail address: hendrik.nowak@naturmuseum.it (H. Nowak).

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ferns, they have a few distinguishing characters and are sometimes separated from the others as "protoleptosporangiate" ferns, but cladistic analysis suggest that they form a monophyletic taxon with the "euleptosporangiate" lineages (Pryer et al., 2004).

The Gleicheniales (Dipteridaceae, Gleicheniaceae, Matoniaceae) are documented from the early Permian (*e.g.*, He et al., 2016, 2020) but could have originated already in the Carboniferous (Halle, 1927; Brousmiche-Delcambre et al., 1997). Schizaeales (Schizaeaceae, Anemiaceae, Lygodiaceae) have first appearances in the Upper Triassic in Arizona (Axsmith, 2009), North Carolina (Axsmith et al., 2018), and Austria (Pott et al., 2018). The Hymenophyllales (Hymenophyllaceae) have an isolated but well-documented first appearance in the Upper Triassic of North Carolina (USA; Axsmith et al., 2001). Specimens of *Coniopteris* Brongniart in d'Orbigny, 1849 from the Triassic of Argentina have been assigned to the Cyatheales (family Dicksoniaceae; *e.g.*, Morel et al., 2010) although they appear more frequently in the fossil record from the Jurassic onwards (Taylor et al., 2009). The Salviniales have a solid fossil record only from the Cretaceous onward, and a few confident appearances in the Jurassic (Santamarina et al., 2018 and ref. therein). However, the leaf genus *Flabellariopteris* Sun in Sun et al., 2014 from the Triassic of China has also been assigned to this order, specifically to the family Marsileaceae (Sun et al., 2014). While this has been contested (Hermsen, 2019), the presence of water ferns in the Triassic would be consistent with molecular clock analyses, since they are commonly placed as a sister clade to the Cyatheales (Knie et al., 2016). It is possible that all orders of leptosporangiate ferns were present by the end of the Triassic (Rothfels et al., 2021), although for some (Polypodiales, Salviniales) there is no fossil evidence yet.

In this paper, we study the intraspecific and interspecific morphological variability of *in situ* spores of leptosporangiate ferns (belonging to the Osmundales, Gleicheniales, and Schizaeales) from the Triassic of Italy and Austria. Our goals are to distinguish characters that can serve to identify specific taxa from those that fall into the normal range of variability, to test if variants in spore morphology can be linked to developmental stages or environmental influence and to determine the frequency of malformed spores.

2. Materials and methods

Samples of *in situ* sporangia were taken from fern macrofossils with fertile structures in organic preservation in the palaeobotanical collections of the Natural History Museum of Vienna, Austria (NHMW; sample numbers with prefix "NHMW-Geo"), the Museum für Naturkunde Berlin (MfN; sample numbers with prefix "MB.Pb."), the Museum of Nature South Tyrol in Bozen/Bolzano, Italy (NMS; sample numbers with prefix "PAL"), and the Swedish Museum of Natural History in Stockholm, Sweden (NRM; sample numbers with prefix "S"). The fossils stem from the Carnian Lunz flora (Lunz Formation) in Austria (see *e.g.*, Dobruskina, 1998; Pott et al., 2018) and the Anisian flora of the Kühwiesenkopf/Monte Prà della Vacca (Dont Formation) in the Dolomites in Northern Italy (see Van Konijnenburg-van Cittert et al., 2006; Kustatscher et al., 2010, 2019; Kustatscher and Van Konijnenburg-van Cittert, 2011).

The samples were macerated using a variant of the method proposed for *in situ* material by Kerp (1990). The details were determined after a series of tests with spores of *Asterotheca merianii* (Brongniart) Stur ex Krasser, 1909 (Nowak et al., in prep.). The organic matter is placed in a glass tube and a small amount of crystalline potassium chlorate (KCl) is added (a little more than the amount of organic matter), then – under a fume hood – 3 ml nitric acid (HNO3) in a 30% solution are added. After each day for the following three days, 1 ml of 67.5% nitric acid is added. On the fifth day, the acid is decanted, and the residue is washed with deionized water and decanted twice. Then, a few drops of 5% potassium hydroxide (KOH) are added to the residue, and after a few seconds diluted with deionized water (faster if there is an instantaneous reaction). The sample is again decanted and washed with deionized water, after which the pH of the water was tested to be neutral.

The macerated residues in the water were examined under a dissecting microscope, and spores or spore masses were manually transferred onto glass slides with a drop of heated (liquefied) glycerin jelly or onto stubs with carbon tabs for SEM analysis. Where possible, some spore masses were carefully pulled apart with a needle to isolate individual spores. The slides were then topped with a cover glass and left to cool down. The finished slides were examined under a Leica DM 2500 LED transmitted light microscope and images were made with a Leica DMC4500 mounted camera. SEM pictures were taken with a ZEISS EVO 40 scanning electron microscope. Measurements were taken from the images with the Fiji distribution of ImageJ version 1.53c (Schindelin et al., 2012). Diagrams presenting the data were made using R version 4.1.0 (R Core Team, 2018), including the packages ggplot2 version 3.3.5 (Wickham, 2016), ggExtra version 0.9 (Attali, 2019), and ggridges version 0.5.3 (Wilke, 2021).

Spores are identified as abortive if they are smaller and darker than regular ones, with an appearance that suggests omnidirectional compression of the spore wall. This often emphasizes the triradiate core structure and distorts the outline. Spores that are simply folded or deformed due to contact with surrounding spores are not included in this group, while some specimens that are compressed along two dimensions or conspicuously small and dark spores that retained a regular shape are considered as uncertain cases.

3. Systematic palaeobotany

Order: Osmundales Bromhead, 1838
Family: Osmundaceae Berchtold et Presl, 1820
Genus: **Todites** Seward, 1900
Type species: Todites williamsonii (Brongniart) Seward, 1900

Todites linnaeifolius (Bunbury) Pott et Bomfleur, 2018
Plate I, 1–2, Plate III, 1–8, Plate VI, 5–6

Selected references (for further references see Van Konijnenburg-van Cittert et al., 2006*;* Pott et al., 2018*):*

1847 *Neuropteris linnææfolia* Bunbury, p. 281, pl. 1
2018 *Todites linnaeifolius* (Bunbury) – Pott et al., p. 22, pl. 10, figs. 9–15; text-fig. 7A–E

Locality: Lunz, Austria.

Stratigraphic horizon: Lunz Formation.

Studied material: NHMW-Geo 1886/0001/0016, NHMW-Geo 1882/0013/3054, S148667-01.

Description: See Pott et al. (2018, p. 23–25).

Comparison: See Pott et al. (2018, p. 25–26).

Description of in situ spores: The spores are trilete, with a distinct trilete mark, a circular to slightly oval amb, and diameters between 31 and 52 (mean: 41.9; n = 173) μm (Figs. 1, 2). Rays of the trilete mark measure 52–100% of the spore radius and often fork at the end. The correlation of radius and leasure length (Fig. 2) is noisy (Pearson's $r = 0.587$), but significant ($p < 0.001$). Spore walls are laevigate or microverrucate and about 1 μm thick.

Spores from specimen NHMW-Geo 1882/0013/3054 (Plate III, 1, 2, 5–8) are on average significantly larger (mean 44.7 μm) than those from NHMW-Geo 1886/0001/0016 (mean 39.2 μm; Plate III, 3, 4). The specimens were sampled in multiple positions, and in both cases the largest spores and larger spores on average came from a sample more towards the base of a secondary pinna (Plate I, 1).

Abortive spores (Plate III, 7, 8) were observed with frequencies of 1.1–12.6% per sample (Fig. 3) – with some uncertain cases.

Discussion: Pott et al. (2018) described *in situ* spores of specimen S148667 as monolete, sometimes with a faint trilete mark. They considered them as possibly immature and suggested that the monolete spores "had not yet developed a prominent trilete mark" (Pott et al.,

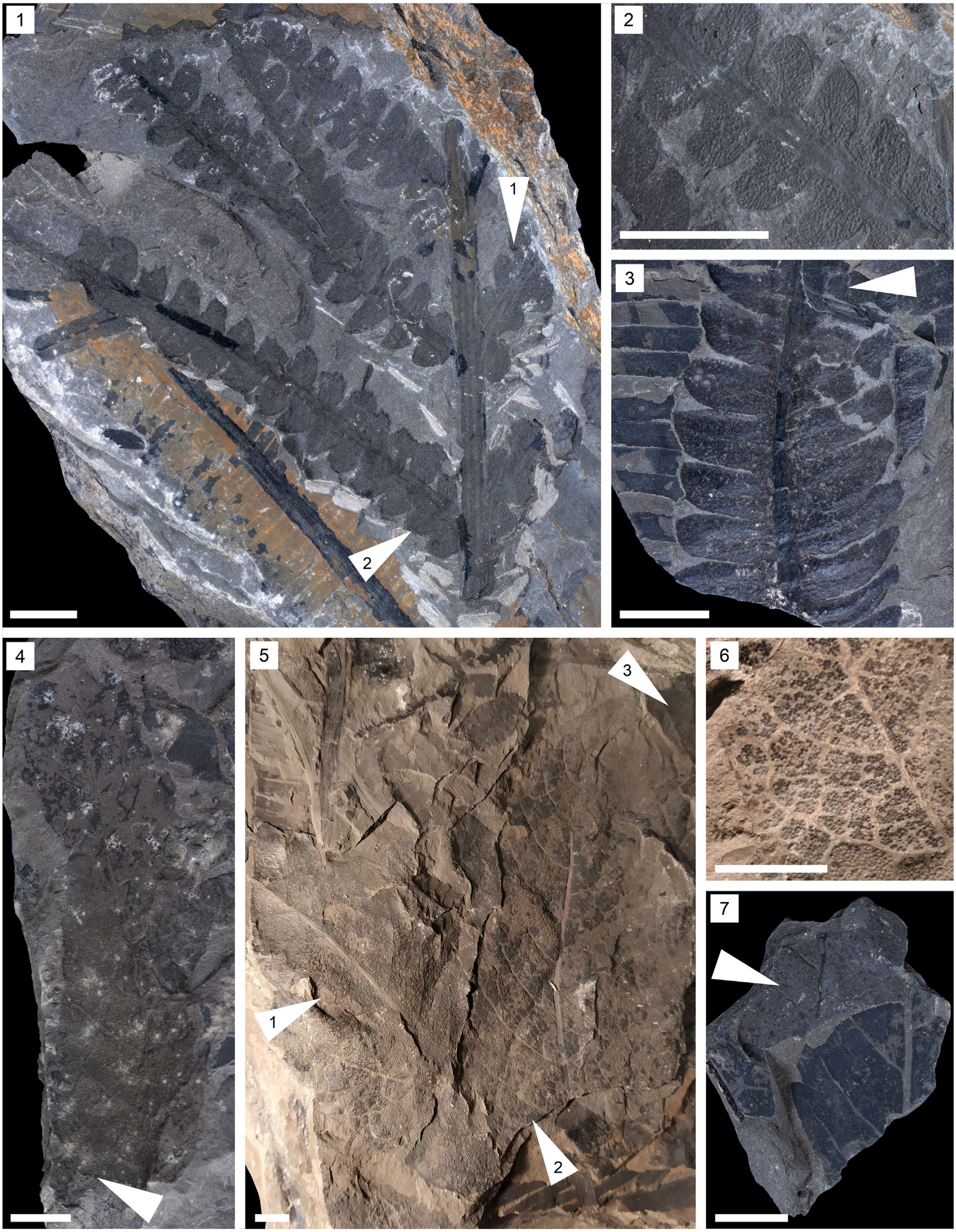

Plate I. Plant macrofossils of Osmundaceae (Figs. 1–3) and Dipteridaceae (Figs. 4–7) from the Carnian Lunz flora. White arrows mark positions of *in situ* samples, numbers on the arrows indicate sample numbers. 1. *Todites linnaeifolius*, NHMW-Geo 1882/0013/3054. 2. Detail of the specimen in Fig. 1. 3. *Todites* sp., NHMW-Geo 1883/0017/5946. 4. *Dictyophyllum serratum*, NHMW-Geo 2010/0102/0172. 5. *Dictyophyllum serratum*, MB.Pb.2019/279. 6. Detail of the specimen in Fig. 5. 7. *Clathropteris* cf. *reticulata*, NHMW-Geo 1878B/0006/9966. Scale bars: 10 mm.

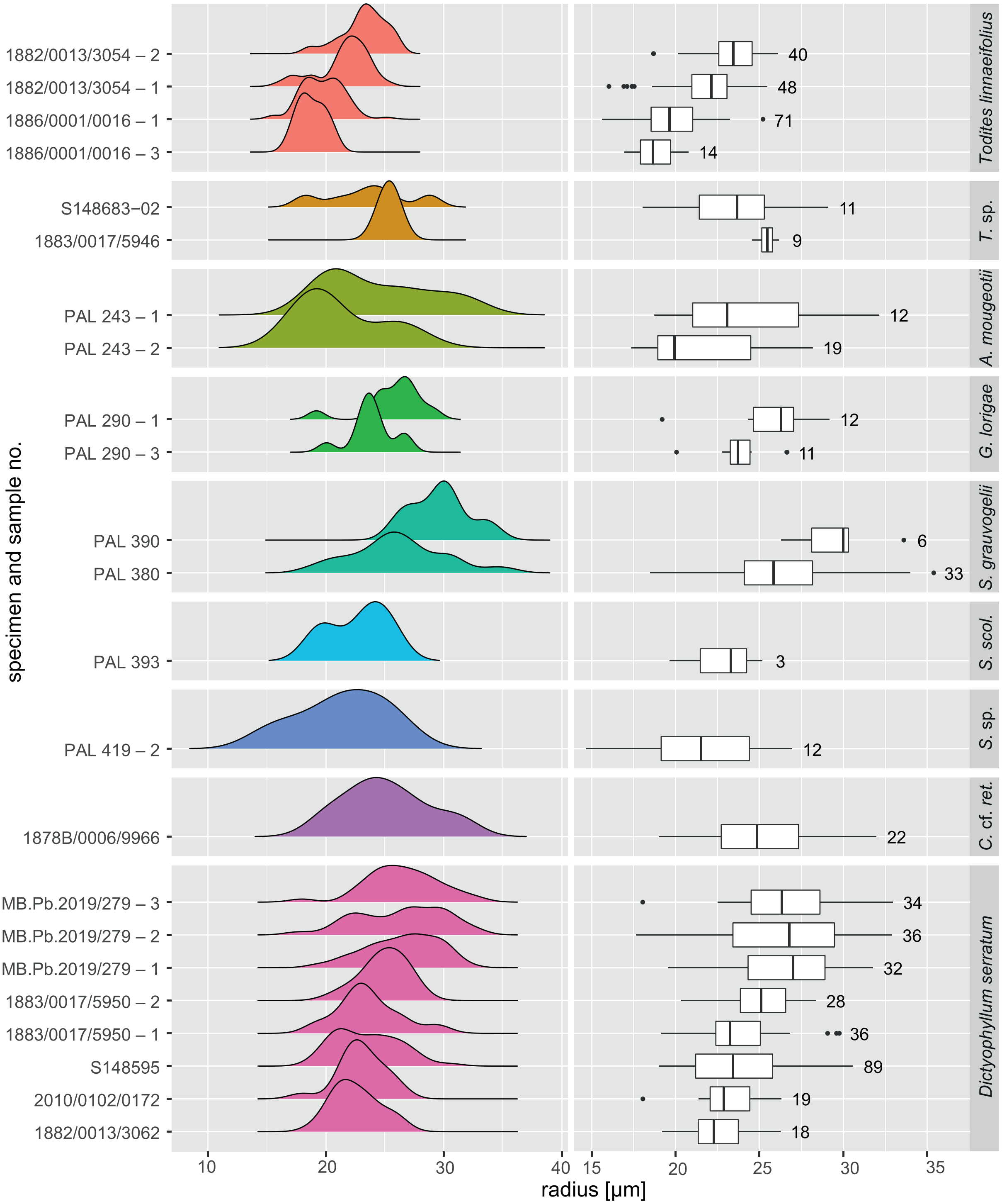

Fig. 1. Size distributions of *in situ* spore radii in individual samples from *Todites linnaeifolius*, *Todites* sp., *Anomopteris mougeotii*, *Gordonopteris lorigae*, *Scolopendrites scolopendrioides*, *Scolopendrites grauvogelii*, *Scolopendrites* sp., *Clathropteris* cf. *reticulata*, and *Dictyophyllum serratum*, presented as ridgeline plots and boxplots. *C.* cf. *ret.* = *Clathropteris* cf. *reticulata*, *T.* = *Todites*, *S.* = *Scolopendrites*, *scol.* = *scolopendrioides*, *G.* = *Gordonopteris*, *A.* = *Anomopteris*.

2018, p. 25). However, an ontogenetic shift from a straight monolete to a trilete condition would be unprecedented. Furthermore, as noted by Pott et al. (2018), monolete spores are untypical for Osmundales. The monolete appearance is more likely to be a result of folding. Neither monolete nor trilete marks were observed in the spores that we obtained from the same specimen. Considering this and the thin walls of these spores, we concur that they are probably immature. Pott et al. (2018) compared the spores of S148667 with dispersed sporomorphs from the palynoflora of Lunz that were assigned by Bharadwaj and Singh (1964) to *Laricoidites intragranulosus* Bharadwaj et Singh, 1964. The latter is a taxon for inaperturate pollen; thus, similarities have to be considered superficial.

The better-developed spores of specimens NHMW-Geo 1882/0013/3054 and NHMW-Geo 1886/0001/0016 are clearly circular, trilete with relatively long rays and laevigate or microverrucate, thereby corresponding to the dispersed genus *Todisporites* Couper, 1958. Their size

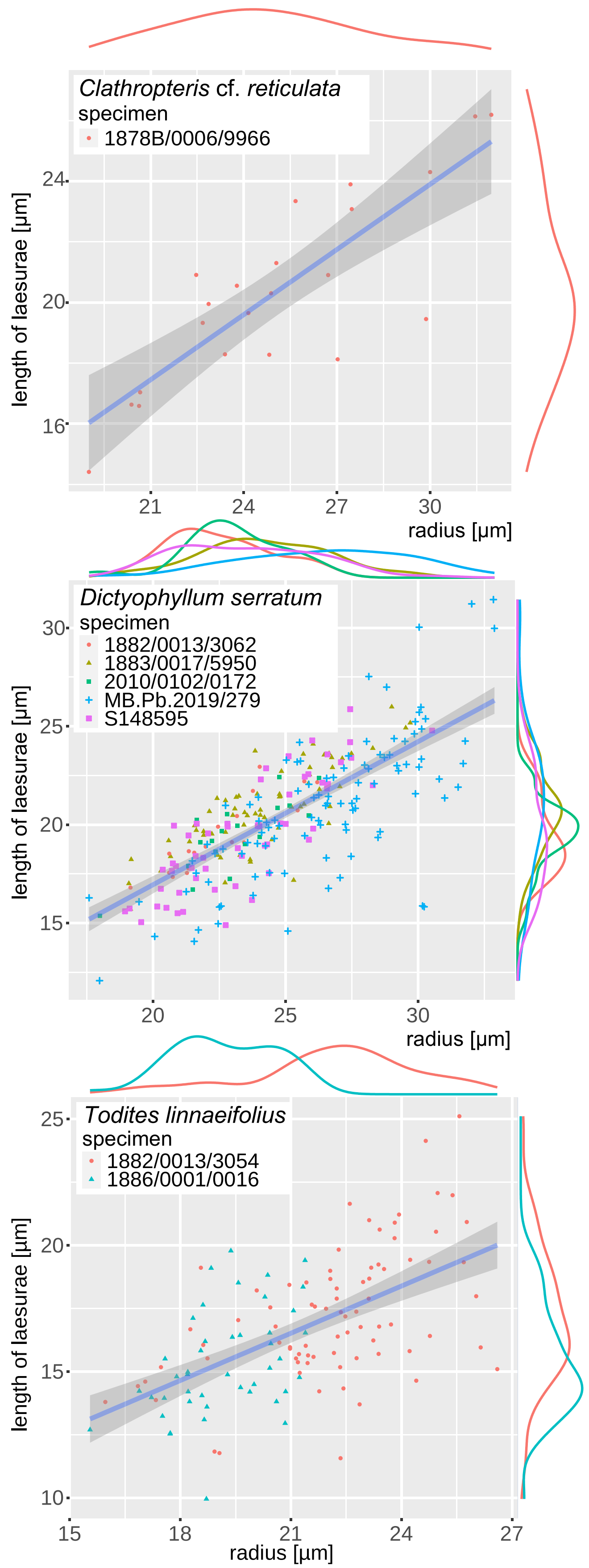

Fig. 2. Scatter plots of spore radii and lengths of laesurae in *Clathropteris* cf. *reticulata*, *Dictyophyllum serratum* and *Todites linnaeifolius*.

range is similar to that of *Todisporites minor* Couper, 1958, a species that is also known from the palynoflora of Lunz (Bharadwaj and Singh, 1964; Roghi et al., 2010). The genus *Todisporites* was introduced by Couper (1958) with the intention of matching the spores of *Todites*. He described *Todisporites major* Couper, 1958 as *in situ* spores of *Todites goeppertianus* (Münster) Krasser, 1922 and *Todites williamsonii* (Brongniart) Seward, 1900, as well as *Todites minor* Couper, 1958 as *in situ* spores of *Todites princeps* (Presl) Gothan, 1914 (see also Van Konijnenburg-van Cittert, 1978; Table 1). Cornet and Traverse (1975) also compared *Todisporites rotundiformis* (Malyavkina) Pocock, 1970 to the spores of *Todites princeps*. The *in situ* spores of *Todites gaillardotii* (Brongniart) Kustatscher et Van Konijnenburg-van Cittert, 2011 have also been compared to *Todisporites* (Kustatscher and Van Konijnenburg-van Cittert, 2011). The spores of *Todites roessertii* (Presl in Sternberg) Krystofovich, 1912, which have been described as spherical, trilete, and smooth, with diameters of 40–45 µm (Van Konijnenburg-van Cittert et al., 2020) fall into the same category. Similarly, Van Konijnenburg-van Cittert (1978) described *in situ* spores of *Todites thomasii* Harris, 1961 as scabrate with a mean spore diameter of 47 µm (41–52 µm). Schweitzer et al. (1997) also compared the spores of *Todites nebbensis* (Brongniart, 1828) Kilpper, 1964 to *Todisporites minor*. However, the former are marked by an irregular granulation forming a kind of reticulum. Granulate-papillate or baculate *in situ* spores, which have been compared to *Osmundacidites* Couper, 1953 and/or *Granulatisporites* Ibrahim, 1933, were found in *Todites recurvatus* Harris, 1931, *T. hartzii* Harris, 1931, *T. crenatus* Barnard, 1965, *T. denticulatus* (Brongniart) Krasser, 1961 (= *Cladotheca undans* in Halle, 1911; Potonié, 1962, 1967; *T. undans* in Couper, 1958 and Dettmann, 1963), and *T. lobatulus* Naugolnykh, 2002, as well as in other osmundaceous ferns such as *Osmundopsis plectrophora* Harris, 1931 (Harris, 1931; Couper, 1958; Potonié, 1962; Van Konijnenburg-van Cittert, 1978; Balme, 1995). The spores of *Todites pseudoraciborskii* (Srebrodolskaja) Schorochova, 1975 from the Upper Triassic of Russia are unusual in that they are triangular and comparable to *Leiotriletes* Potonié et Kremp, 1954 or *Deltoidospora* Miner, 1935 (Schorochova, 1975; Balme, 1995), which Balme (1995) considered to be a possible result of immaturity or degradation. Apart from these general descriptions (Table 1), a wide range in spore diameter within one sporangium and between various preparation methods has been observed (Van Konijnenburg-van Cittert, 1978).

Todites sp.
Plate I, 3, Plate III, 9–14, Plate VI, 7.
Locality: Lunz, Austria.
Stratigraphic horizon: Lunz Formation.
Studied material: NHMW-Geo 1883/0017/5946, S148683-02.

Description: Both studied specimens are small fertile pinna fragments; NHMW-Geo 1883/0017/5946 (Plate I, 3) shows pinnules that adhere at their base, and vary in length between 10 and 12 mm, with a width between 5 and 6 mm. The lower surface is covered with sporangia just as in S148683, where the pinnule length varies between 1.0 and 1.1 mm, and the width between 6 and 7 mm. In both specimens only the midrib is visible, while secondary venation is obscured due to the sporangia.

Comparison: The two specimens have not been included by Pott et al. (2018) in their description of ferns from the Lunz flora, and differ from the species presented therein. The specimens resemble *Cladophlebis remota* (Presl) Van Konijnenburg-van Cittert et al., 2006 due to the presence of a distinct midvein, the attachment with the entire base and the subtriangular shape of the pinnules. They differ, however, in the stouter rachis, the more rounded pinnules and apices, and the oppositely

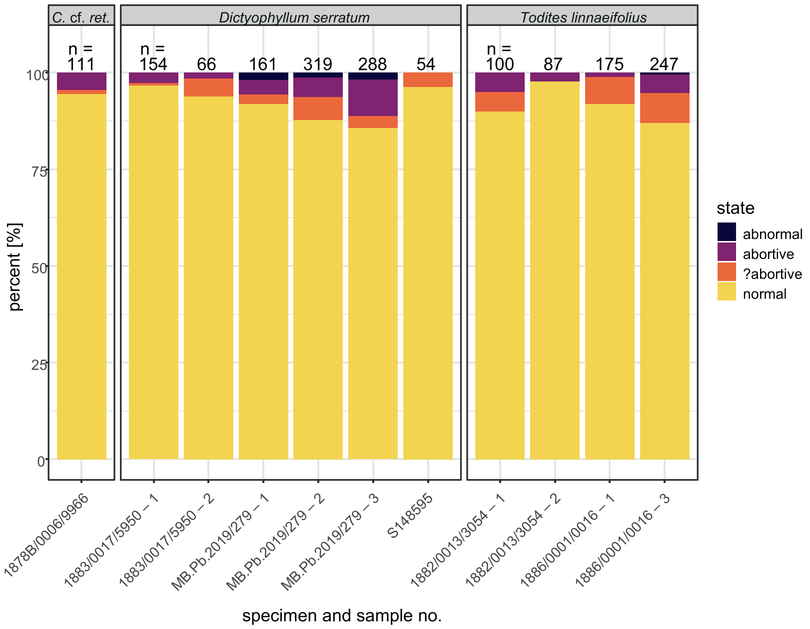

Fig. 3. Percentages of abortive/abnormal spores per sample in *Clathropteris* cf. *reticulata*, *Dictyophyllum serratum* and *Todites linnaeifolius*. *C.* cf. *ret.* = *Clathropteris* cf. *reticulata*.

attachment of the pinnae. Fertile leaves of *C. remota* are as yet unknown. The observed differences could be because the specimen presented here is fertile. Since the relationship between these fertile leaf fossils and *C. remota* is unclear, for the moment we prefer to keep it in open nomenclature.

Description of in situ spores: The spores are trilete, with a subcircular or slightly triangular amb, a more or less distinct trilete mark, and a diameter of 36 to 58 (mean: 48.7; n = 20) μm (Fig. 1). Rays of the trilete mark are about 2/3 to 3/4 of the radius. The spore wall is *ca.* 1–1.5 μm thick. The ectexine of spores from specimen NHMW-Geo 1883/0017/5946 shows a uniform, dense ornamentation with verrucae that are 2–4 μm wide, 0.5–1.0 μm high, and are partially fused to rugulae (Plate III, 9–12). Only a single cluster of 13 spores was obtained from specimen NHMW-Geo 1883/0017/5946, which are close in size (49–52 μm), while specimen S148683–02 yielded a sporangium with spores varying between 36 and 58 μm in diameter and with an inconsistent (partially laevigate) ornamentation (Plate III, 13–14). Abortive spores were not identified with certainty.

Discussion: The spores of specimen NHMW-Geo 1883/0017/5946, due to their general form and uniform verrucate and rugulate ornamentation, correspond to the dispersed genus *Verrucosisporites* Ibrahim, 1933. This genus was reported to be one of the most common in the palynoflora recovered from a coal seam in the Lunz Formation near Lunz (Bharadwaj and Singh, 1964; Roghi et al., 2010). This includes *Verrucosisporites morulae* Klaus, 1960, to which the spores of *Todites* sp. are comparable. It should be noted that Bharadwaj and Singh (1964) distinguished three other species of *Verrucosisporites* in the palynoflora of Lunz, with one criterion being a more or less subcircular shape. However, some of the specimens figured as *V. morulae* also show a tendency to a subcircular amb (Bharadwaj and Singh, 1964, pl. 3, figs. 61–63) that is comparable to our specimens. The spores of specimen S148683–02 are probably immature, considering their inconsistent, *i.e.*, partially laevigate, ornamentation. The *in situ* spores of *Todites* sp. differ from those of *Todites linnaeifolius* and from other *Todites* species in the presence of a coarse, verrucate and rugulate ornamentation (Table 1; see also the discussion on *Todites linnaeifolius* above).

Family:?Osmundaceae Berchtold and Presl, 1820
Genus: **Anomopteris** Brongniart, 1828a emend. Grauvogel-Stamm et Grauvogel, 1980

Type species: Anomopteris mougeotii Brongniart, 1828b emend. Grauvogel-Stamm et Grauvogel, 1980

Anomopteris mougeotii Brongniart, 1828b emend. Grauvogel-Stamm et Grauvogel, 1980
Plate II, 5, Plate IV, 1–6, Plate VI, 10–12

Selected references (for further references see Van Konijnenburg-van Cittert et al., 2006*):*

1828a *Anomopteris mougeotii* Brongniart, p. 60, 190, *nomen nudum*
1828b *Anomopteris mougeotii* Brongniart, p. 439
1828c *Anomopteris mougeotii* Brongniart, p. 258, pl. 79–81
1980 *Anomopteris mougeotii* Brongniart – Grauvogel-Stamm and Grauvogel, p. 54, pls 1–6, text-figs. 1, 2
2006 *Anomopteris mougeotii* Brongniart – Van Konijnenburg-van Cittert et al., p. 954, pl. 4, figs. 1, 3
2019 *Anomopteris mougeotii* Brongniart – Kustatscher et al., p. 10, fig. 6B

Locality: Kühwiesenkopf/Monte Prà della Vacca, Italy.

Stratigraphic horizon: Dont Formation.

Studied material: PAL 240, PAL 243, PAL 244, PAL 245, PAL 247, PAL 249, PAL 250.

Description: See Van Konijnenburg-van Cittert et al. (2006, p. 954).

Comparison: See Van Konijnenburg-van Cittert et al. (2006, p. 954–955).

Description of in situ spores: Sporangia are ovoid, *ca.* 350 μm long and 300 μm wide, with an estimate of 200–300 (possibly 256) spores in one sporangium. The spores are trilete, with a circular to slightly triangular amb, ranging from 35 to 64 (mean: 45.0; n = 31) μm (Fig. 1). Rays of the trilete mark are often indistinct, reaching *ca.* 1/2 to 2/3 the length of the radius. The ectexine is granulate (microverrucate/microgemmate) to verrucate/gemmate, microreticulate, and punctate with dense elements of around 1 μm width and up to *ca.* 0.5 μm height. Spore walls are around 1 μm thick and punctate. A few spores in PAL 247 and PAL 249 are laevigate. Abortive spores were not identified with certainty.

Discussion: Only PAL 243 yielded numerous spores and complete sporangia, and these were the basis for their description. PAL 247 and 249 yielded incomplete sporangia with poor preservation. Only a few spores were obtained from PAL 244 and 245. Such occasional, isolated spores may at least in part be foreign components. In fact, a sample

Table 1
Overview of Permian–Jurassic osmundaceous fern species with reported *in situ* spores discussed in the text. References: 1 = Pott et al. (2018); 2 = Kustatscher and Van Konijnenburg-van Cittert (2011); 3 = Ash (1969); 4 = Litwin (1985); 5 = Balme (1995); 6 = Harris (1931); 7 = Lundblad (1950); 8 = Couper (1958); 9 = Potonié (1962); 10 = Van Konijnenburg-van Cittert (1978); 11 = Schenk (1884); 12 = Nathorst (1908); 13 = Thomas (1911); 14 = Menéndez (1956); 15 = Harris (1961); 16 = Potonié (1967); 17 = Krassilov (1969); 18 = Delle (1967); 19 = Andrews in Boureau (1970); 20 = Cornet and Traverse (1975); 21 = Schweitzer et al. (1997); 22 = Van Konijnenburg-van Cittert et al. (2020); 23 = Schorochova (1975); 24 = Barnard (1965); 25 = Taylor and Taylor (1993); 26 = Halle (1911); 27 = Dettmann (1963); 28 = Naugolnykh (2002).

Species	Stratigraphy	Outline	Diameter [μm]	Ornamentation	Comparable dispersed taxa	References
Todites linnaeifolius (Bunbury) *sensu* Pott et al., 2018	Carnian	Circular to subcircular or elliptic	31–58	Laevigate to microverrucate/granulate	*Todisporites minor* Couper, 1958	1, this work
T. sp.	Carnian	Subcircular	36–58	Verrucate	*Verrucosisporites morulae* Klaus, 1960	This work
T. gaillardotii (Brongniart) Kustatscher et Van Konijnenburg-van Cittert, 2011	Ladinian	Circular	35–51	Laevigate	*Todisporites*	2
T. fragilis Daugherty emend. Ash, 1969	Carnian	Circular	26–42	Granulate/conate, elements <1 μm long, contact area unornamented	*Osmundacidites parvus* De Jersey, 1962	3, 4, 5
T. goeppertianus (Münster) Krasser, 1922	Rhaetian–Lower Jurassic	Circular	46–62	Laevigate (granulate according to Potonié, 1962)	*Todisporites* (?) / *Cyclogranisporites* (?)	4, 5, 6, 7, 8, 9, 10
T. williamsonii (Brongniart) Seward, 1900	Rhaetian–Middle Jurassic	Circular	40–80	Scabrate/laevigate	*Todisporites major* Couper, 1958 / *Punctatisporites*	5, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19
T. princeps (Presl) Gothan, 1914	Rhaetian–Middle Jurassic	Circular	20–43	Scabrate	*Todisporites minor* Couper, 1958 / *T. rotundiformis* (Malyavkina) Pocock, 1970	4, 5, 6, 8, 10, 15, 19, 20
T. nebbensis (Brongniart) Kilpper, 1964	Rhaetian	More or less circular	24–40	Granules, often fused into irregular reticulum	*Todisporites minor* Couper, 1958 (?)	21
T. roessertii (Presl in Sternberg) Krystofovich, 1912	Rhaetian	Circular	40–45	Laevigate	*Todisporites* (?)	22
T. pseudoraciborskii (Srebrodolskaja) Schorochova, 1975	Upper Triassic	Triangular	50	Laevigate	*Leiotriletes*; *Deltoidospora*	23, 5
T. hartzii Harris, 1931	Rhaetian–Lower Jurassic	Circular	39–51	Granulate	*Osmundacidites*	4, 5, 6, 8, 9, 10
T. recurvatus Harris, 1931	Rhaetian–Middle Jurassic	Circular	38	Thin-walled and laevigate or thick-walled and granulate/baculate with somewhat conical elements	*Granulatisporites*; *Osmundacidites*	4, 5, 6, 8, 9, 19
T. crenatus Barnard, 1965	Rhaetian–Jurassic	Circular	20–37	Granules, baculae or spines	*Osmundacidites*	4, 5, 21, 24
T. thomasii Harris, 1961	Middle Jurassic	More or less circular	40–52	Subgranulate	?	5, 10, 15, 16, 25
T. denticulatus (Brongniart) Krasser, 1961 (= Cladotheca undans in Halle, 1911, Potonié, 1962, 1967; T. undans in Couper, 1958 and Dettmann, 1963)	Jurassic	Circular or rarely convex triangular	26–62	Granulate/subgranulate/subconate/subverrucate	*Granulatisporites*; *Osmundacidites wellmanii* Couper, 1953	4, 5, 6, 9, 10, 15, 16, 26, 27
T. lobatulus Naugolnykh, 2002	upper Permian	Subcircular/subtriangular?	?	Granulate	*Osmundacidites*	28
Osmundopsis plectrophora Harris, 1931	Jurassic	Circular	44–57	Granulate/baculate	*Osmundacidites wellmanii* Couper, 1953	5, 8, 6, 9, 10

from PAL 243 and PAL 245 each contained a certainly foreign bisaccate pollen grain, evidencing some contamination. However, most of the spores in PAL 244 and 245 are consistent with those found in PAL 243.

In situ spores of *Anomopteris mougeotii* have previously been described from the Grès à Voltzia by Grauvogel-Stamm and Grauvogel (1980) as trilete with a distinct mark, circular, having a finely punctate exine and sizes of 25–40 μm. Our material differs in that almost all spores have a granulate to verrucate/gemmate surface ornamentation and generally larger sizes. They might have been more mature than the type material from the Grès à Voltzia. The few spores without distinct ornamentation are probably a result of poor preservation. Grauvogel-Stamm and Grauvogel (1980) determined that *Punctatisporites fissus* Leschik, 1955 was most similar to the *in situ* spores of *A. mougeotii* from the Grès à Voltzia. Balme (1995), based on the figures of Grauvogel-Stamm and Grauvogel (1980), considered these spores to be granulate and assigned them to *Osmundacidites*. The spores of *A. mougeotii* from Kühwiesenkopf are with few exceptions comparable to the genus *Osmundacidites* as well.

Genus: **Gordonopteris** Van Konijnenburg-van Cittert et al., 2006
Type species: Gordonopteris lorigae Van Konijnenburg-van Cittert et al., 2006

Gordonopteris lorigae Van Konijnenburg-van Cittert et al., 2006
Plate II, 4, Plate III, 15–20, Plate VI, 8–9
Selected references (for further references see Van Konijnenburg-van Cittert et al., 2006*):*
2006 *Gordonopteris lorigae* Van Konijnenburg-van Cittert et al., p. 955, pl. 3; text-figs. 4, 5D
2019 *Gordonopteris lorigae* Van Konijnenburg-van Cittert et al. – Kustatscher et al., p. 10, fig. 7C
Locality: Kühwiesenkopf/Monte Prà della Vacca, Italy.

Stratigraphic horizon: Dont Formation.

Studied material: PAL 257, PAL 290, PAL 296, PAL 308, PAL 324.

Description: See Van Konijnenburg-van Cittert et al. (2006, p. 955–956).

Comparison: See Van Konijnenburg-van Cittert et al. (2006, p. 956).

Description of in situ spores: The spores are trilete, with a circular to oval amb and diameters of 38–58 (mean: 49.7; n = 23) μm (Fig. 1). Rays of the trilete mark measure about 3/4 of the radius. The spore walls are *ca.* 0.5–1.0 μm thick. Surfaces are smooth or showing a low-relief sculpture with grana or verrucae up to 3 μm wide and up to *ca.* 0.5 μm high. Spores from individual sporangia or spore clusters appear to have the same ornamentation. Clusters with a more or less pronounced sculpture were found in all specimens. Clusters of laevigate spores were present in PAL 290 and PAL 296. In the case of PAL 290, spores with the best-developed verrucae and those with a laevigate or microverrucate sculpture came even from neighboring sporangia (compare Plate III, 16–18 and 19, 20). Two abortive spores were observed in a sample from PAL 290.

Discussion: The spores that were retrieved are mostly part of dense and solid spore masses, which hinders detailed analyses. Numerous isolated spores were only obtained from PAL 290. Based on observations so far, the presence of pronounced sculpture elements appears to be consistent within individual sporangia. Since these apparently more mature and more immature sporangia can occur side by side on the same plant fossil and even in the same sample, this is unlikely to be an effect of preservation or maceration, and more likely represents asynchronous sporogenesis.

The spores of *Gordonopteris lorigae* have been described by Van Konijnenburg-van Cittert et al. (2006, p. 955) as "globose, trilete, around 45–60 μm in diameter, exospore finely punctate." Kustatscher et al. (2019) compared them to the dispersed genus *Punctatisporites* Ibrahim, 1933. We cannot confirm a punctate sculpture in our samples. The unornamented spores rather correspond to the dispersed genus *Todisporites*, and due to their size, they mostly overlap with *T. major*, a species that has been compared to the spores of *Todites williamsonii* and *Todites goeppertianus* (Couper, 1958; Van Konijnenburg-van Cittert, 1978; see above; Table 1). The more ornamented spores in our material may approach *Verrucosisporites*. Since in all observed cases the relief is relatively shallow, it is conceivable that the spores are not fully mature, and that *Verrucosisporites* may have been the final form. The palynoflora of the Dont Formation at the Kühwiesenkopf section has been reported to contain various species of the genera *Punctatisporites*, *Todisporites*, and *Verrucosisporites* (Kustatscher and Roghi, 2006; Kustatscher et al., 2010).

Genus: **Scolopendrites** Göppert, 1836

Type species: Scolopendrites scolopendrioides (Brongniart) Van Konijnenburg-van Cittert et al., 2006

Scolopendrites scolopendrioides (Brongniart) Van Konijnenburg-van Cittert et al., 2006

Plate II, 1, Plate IV, 9–12

Selected references (for further references see Van Konijnenburg-van Cittert et al., 2006):

1828a *Filicites scolopendrioides* Brongniart, p. 190, *nomen nudum*

1828b *Filicites scolopendrioides* Brongniart, p. 443, pl. 18, fig. 2

1828c *Filicites scolopendrioides* Brongniart, p. 388, pl. 137, figs. 2–3

2006 *Scolopendrites scolopendrioides* (Brongniart) – Van Konijnenburg-van Cittert et al., p. 950, pl. 2, figs. 1–3, 5–6

2019 *Scolopendrites scolopendrioides* (Brongniart) – Kustatscher et al., p. 10, fig. 7A

Locality: Kühwiesenkopf/Monte Prà della Vacca, Italy.

Stratigraphic horizon: Dont Formation.

Studied material: PAL 395.

Description: See Van Konijnenburg-van Cittert et al. (2006, p. 952).

Comparison: See Van Konijnenburg-van Cittert et al. (2006, p. 952).

Description of in situ spores: The spores are trilete, with a circular amb, an often indistinct trilete mark, and a diameter of 39–50 (mean: 45.4; n = 3) μm (Fig. 1). The sculpture is laevigate or microverrucate to verrucate. The spores are present as rather solid clusters and only a few spores could be observed in detail. Abortive spores were not identified.

Discussion: Because of the low number of observations, the range of variation for the *in situ* spores of this species is probably not completely represented. The spores of *Scolopendrites scolopendrioides* and *S. grauvogelii* Van Konijnenburg-van Cittert et al., 2006 (see below) were both first described by Van Konijnenburg-van Cittert et al. (2006, p. 952–953) as "trilete, circular in equatorial outline, with a diameter of 35–45 μm and the exospore is scabrate to granulate." They considered the spores of the two species to be indistinguishable. By contrast, we found significant differences between the spores of *S. scolopendrioides* and *S. grauvogelii*; *e.g.*, slightly larger sizes than those originally described for the spores of *S. scolopendrioides*, but considerably larger sizes for *S. grauvogelii* (Table 2; see also description and discussion for *S. grauvogelii* below).

Kustatscher et al. (2019) considered the *in situ* spores of *Scolopendrites scolopendrioides* as possibly immature versions of *Osmundacidites*, whereas they compared psilate (= laevigate) spores to *Todisporites*. Both *Osmundacidites* and *Todisporites* have been reported from the palynoflora of the Dont Formation at the Kühwiesenkopf section (Kustatscher and Roghi, 2006; Kustatscher et al., 2010).

Scolopendrites grauvogelii Van Konijnenburg-van Cittert et al., 2006

Plate II, 3, Plate IV, 13–20, Plate VI, 13–14

Selected references (for further references see Van Konijnenburg-van Cittert et al., 2006):

2006 *Scolopendrites grauvogelii* Van Konijnenburg-van Cittert et al., p. 952, pl. 2, figs. 4, 7–9; text-fig. 3

2019 *Scolopendrites grauvogelii* Van Konijnenburg-van Cittert et al. – Kustatscher et al., p. 10, fig. 7B

Locality: Kühwiesenkopf/Monte Prà della Vacca, Italy.

Stratigraphic horizon: Dont Formation.

Studied material: PAL 376, PAL 387, PAL 380, PAL 390, PAL 413.

Description: See Van Konijnenburg-van Cittert et al. (2006, p. 952–953).

Comparison: See Van Konijnenburg-van Cittert et al. (2006, p. 953).

Description of in situ spores: The spores are trilete, with a circular amb, an indistinct mark of about 1/2 the length of the radius, and a diameter of 37–71 (mean: 53.4; n = 39) μm (Fig. 1). The sculpture is laevigate or granulate (microverrucate/microgemmate). The wall is 0.5–1 μm thick, commonly around 0.7–0.8 μm. In many cases, the spores show a patchy ornamentation across their surface, suggesting an incomplete fusion with the tapetum (*e.g.*, Plate VI, 13–14). Abortive spores were not identified.

Discussion: The spores of *S. grauvogelii* have been described by Van Konijnenburg-van Cittert et al. (2006) and Kustatscher et al. (2019) as indistinguishable from those of *S. scolopendrioides* (see above). The newly analyzed spores are with few exceptions larger (37–71 μm) than the previously described size range (35–45 μm). The *in situ* spores of *S. grauvogelii* studied by Van Konijnenburg-van Cittert et al. (2006) came from specimen PAL 380, and upon checking their original material, we found that they show similarly large and even larger sizes (up to 79 μm) than those measured in the new samples. In contrast, the sizes of the spores of *S. scolopendrioides* in the material studied by Van Konijnenburg-van Cittert et al. (2006) are similar to only slightly larger compared to the original description. A slight difference was probably due to alterations caused by the preparation method or mounting medium over time and/or due to different calibrations for the measurements. Because of the possibility of alterations and effects of the different maceration protocols, measurements from older material are not included in our description.

The spores of *S. grauvogelii* are also for the most part larger than those we found in *S. scolopendrioides* (see above; Table 2). In addition, none of the new specimens show a verrucate ornamentation. The *in*

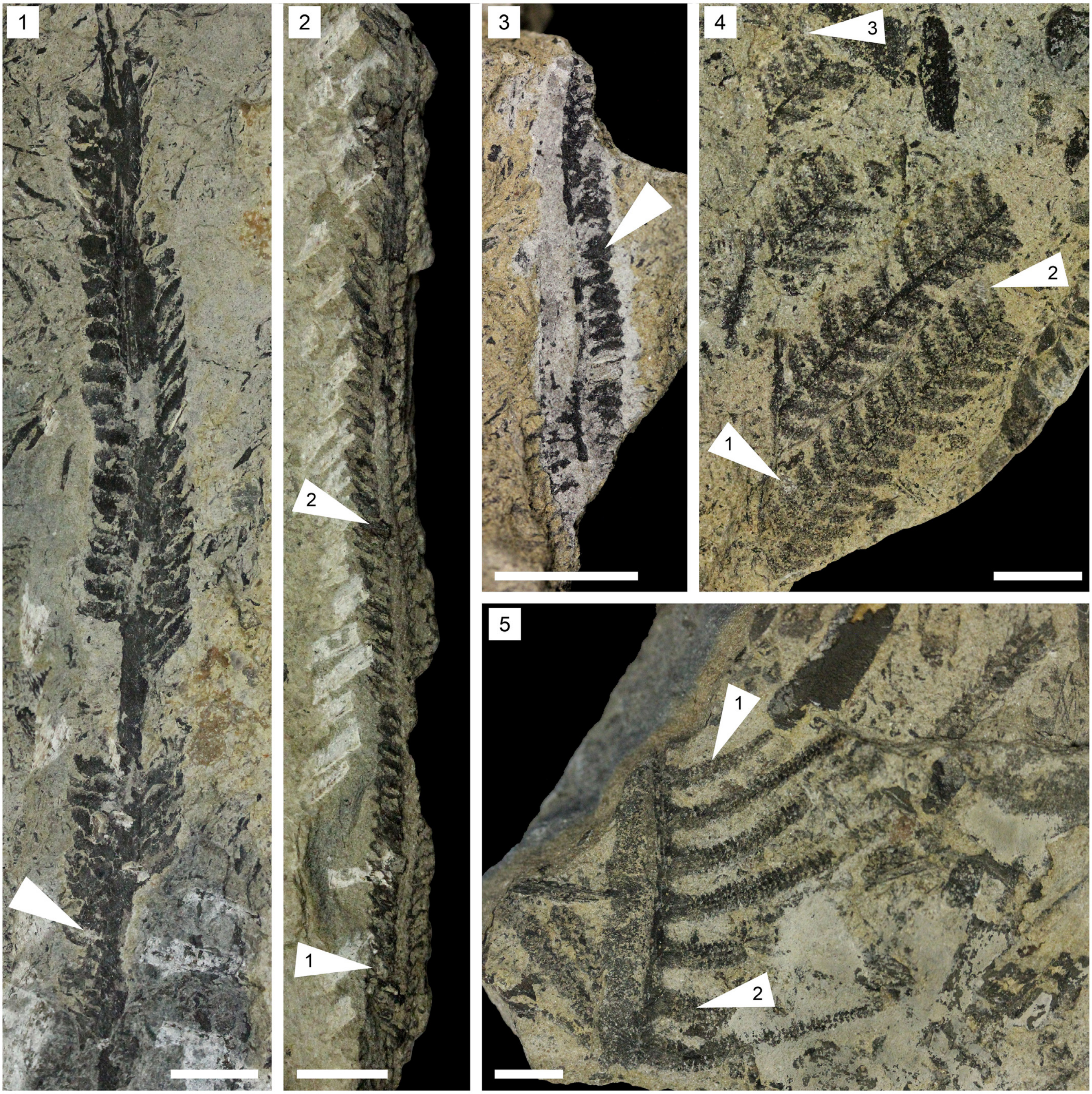

Plate II. Plant macrofossils of ?Osmundaceae from the Anisian Kühwiesenkopf/Monte Prà della Vacca flora. White arrows mark positions of *in situ* samples. 1. *Scolopendrites scolopendrioides*, PAL 395. 2. *Scolopendrites* sp., PAL 419. 3. *Scolopendrites grauvogelii*, PAL 380. 4. *Gordonopteris lorigae*, PAL 290. 5. *Anomopteris mougeotii*, PAL 23. Scale bars: 10 mm.

situ spores can be compared to the dispersed genus *Todisporites*. However, the latter normally has longer laesurae (≥70% of the radius; Couper, 1958). The relatively short laesurae and – in some spores – thin spore walls resemble *Calamospora* Schopf, Wilson et Bentall, 1944. *Calamospora* is commonly associated with equisetophytes but has been found in other plants as well (*e.g.*, Balme, 1995). *Todisporites* and *Calamospora* are both present in the Lunz palynoflora (Bharadwaj and Singh, 1964; Roghi et al., 2010).

Scolopendrites sp.
Plate II, 2, Plate IV, 7–8, Plate VI, 15–16
Locality: Kühwiesenkopf/Monte Prà della Vacca, Italy.
Stratigraphic horizon: Dont Formation.
Studied material: PAL 419.

Description: PAL 419 (Plate II, 2) is an imperfectly preserved *Scolopendrites* fragment, 126 mm long and up to 8 mm wide. The rachis is 1–1.5 mm wide. The sporophylls are up to 4 mm wide and inclined with an angle of 55–60° towards the base of the frond fragment. It was not included in the description of *Scolopendrites* material in Van Konijnenburg-van Cittert et al. (2006) because of its poor preservation but the sporangia yielded sufficiently well-preserved spores to allow a description.

Comparison: The specimen is not confidently assignable to either *Scolopendrites grauvogelii* or *S. scolopendrioides* because of its poor preservation and therefore here assigned to *Scolopendrites* sp.

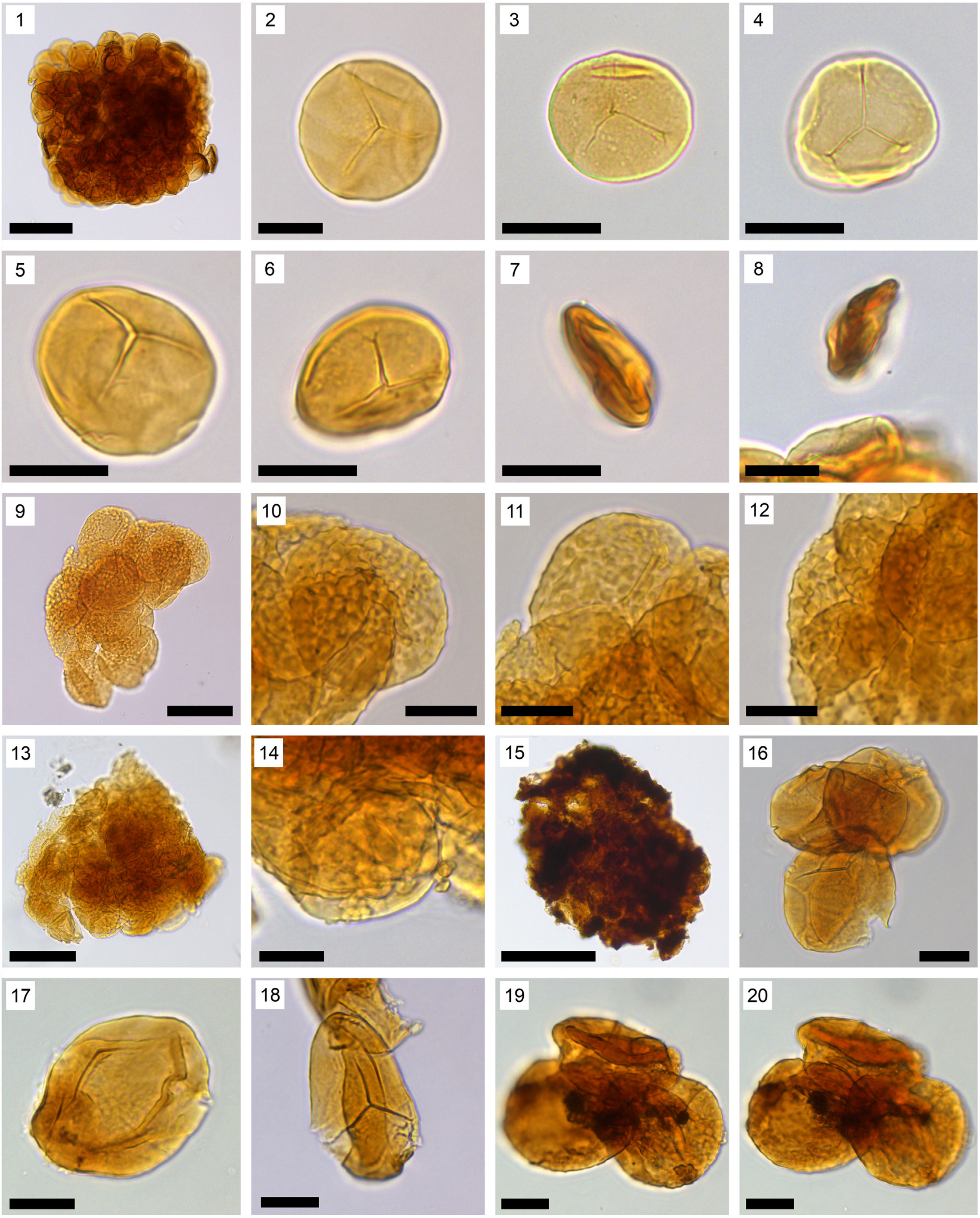

Plate III. *In situ* spores of *Todites linnaeifolius* and *Todites* sp. from the Carnian Lunz flora, and *Gordonopteris lorigae* from the Anisian Kühwiesenkopf/Monte Prà della Vacca flora. 1–8. *Todites linnaeifolius*. 1. Sporangium, NHMW-Geo 1882/0013/3054, sample 1. 2. Well-developed spore in polar view showing the trilete mark, NHMW-Geo 1882/0013/3054, sample 1. 3. Spore in polar view with microverrucate surface, NHMW-Geo 1886/0001/0016, sample 3. 4. Spore in polar view with laevigate surface and folds, NHMW-Geo 1886/0001/0016, sample 1. 5. Spore in oblique view, NHMW-Geo 1882/0013/3054, sample 1. 6. Unusually small spore with laevigate surface, NHMW-Geo 1882/0013/3054, sample 1. 7 and 8. Abortive spores, NHMW-Geo 1882/0013/3054, sample 1. 9–14. *Todites* sp. 9. Cluster of spores, NHMW-Geo 1883/0017/5946. 10–12. Details of Fig. 9, spores showing verrucate ornamentation. 13. Fragment of a sporangium, S148683–02. 14. Detail of Fig. 13, spore with probable remains of the tapetum. 15–20. *Gordonopteris lorigae*. 15. Sporangium, PAL 257, sample 2. 16. Three spores, PAL 290, sample 1. 17. Single spore with weakly developed ornamentation, PAL 290, sample 1. 18. Folded spore with conspicuous trilete mark, PAL 290, sample 1. 19 and 20. Three spores with verrucate ornamentation, with different focus, PAL 290, sample 1. Scale bars: Figs. 1, 15: 100 μm, Fig. 9: 50 μm, all others: 20 μm.

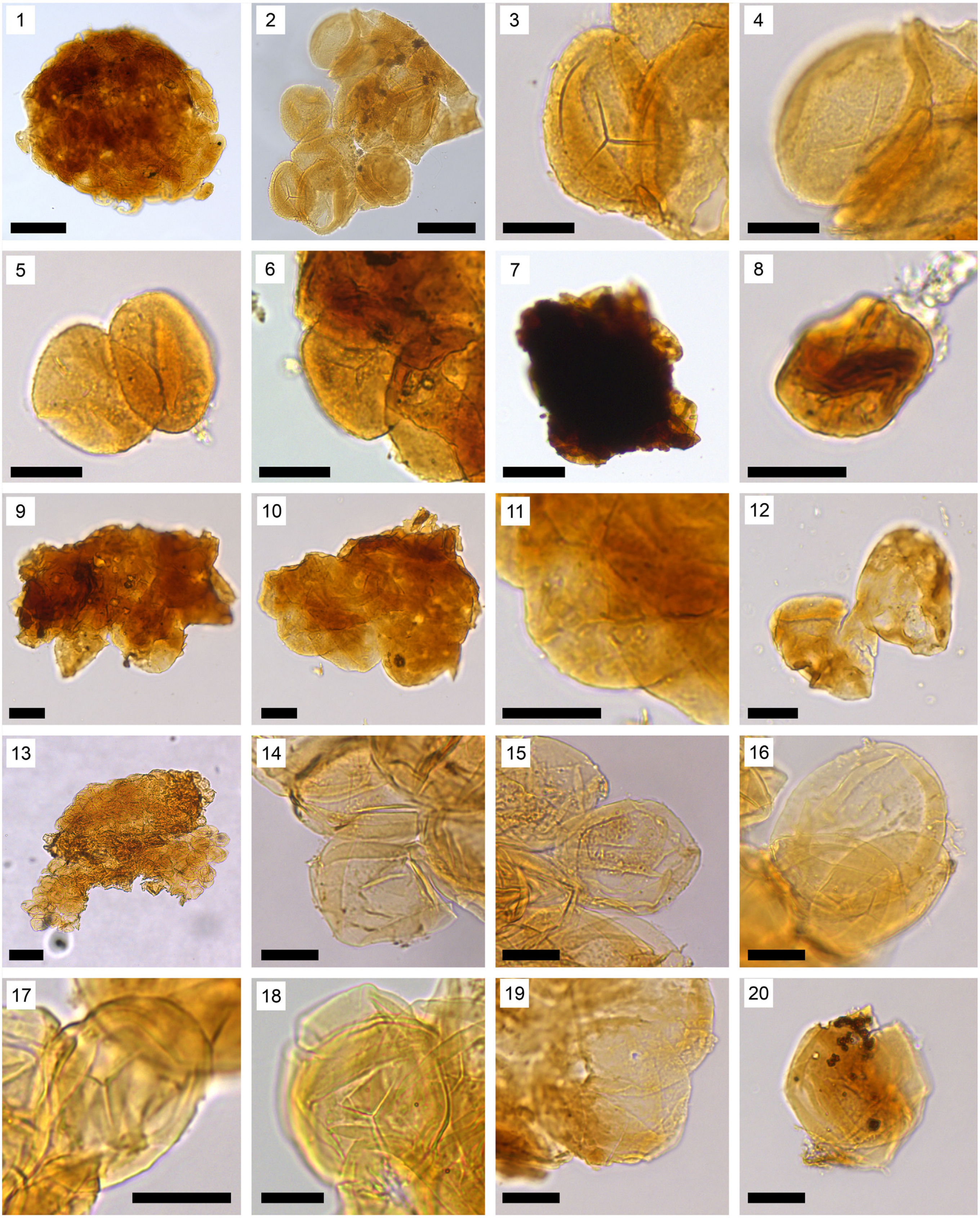

Plate IV. *In situ* spores of *Anomopteris mougeotii*, *Scolopendrites* sp., *S. scolopendrioides*, and *S. grauvogelii* from the Kühwiesenkopf/Monte Prà della Vacca flora. 1–6. *Anomopteris mougeotii*, PAL 243, sample 1. 1. Sporangium. 2. Spore cluster. 3 and 4. Details of Fig. 2. 5. Two spores. 6. Spore with a pronounced convex triangular outline and long laesurae. 7–8. *Scolopendrites* sp. 7. Spore cluster, PAL 419, sample 1. 8. Single spore, PAL 419, sample 2. 9–12. *Scolopendrites scolopendrioides*, PAL 395. 9 and 10. Spore clusters. 11. Detail of Fig. 10. 12. Spore fragments. 13–20. *Scolopendrites grauvogelii*. 13. Sporangia, PAL 380. 14 and 15. Details of Fig. 13. 16–18. Spores with laevigate exine and visible trilete marks, PAL 380. 19 and 20. Spores with microverrucate ornamentation, PAL 390. Scale bars: Figs. 1, 13: 100 μm, Figs. 2, 7: 50 μm, all others: 20 μm.

Table 2
Overview of possible osmundaceous fern species with *in situ* spores discussed in the text. References: 1 = Balme (1995); 2 = Grauvogel-Stamm and Grauvogel (1980); 3 = Van Konijnenburg-van Cittert et al. (2006); 4 = Kustatscher et al. (2019).

Species	Stratigraphy	Outline	Diameter [μm]	Ornamentation	Comparable dispersed taxa	References
Anomopteris mougeotii Brongniart, 1828	Anisian	Circular to slightly triangular	25–64	Granulate to verrucate/gemmate, microreticulate, punctate	*Osmundacidites*	1, 2, this work
Gordonopteris lorigae Van Konijnenburg-van Cittert et al., 2006	Anisian	Circular to oval	38–58	Laevigate or granulate/verrucate	*Todisporites*; *Verrucosisporites*	3, 4, this work
Scolopendrites scolopendrioides (Brongniart) Van Konijnenburg-van Cittert et al., 2006	Anisian	Circular	39–50	Laevigate or microverrucate	*Todisporites*; *Osmundacidites*	3, 4, this work
S. grauvogelii Van Konijnenburg-van Cittert et al., 2006	Anisian	Circular	37–71	Laevigate or granulate	*Todisporites*; *Calamospora*	3, 4, this work
S. sp.	Anisian	Circular	29–54	Laevigate/granulate/microverrucate to verrucate	*Todisporites*; *Osmundacidites*	this work

Description of in situ spores: The spores are trilete, with a circular amb, an often indistinct mark, and a diameter of 29–54 (mean: 42.8; n = 12) μm (Fig. 1). The exine is *ca.* 0.5–1.5 μm thick. The sculpture is laevigate or granulate/microverrucate to verrucate. Abortive spores were not identified.

Discussion: The spores are generally similar to those of *Scolopendrites scolopendrioides* (see above; Table 2). They can likewise be compared to the dispersed taxa *Todisporites* and *Osmundacidites*. Their documented size range is wider than that of the spores of *S. scolopendrioides* in both its lower and upper limits. The size range also with the spore sizes of *S. grauvogelii*, but the latter are larger on average and reach larger sizes overall (up to 71 μm).

Order: Gleicheniales Schimper, 1869
Family: Dipteridaceae (Diels) Seward et Dale, 1901
Genus: **Clathropteris** Brongniart, 1828a
Type species: Clathropteris meniscioides (Brongniart) Brongniart, 1828a

Clathropteris cf. *reticulata* Kurr ex Heer, 1877
Plate I, 7, Plate V, 13–20, Plate VI, 4
Selected references (for further references see Pott et al., 2018*):*
1864 *Clathropteris reticulata* Kurr *ms.*
1877 *Clathropteris reticulata* Kurr – Heer, p. 73, pl. 25, figs. 4–6
2018 *Clathropteris reticulata* Kurr – Pott et al., p. 29, pl. 15, figs. 1–8; pl. 16; text-figs. 9E–G
Locality: Lunz, Austria.
Stratigraphic horizon: Lunz Formation.
Studied material: NHMW-Geo 1878B/0006/9966.

Description: NHMW-Geo 1878B/0006/9966 (Plate I, 7) is a small (*ca.* 40 mm × 30 mm) slab with partly sterile and partly fertile *Clathropteris* frond fragments. The fertile frond fragment does not show the characters of the margin and the organization of the frond, while the sterile fragment clearly shows a dentate margin. The primary vein and the secondary veins of the fertile fragment are distinct, but no clear tertiary venation could be distinguished. The sporangia yielded well-preserved spores.

Comparison: The examined specimen is incomplete, in particular the leaf margin is missing, therefore the assignment to *Clathropteris reticulata* is only tentative. It is labelled "*Dictyophyllum acutilobum* Schenk". Its spore morphology is consistent with *Clathropteris reticulata* (see below).

Description of in situ spores: Sporangia are approximately circular, measuring *ca.* 300–450 μm in diameter. The spores are trilete and rounded triangular with slightly concave sides. The mark is distinct and straight to slightly undulating. The spore radius ranges from 19 to 32 μm, with a mean of 24.6 μm (n = 22; Fig. 1). Rays of the trilete mark measure 65–93% of the radius, very rarely bifurcating at the end. The lengths of radii and leasurae are linearly correlated (Pearson's $r = 0.831$; $p << 0.001$; Fig. 2). The exine is *ca.* 0.7–1.5 μm thick without the sculptural elements. The surface shows a microreticulate ornamentation, a weakly pronounced to inconspicuous margo (kyrtome-like thickening), and sparse microverucae/verrucae or short baculae (up to *ca.* 1 μm long) with varying density. The ornamentation is sometimes more pronounced on the proximal side (Plate V, 17, 18). In specimens with a more pronounced margo, the exine tends to be noticeably thinner in the gap between the laesurae and the margo (Plate V, 15). Certain and probably abortive spores make up 4.5–5.4% of the counted spores (n = 111; Fig. 3).

Discussion: The spores may be assigned to three basic types: 1) Spores without a pronounced margo; 2) Spores with a pronounced margo and thinning along the laesurae; 3) Abortive spores with a compressed and dark appearance. However, transitional cases between these types exist as well. Additionally, 9% of the spores are compressed and may represent normal or abortive spores.

Pott et al. (2018) compared the spores of *Clathropteris reticulata* to the dispersed taxon *Lunzisporites sparsus* Bharadwaj et Singh, 1964, which has been described from the palynoflora of Lunz (Bharadwaj and Singh, 1964; Table 3). *Lunzisporites sparsus* is marked by a sparse, (micro-)verrucate-baculate ornamentation, with elements being 0.5 μm high and about 1 μm broad, as well as a trilete mark 3/4 of the radius (Bharadwaj and Singh, 1964). The spores extracted from NHMW-Geo 1878B/0006/9966 conform to this type in the sparsity and type of sculptural elements. However, the baculate elements in our material and in the material described and figured by Pott et al. (2018) are higher (respectively up to 1 μm and 2 μm) and the laesurae are frequently longer (up to 12/13 and 5/6, respectively) than what is described for *L. sparsus*. This may be explained by the holotype representing an extreme case of a broader spectrum. Bharadwaj and Singh (1964) only figured and cited one specimen; it is therefore not clear how many other spores were considered to determine possible variations within the species. The Lunz palynoflora contains two other species of *Lunzisporites* Bharadwaj et Singh, 1964: *L. lunzensis* Bharadwaj et Singh, 1964 and *L. pallidus* Bharadwaj et Singh, 1964, which are distinguished by a higher density of verrucae and baculae and by more pronounced thickenings (margos) between the rays compared to *L. sparsus*. Lund (1977) considered *Lunzisporites* as a junior synonym of *Trachysporites* Nilsson, 1958, and recombined *L. sparsus* as *Trachysporites sparsus* (Bharadwaj et Singh) Lund, 1977. Moreover, those elements in which the ornamentation is smaller than 1 μm, could have been classified also within the genus *Intrapunctisporis* Krutsch 1959, if found dispersed in the fossil record.

The spores of *Clathropteris obovata* Ôishi, 1932 from the Upper Triassic in Sichuan, China share many characteristics with those of *Clathropteris* cf. *reticulata* (Table 3); they mainly differ in the sculpture elements being coarser (up to 1.5 μm long and 1 μm broad; Wang et al., 2015). Those spores conform to the *Trachysporites*-type as well. From the type species of *Clathropteris*, *C. meniscioides*, *in situ* spores are known from the late Carnian of the Newark Basin, USA (Cornet and Traverse, 1975) and from Rhaetian to Liassic beds in Greenland (Harris, 1931; Balme, 1995) and Germany (Schenk, 1867; Potonié, 1962; Van Konijnenburg-van Cittert et al., 2020). These spores have been compared to *Converrucosisporites* Potonié et Kremp, 1954 and *Granulatisporites*. Likewise, spores of *C. walkeri* Daugherty emend. Ash,

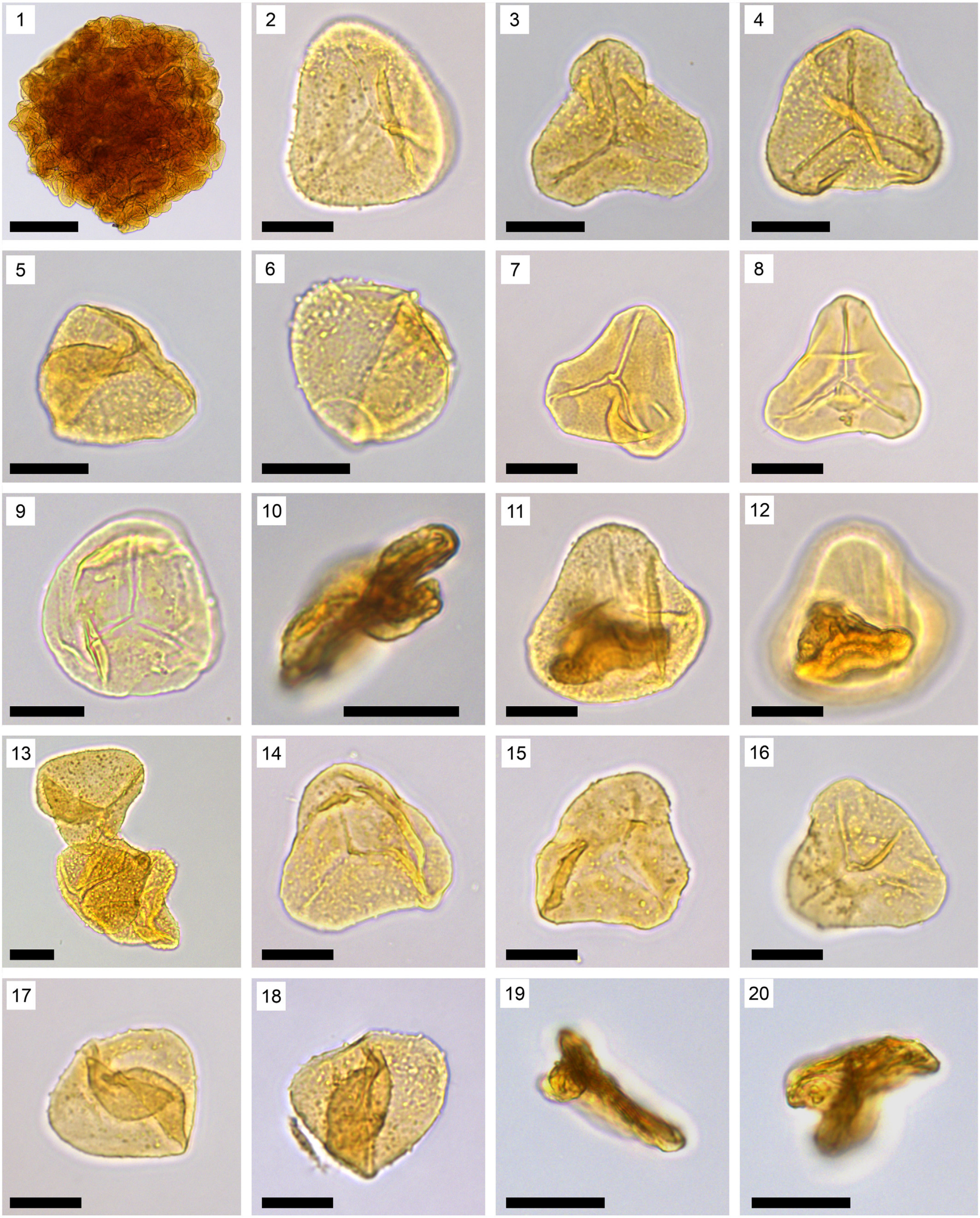

Plate V. *In situ* spores of *Dictyophyllum serratum* and *Clathropteris* cf. *reticulata* from the Lunz flora. 1–12. *Dictyophyllum serratum*. 1. Sporangium, NHMW-Geo 1883/0017/5950, sample 2. 2. Spore with well-developed, protruding surface elements, MB.Pb.2019/279, sample 2. 3 and 4. Spores with short curvaturae imperfectae, NHMW-Geo 1883/0017/5950, sample 2. 5 Spore in oblique view, NHMW-Geo 1883/0017/5950, sample 2. 6. Spore in lateral view with sculpture elements primarily on the proximal half, NHMW-Geo 1883/0017/5950, sample 1. 7. Spore with microreticulate ornamentation, NHMW-Geo 2010/0102/0172. 8. Spore with laevigate surface and exine thinning between trilete mark and margo, NHMW-Geo 2010/0102/0172. 9. Thin-walled, laevigate and nearly circular abnormal spore, MB.Pb.2019/279, sample 3. 10. Abortive spore, NHMW-Geo 1883/0017/5950, sample 2. 11 and 12. Abortive spore in front of a well-developed grain, MB.Pb.2019/279, sample 2. 13–20. *Clathropteris* cf. *reticulata*, NHMW-Geo 1878B/0006/9966. 13. Small cluster of spores. 14–16. Single spores in polar view. 17 and 18. Spores in lateral view. 19 and 20. Abortive spores. Scale bars: Fig. 1: 100 μm, all others: 20 μm.

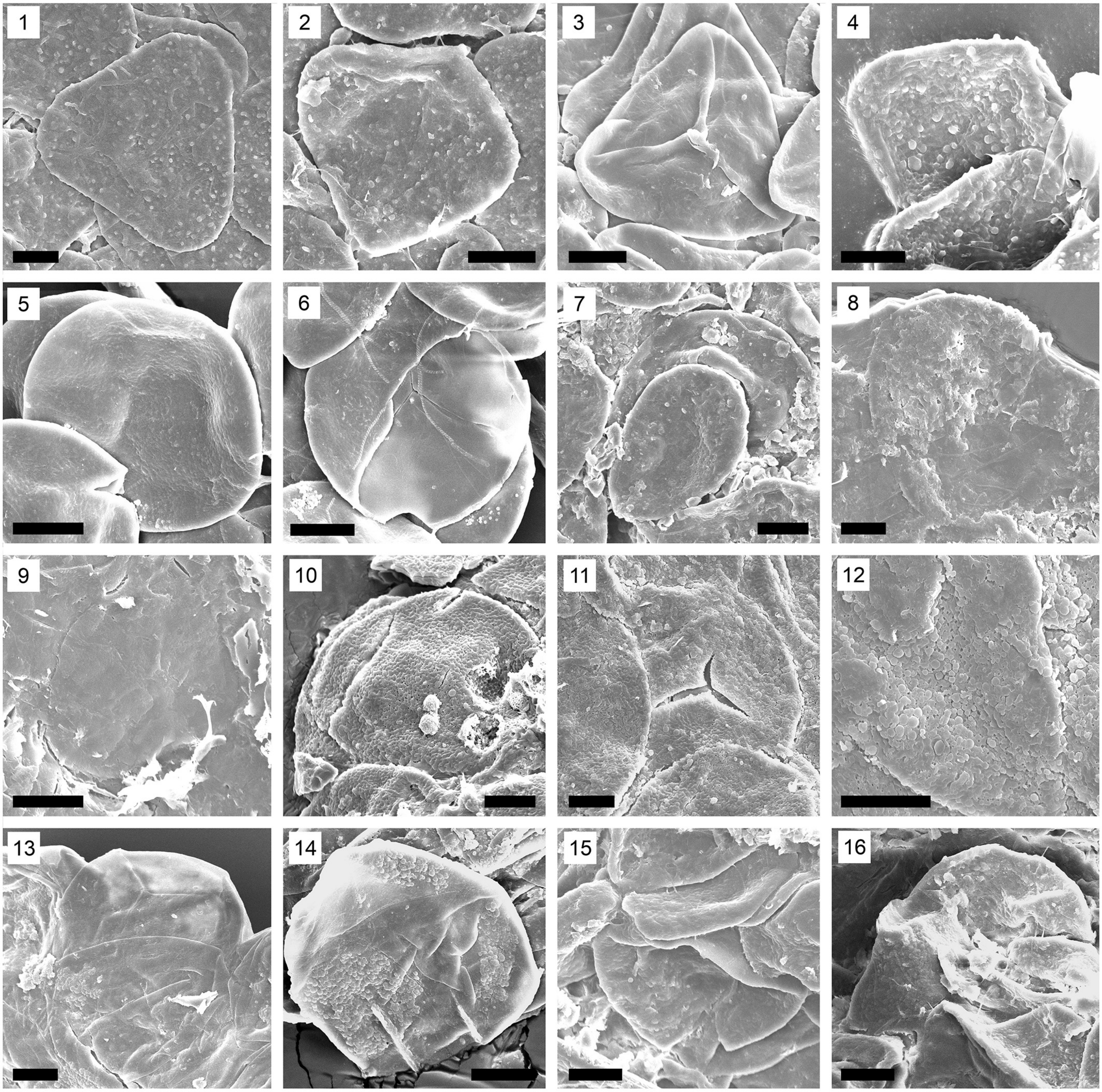

Plate VI. SEM pictures of *in situ* spores. 1. *Dictyophyllum serratum*, spore in distal polar view, NHMW-Geo 1883/0017/5950, sample 1. 2. *Dictyophyllum serratum*, spore in lateral view, NHMW-Geo 1883/0017/5950, sample 2. 3 *Dictyophyllum serratum*, spore with laevigate to microfoveolate sculpture and notable intraradial thickenings, S148595. 4. *Clathropteris* cf. *reticulata*, NHMW-Geo 1878B/0006/9966. 5. *Todites linnaeifolius*, spore displaying microverrucate ornamentation, NHMW-Geo 1882/0013/3054, sample 2. 6. *Todites linnaeifolius*, fragmented spore displaying inner surface of the exine and laesurae, NHMW-Geo 1882/0013/3054, sample 2. 7. *Todites* sp., spores with imperfect verrucate ornamentation, S148683–02. 8. *Gordonopteris lorigae*, unornamented spores with probable remains of the sporangial wall, PAL 257, sample 1. 9. *Gordonopteris lorigae*, unornamented spore with faint trilete mark, PAL 257, sample 2. 10. *Anomopteris mougeotii*, spore with granulate to gemmate, microreticulate, and punctate surface. PAL 243, sample 1. 11. *Anomopteris mougeotii*, spores with granulate to gemmate and punctate surface showing a trilete mark, PAL 243, sample 2. 12. Detail of 11. 13 and 14. *Scolopendrites grauvogelii*, spores with laevigate and partially granulate surface, PAL 380. 15. *Scolopendrites* sp., spores with granulate ornamentation, PAL 419, sample 1. 16. *Scolopendrites* sp., spores with granulate ornamentation, PAL 419, sample 2. Scale bars: 10 μm.

1969 from Arizona and New Mexico, USA have been compared to *Converrucosisporites* and *Granulatisporites* (Ash, 1969; Litwin, 1985; Balme, 1995; Wang et al., 2015; Table 3). However, the mixture of sculpture elements of different types in the spores of both *C. meniscioides* and *C. walkeri* is typical for *Trachysporites*. They partly differ from the spores of *C.* cf. *reticulata* in a higher density of sculpture elements, but there is some overlap.

Genus: **Dictyophyllum** Lindley et Hutton, 1834
Type species: *Dictyophyllum rugosum* Lindley et Hutton, 1834.

Dictyophyllum serratum (Kurr ex Schimper) Frentzen, 1922
Plate I, 5–6, Plate V, 1–12, Plate VI, 1–3
Selected references (for further references see Pott et al., 2018*):*
1869 *Camptopteris serrata* Kurr – Schimper, p. 632, pl. 42, fig. 4

Table 3
Overview of dipteridacean fern species with reported *in situ* spores discussed in the text. References: 1 = Pott et al. (2018); 2 = Balme (1995); 3 = Harris (1931); 4 = Potonié (1967); 5 = Van Konijnenburg-van Cittert et al. (2020); 6 = Sierotin (1962); 7 = Couper (1958); 8 = Potonié (1962); 9 = Schenk (1867); 10 = Harris (1944); 11 = Guignard et al. (2009); 12 = Schweitzer et al. (2009); 13 = Harris (1961); 14 = Delle (1967); 15 = Thomas (1922); 16 = Cornet and Traverse (1975); 17 = Ash (1969); 18 = Litwin (1985); 19 = Wang et al. (2015); 20 = Vladomirovitch (1950); 21 = Krassilov (1969).

Species	Stratigraphy	Outline	Diameter [μm]	Ornamentation	Comparable dispersed taxa	References
Dictyophyllum serratum (Kurr ex Schimper) Frentzen, 1922	Carnian	Rounded triangular with concave or rarely convex sides	38–55	Laevigate to microfoveolate or (micro-)reticulate/rugulate, sometimes with gemmae and clavae	*Trachysporites*; *Leiotriletes*; *Concavisporites*	1, this work
D. exile (Brauns) Nathorst, 1878	Rhaetian	Rounded triangular with straight to convex sides	50–60	Laevigate/punctate	*Cyathidites*; *Deltoidospora*	2, 3, 4, 5, 6
D. muensteri (Göppert) Nathorst, 1878	Rhaetian–Lower Jurassic	Rounded triangular with convex sides	65	Laevigate/punctate	*Dictyophyllidites mortonii* (De Jersey) Playford et Dettmann, 1965 / *Dictyophyllidites paramuensteri* Cornet et Traverse, 1975 / *Triplanosporites*	2, 3, 4, 7, 8
D. nilssonii (Brongniart) Göppert, 1846	Rhaetian–Lower Jurassic	Rounded triangular with convex sides	26–42	Laevigate/granulate	*Dictyophyllidites harrisii* Couper, 1958	2, 3, 4, 7, 8, 9, 10, 11, 12
D. rugosum Lindley et Hutton, 1834 emend. Harris, 1961	Middle Jurassic	Rounded triangular with concave to convex sides	33–58	Laevigate	*Dictyophyllidites harrisii* Couper, 1958	2, 4, 7, 8, 10, 13, 14, 15
Clathropteris cf. *reticulata* Kurr ex Heer, 1877	Carnian	Rounded triangular, concave sides	39–45	Microreticulate, sparse microverrucae/verrucae or baculae	*Trachysporites sparsus* (Bharadwaj et Singh) Lund, 1977; *Intrapunctisporis* Krutsch, 1959	this work
C. reticulata Kurr ex Heer, 1877	Carnian	Rounded triangular with straight to concave sides	33–51	Rugulate, verrucate/baculate	*Trachysporites sparsus* (Bharadwaj et Singh) Lund, 1977	1
C. meniscioides (Brongniart) Brongniart, 1828	Carnian–Lower Jurassic	Roundish to rounded triangular	40	Baculate/papillate	*Granulatisporites infirmus* (Balme) Cornet et Traverse, 1975; *Converrucosisporites cameronii* (de Jersey) Playford et Dettmann, 1965	2, 3, 5, 8, 9, 16
C. walkeri Daugherty emend. Ash, 1969	Upper Triassic	Rounded triangular with concave to convex sides	22–65	Conate/baculate	*Converrucosisporites*; *Granulatisporites*	2, 17, 18, 19
C. obovata Ôishi, 1932	Upper Triassic–Jurassic	Rounded triangular with concave sides	22–65	Laevigate(?) or verrucate/baculate/granulate	*Converrucosisporites*; *Conbaculatisporites*; *Dictyophyllidites* (?)	2, 7, 19, 20, 21

1922 *Dictyophyllum serratum* (Kurr) – Frentzen, p. 35, pl. 3, fig. 1
2018 *Dictyophyllum serratum* (Kurr) – Pott et al., 31, pl. 15, figs. 9–17; pl. 17; text-fig. 9A–D

Locality: Lunz, Austria.

Stratigraphic horizon: Lunz Formation.

Studied material: NHMW-Geo 1882/0013/3062, NHMW-Geo 1883/0017/5950, NHMW-Geo 1885/0012/4013, NHMW-Geo 2010/0102/0172, MB.Pb.2019/279, S148595.

Description: See Pott et al. (2018, p. 33).

Comparison: See Pott et al. (2018, p. 33–34).

Description of in situ spores: The spores are trilete, with a rounded triangular or subtriangular amb, having commonly slightly concave, rarely convex sides. Rays of the trilete mark are distinct and straight to slightly undulating. The spore radius ranges from 17.6 to 32.9 (mean: 24.6; n = 292) μm (Fig. 1). Laesurae measure 52–100% of the radius, with a significant linear correlation (Pearson's $r = 0.753$; $p << 0.001$; Fig. 2). The surface shows a (micro-)reticulate or rugulate ornamentation (Plate VI, 1, 2), a more or less pronounced margo (*e.g.*, Plate VI, 3), and sometimes free-standing sculpture elements such as gemmae or clavae (Plate V, 2, 6, Plate VI, 1, 2). The exine is *ca.* 0.7–1 μm thick without the sculptural elements. Some spores are laevigate or microfoveolate, with this condition being rare in most samples, except for specimens S148595 and NHMW-Geo 2010/0102/0172, which yielded consistently laevigate (Plate V, 8) to microfoveolate (Plate VI, 3) or (micro-)reticulate (Plate V, 7) spores without free-standing sculpture elements. Abortive spores occur with frequencies of 0–12.5% (Fig. 3).

Discussion: In situ spores of *Dictyophyllum serratum* have previously been described by Pott et al. (2018) and compared to *Lunzisporites pallidus*. Our material shows essentially the same characteristics and for the most part could equally be assigned to *L. pallidus*. The ornamentation with a mixture of verrucae and baculae is the most distinguishing feature of the genus *Lunzisporites*. The characteristic of *L. pallidus* is that the ornamentation elements are dense, but separated, whereas they are basally confluent in *L. lunzensis* and sparse in *L. sparsus* (Bharadwaj and Singh, 1964). Pott et al. (2018) determined from SEM studies that “bacula are only present on the distal face,” which we cannot confirm for our material. Some of our spores could be assigned also to the dispersed genus *Trachysporites* Nilson, 1958 due to the mixed sculpture elements, while other spores are without protruding sculptural elements, and thus more comparable to *Leiotriletes* or *Concavisporites* Delcourt et Sprumont, 1955. Both *Trachysporites* (= *Lunzisporites*) and *Leiotriletes* are common components of the Lunz palynoflora (Bharadwaj and Singh, 1964). Laevigate spores of *D. serratum* strongly resemble those of *D. rugosum* Lindley et Hutton emend. Harris, 1961 from the middle Jurassic of Yorkshire (Couper, 1958; Harris, 1961; Potonié, 1967) and of *D. nilssonii* (Brongniart) Göppert, 1846 from the Rhaetian and Lower Jurassic of Greenland (Schenk, 1867; Harris, 1931; Couper, 1958; Potonié, 1962, 1967) and China (Guignard et al., 2009; Table 3). However, *in situ* spores of the latter species from Iran described by Schweitzer et al. (2009) are larger (55–60 μm) and granulate. The spores of *D. rugosum* have been associated with the dispersed species *Dictyophyllidites harrisii* Couper, 1958. The spores of *D. exile* (Brauns) Nathorst, 1878 from the Rhaetian of Sweden and Germany are similarly unornamented or punctate, but – with diameters of 50–60 μm – larger than most of the spores of *D. serratum* (Harris, 1931; Sierotin, 1962; Potonié, 1967; Van Konijnenburg-van Cittert et al., 2020). The spores of *D. muensteri* (Göppert) Nathorst, 1878 from the Rhaetian–Liassic of Greenland are also described as larger (65 μm in diameter) and smooth or punctate (Harris, 1931; Couper, 1958; Potonié, 1962, 1967; Balme, 1995). They have been compared to *Dictyophyllidites* Couper, 1958 and *Triplanosporites* Pflug in Thompson et Pflug, 1953.

4. Discussion

4.1. Size variation

The *in situ* spores within individual sporangia show considerable size variation, with the larger spores in some cases having more than twice the diameter of the smaller ones. While these size ranges tend to overlap across the studied individuals, they do show significant differences in their statistical distribution and in the documented minimum and maximum sizes. These differences occur between species (Fig. 1; Tables 1–3), but also between individuals and even between sampling points on the same plant fossil (Figs. 1, 2).

Although spore sizes are often thought to be consistent for a particular species, extant ferns can show similar variation (Barrington et al., 1986). A noticeable size variation was also observed in Jurassic osmundaceous spores (Van Konijnenburg-van Cittert, 1978). In the fossil spores, a part of the general size variation within sporangia can be attributed to distortions of the spore walls due to compression. Although highly folded spores were not included in the measurements, very few are undistorted. Another factor for the variation within and between individuals are the different states of maturation of the spores. It is a well-known caveat of *in situ* sporomorphs that they are usually more or less immature, since fully developed spores and pollen are soon dispersed. Spores of extant osmundaceous ferns have been shown to increase significantly in size while maturing (Peabody, 1964). Among other things, during sporogenesis, the spore wall gains additional or thickens existing layers and increases slightly in size (Lugardon, 1972, 1974, 1990). This is also related to the development of ornamentation (see below). Furthermore, the spores of the same plant may mature diachronously. We have documented a few cases in which sporangia from different positions on a frond displayed divergent maximum and average sizes, which may be related to asynchronous sporogenesis (Fig. 1).

Ploidy levels or genome size are usually regarded as the most important factor determining cell/spore size differences between species or populations (Barrington et al., 1986, 2020). However, a comparison of nuclei in permineralized cells of an osmundaceous fern from the Lower Jurassic with a recent relative provided evidence that at least in this lineage, genome size may have been stable until today (Bomfleur et al., 2014), whereas *in situ* spore sizes do show significant differences across time (Van Konijnenburg-van Cittert, 2000). In addition to ploidy, reproduction adaptations and environmental factors have been shown to influence spore size as well and may produce differences between species and habitats, respectively (Barrington et al., 1986, and references therein).

In the cases of the two genera of which we analyzed more than one species (*Scolopendrites* and *Todites*), spore sizes did in fact differ between species, with *Todites* sp. and *Scolopendrites grauvogelii* having mostly larger spores than *T. linnaeifolius*, *S. scolopendrioides* and *Scolopendrites* sp., respectively. Since this pattern holds true across multiple samples and the specimens came from the same localities, this is likely a reflection of genome sizes. However, the overall sample size is small, and at least *Todites linnaeifolius* shows even higher intraspecific variation (with mean spore diameters per sample ranging from 37.6 to 46.5 μm) compared to *Todites* sp. (mean spore diameters per sample ranging from 47.0 to 50.7 μm; Fig. 1). These differences in dimensions cannot be linked in our case to different ways of preparations as observed previously by Van Konijnenburg-van Cittert (1978), since in our case all samples were treated with a standardized method.

4.2. Morphological variation

The general outlines of the spores described here are relatively consistent for individual species. Only *Dictyophyllum serratum* has delivered several spores that deviate from the usual concave triangular outline to a pronounced convex form (Plate V, 9). These cases can be regarded as abnormal (see below). The tendency of spores found in *Todites* sp. and *Anomopteris mougeotii* to show a slightly triangular outline (Plate III, 11, 12, Plate IV, 3, 6) can be seen as a deviation from the normally circular form that is common in osmundalean spores in general. Potonié (1962) considered a more triangular appearance in osmundalean spores as a sign of immaturity.

Surface ornamentation varies more regularly, but again *Dictyophyllum serratum* is the best example due to its spores normally having a distinct positive ornamentation. In all samples of this species, spores with reduced ornamentation are frequent (Plate V, 7, Plate VI, 3), while in rare cases, the surface is completely smooth (Plate V, 8). If found dispersed in the sediment, these differently ornamented spores would be assigned to different genera (*Trachysporites* or *Concavisporites*), since ornamentation is one of the most obvious, and therefore important, characters for the distinction of sporomorph morphotaxa. The co-occurrence of these forms *in situ* thus suggests that dispersed genera are prone to overestimate the biological diversity of fern spores. On the other hand, simple, unornamented morphologies like those of *Concavisporites* and *Todisporites* may be the product of underdeveloped or imperfectly preserved spores from different fern species; *e.g.*, the spores of *Dictyophyllum* and *Clathropteris* would be essentially indistinguishable without a structured outer exospore and perispore.

The differences between the spores of *Anomopteris mougeotii* from the Grès à Voltzia in France (punctate) and from the Dont Formation of the Kühwiesenkopf/Monte Prà della Vacca (granulate to verrucate) – if they are not a matter of interpretation (comp. Grauvogel-Stamm and Grauvogel, 1980; Balme, 1995) – might be caused by the former being in a relatively more immature state. It is also possible that the local environments had an effect on the development of the spores or on their preservation.

Spores comparable to *Osmundacidites* and *Todisporites* similar to what we found in *Todites* spp. and the possible osmundaceous ferns of the Kühwiesenkopf/Monte Prà della Vacca flora are regularly found in fossil Osmundales and are even common in extant representatives (Van Konijnenburg-van Cittert, 1978, 2000). Van Konijnenburg-van Cittert (2000) distinguished three basic types of osmundaceous *in situ* spores, based on the sculpture of their exospore; *Osmundopsis*-type (with partly fused granulate or baculate elements), *Todites hartzii*-type (with unfused granules) and *Todites williamsonii*-type (almost laevigate). All of the above described *in situ* spores of ferns tentatively assigned to the Osmundales, as well as those of *Todites* spp. fall into the established morphospace for osmundaceous spores.

4.3. Abnormal spores

In some samples, an increased frequency of spores that are considered abortive (Plate III, 7, 8, Plate V, 11–12, 19, 20) or otherwise having an abnormal shape (Plate V, 9) was observed. Although the exact numbers are difficult to determine due to the distortion of the spores relative to their positions in the compacted sporangia, it appears that samples from the same individual plant have similarly high or low frequencies of abortive spores. The specimen with the highest number of abortive spores (MB.Pb.2019/279) also yielded several developed, but abnormal spores. This suggests that the occurrence of abortive/abnormal spores reflects a systemic, rather than a local defect of the plant. Such cases are known from extant ferns, and are generally ascribed to genetic causes, especially (natural) hybridization (Barrington et al., 1989).

The increased occurrence of abnormal spores and pollen grains in dispersed assemblages from beds corresponding to the end-Permian and end-Triassic mass extinction intervals points to a likely influence of environmental stress factors (Gravendyck et al., 2020; Chu et al., 2021). These did not affect all taxa equally. Ferns, with few exceptions, are not adapted to stressed environments (Van Konijnenburg-van

Cittert, 2002). Information about their reproductive responses to such conditions over time are lacking, but abnormal sporomorphs may provide clues, if more data points are gathered and patterns can be identified. Abortive spores in particular are probably an under-reported category, because their status might not be obvious without a connection to other, well-developed spores of the same type. We hope that our examples may inspire other palynologists to look out for them.

5. Conclusions

Our findings show significant intraspecific variations in the sizes and ornamentation of *in situ* spores from Triassic leptosporangiate ferns. Both can vary within and between individuals or localities. The causes of size variation are difficult to determine but are most likely a combination of genome size, immaturity, and normal spread. Differences in ornamentation are linked primarily to the degree of immaturity of the spores. The presence or absence of certain sculptural elements in the spores of *Dictyophyllum serratum* would be diagnostic for different genera in dispersed spores. Moreover, spores lacking in sculpture elements are prone to converge in simpler "waste-basket taxa". Further comparisons between specimens of the same species from different localities might reveal if or to what extent ecological and/or preservational effects play a role in the general variation of *in situ* spores and in particular in the occurrence of frequent abortive spores.

Such effects need to be taken into account when dispersed sporomorph assemblages are interpreted or when *in situ* spores are used as indicators for the affinity of a plant macrofossil taxon. That said, the spores found in several fern species of the Kühwiesenkopf/Monte Prà della Vacca flora are consistent with their tentative assignment to the Osmundales.

Declaration of Competing Interest

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

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