Ferns and fern allies in the Rhaetian flora of Wüstenwelsberg, Bavaria, Germany

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Abstract

The Rhaetian flora from Wüstenwelsberg (Franconia, southern Germany) comprises a diverse array of cryptogam plants. Twelve species of lycophytes, sphenophytes and ferns are identified and described by means of macromorphology and in situ spores, when present. The study is part of the ongoing examination of this recently excavated and excellently preserved fossil plant assemblage. In total, two lycophyte taxa (Lepacyclotes and Selaginellites) and one sphenophyte (Equisetites) have been identified. Ferns are represented by eight species in three families; Osmundaceae with one Todites and two Cladophlebis species; Matoniaceae with two Phlebopteris species, and Dipteridaceae with Clathropteris, Dictyophyllum and Thaumatopteris with one species each. Curled fern fronds have been attributed to the fossil-genus Spiropteris. Besides several key Rhaetian taxa, two key taxa for Hettangian floras, Phlebopteris angustiloba and Thaumatopteris brauniana, are present in Wüstenwelsberg, albeit not in large numbers. The comparison of the flora from Wüstenwelsberg with adjacent Rhaetian floras revealed distinct local differences in the respective floras, which are discussed in the light of paleogeography involving dispersal patterns or mechanisms and adaptations of the plants.

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1. Introduction

The fossil flora from the uppermost Triassic and lowermost Jurassic strata of Upper Franconia (Bavaria, Germany), more widely known as the “Rhaeto-Liassic flora” of Upper Franconia, has received considerable scholarly attention recently (for references see Van Konijnenburg-van Cittert et al., 2014, 2016, 2017, 2018a, 2018b; Pott et al., 2016). Most of the outcrops include Hettangian (Lower Jurassic) sediments and are spread in a wide area around the towns of Bayreuth and Nuremberg (see e.g., Gotham, 1914). However, a few localities around the town of Coburg are Rhaetian (Upper Triassic) in age (see e.g., Kelber and Van Konijnenburg-van Cittert, 1997; Van Konijnenburg-van Cittert et al., 2014; Pott et al., 2016). These include a quarry near Wüstenwelsberg where systematic sampling during the past uncovered more than 40 different species of fossil plants. The flora of Wüstenwelsberg is currently under thorough study, and several species and taxa have been described by Bonis et al. (2010), Zavialova and Van Konijnenburg-van Cittert (2011), Van Konijnenburg-van Cittert et al. (2014, 2016, 2017, 2018a, 2018b) and Pott et al. (2016).

In this paper, we describe the cryptogams that were present in the flora of Wüstenwelsberg; these include ferns, and, to a lesser extent, sphenophytes and lycophytes. The latter are represented by Lepacyclotes sp. (Isoetales) and Selaginellites cohurgensis Van Konijnenburg-van Cittert et al., 2014, (Selaginellales, see Van Konijnenburg-van Cittert et al., 2014, 2016, 2017, 2018a, 2018b) and Pott et al. (2016). Sphenophytes are represented by one species only, viz. Equisetites laevis Halle, 1908. The ferns constitute a dominant group in the plant assemblage, just as the seed ferns, cycads and Bennettiales (Van Konijnenburg-van Cittert et al., 2018b, and references therein). The diverse fern flora includes Todites roessertii (Presl) Kryštufčík, 1912, Cladophlebis scoresbyensis Harris, 1926, Cladophlepis sp. (with a cuticle), Phlebopteris muensteri (Schenk) Hirmer and Höhhammer, 1936, Phlebopteris angustiloba, Clathropteris...
The ecology and environment of the entire flora are discussed as well as its habitat, with a focus on the cryptogams; in addition, we compare the composition of the Rhaetian flora of Franconia with the Rhaetian and Hettangian floras of East Greenland (Jameson Land), Sweden (Scania), Poland, Ukraine (Donets Basin) and Iran, and discuss potential relationships, biogeography and dispersal patterns.

2. Material and methods

2.1. The Wüstenwelsberg quarry

The studied section is located in a sandstone quarry near the village of Wüstenwelsberg, approximately 20 km SW of Coburg, Germany (Fig. 1). The sediments were deposited in the Germanic Basin and are characterized by an alternation of clay and sandstone layers (for details see Bonis et al., 2010; Pott et al., 2016; Van Konijnenburg-van Cittert et al., 2018b). The plant fossils come from clay layers, one of which is the so-called “Hauptton” that can be up to 10 m thick. Most of the specimens originate from this horizon (level 3 in Bonis et al., 2010). Almost all layers in the section are Rhaetian in age, only the uppermost one (without any macrofossil remains but with palynomorphs) might be Hettangian in age (Bonis et al., 2010).

2.2. Description of the fossil material

The fossil leaf material used in this study originates from fieldtrips by some of the authors (SS, GD, JHAvKvC). The fossils are stored in the collections of the Laboratory of Palaeobotany and Palynology, University of Utrecht (The Netherlands; UU numbers) and in the private collections of Stefan Schmeißner (Kulmbach, Germany; numbers preceded by Q) and Günter Dütsch (Untersteinach, Germany; numbers containing the acronym wü). The plant fossil remains are mainly compression fossils of relatively small size, giving only information on the macromorphology. Some fertile fern specimens yielded in situ spores and so contributed to our knowledge of this Rhaetian flora.

2.3. Methods

In situ spores were prepared by picking sporangia from fertile specimens. These were macerated according to the standard procedure using Schulze’s reagent (30% HNO₃ with a few crystals of KClO₃) and subsequently treated with 5–10% ammonia (NH₄OH) or potassium hydroxide (KOH). Macerated sporangia were rinsed with water and dehydrated in glycerine. Then they were separated with needles so that separate spores could be seen, or spore clusters in the case of immature sporangia. These were embedded in glycerine jelly and sealed with transparent nail polish or paraplast. The slides are stored in the collection of the Laboratory of Palaeobotany and Palynology, Utrecht University, and in the private collections of SS and GD. Slides and specimens of the latter two collections will be donated to a publicly available collection after the research on the Wüstenwelsberg flora has been completed.

The macrofossil specimens were photographed with a Nikon D80/Nikkor AF-S Mikro 60-mm 1:2.8G ED system digital camera and partly with a Panasonic DMC-FZ1000 with a Leica DC Vario-Elmarit 1:2.8–4.0/9.1–146 lens. Oblique lighting and polarizing filters in front of the camera lenses and the lights were used to enhance contrast and fine details. Spores were analyzed with an Olympus BH2 light microscope.

3. Systematic paleobotany

3.1. Lycophyta

Order: Isoetales Prantl, 1874
Family: Isoetaceae Reichenbach, 1828
Genus: Lepacyclotes Emmons, 1856

Diagnosis and discussion: See Emmons (1856), Retallack (1997), Kustatscher et al. (2010), Bauer et al. (2015).

Type species: Lepacyclotes circularis Emmons, 1856, from the Late Triassic (Carnian) of Ellingtons, North Carolina, USA (see Retallack, 1997).

Lepacyclotes sp.

Plate I, 1–2

Description: One specimen (20wü04) in the Wüstenwelsberg flora yields lycophyte remains, albeit not too well preserved (Plate I, 1).
specimen is 25 mm wide and 21 mm long and contains at least two concentric circles, each of some 24 sporophylls. Each spatulate sporophyll is c. 8 mm long and 3 mm wide basally. Distally, each sporophyll terminates in an indistinct, incomplete fibrous apex (Plate I, 2). As the sporophylls partly overlie each other, no more details could be observed.

Remarks: This lycophyte specimen resembles Lepacyclotes bechstaedtii Kustatscher et al., 2010, from the Anisian flora of Kühwiesenkopf (Kustatscher et al., 2010, and esp. their pl. 5, fig. 6), although it is distinctly smaller in size. Hence, we attribute the Wüstenwelsberg specimen to Lepacyclotes sp. as its preservation is too poor to assign it to a known species.

NB: Aratrisporites spores (recorded in situ from Lepacyclotes species, see Grauvogel-Stamm and Duringer, 1983) were found dispersed in the Wüstenwelsberg section (Bonis et al., 2010).

Comparison to other German Late Triassic to Early Jurassic Lepacyclotes species reveals that sporophylls of the well-known Carnian species L. zeilleri (Fliche) Retallack, 1997 are much larger in size than the present ones (15–45 × 20 mm, versus 8 × 3 mm) (Port et al., 2018). The Hettangian species L. kirchneri Bauer et al., 2015 is more similar in size to the present specimen although still larger; L. kirchneri sporophylls measure c. 11 × c. 5 mm without their elongate apical processes.

Material examined: 20wü04.

Order: Selaginellales Prantl, 1874
Family: Selaginellaceae Willkomm, 1854
Genus: Selaginellites Zeiller, 1906

Diagnosis and discussion: See Zeiller (1906), Van Konijnenburg-van Cittert et al. (2014).

Type species: Selaginellites suisii (Zeiller) Zeiller, 1906 from the Late Carboniferous (Stephanian) of Blanzy, France.

Selaginellites coburgensis Van Konijnenburg-van Cittert et al., 2014.

Order: Selaginellales Prantl, 1874
Family: Selaginellaceae Willkomm, 1854
Genus: Selaginellites Zeiller, 1906

Diagnosis and discussion: See Zeiller (1906), Van Konijnenburg-van Cittert et al. (2014).

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Type species: Selaginellites suisii (Zeiller) Zeiller, 1906 from the Late Carboniferous (Stephanian) of Blanzy, France.

Selaginellites coburgensis Van Konijnenburg-van Cittert et al., 2014.
the cryptogam flora from Wüstenwelsberg, we figure two good specimens here that so far have not been figured (Plate I, 3–4).

*Material examined:* Q118/02, 119/02, 120/02, 121/02, 209/02, 210/02, 326/03, 397/04, 412/05, 421/05, 441/06, 608/08, 736/09, 737/09, 881/11, 882/11, 885/11, 897/12, 916/13, 956/14, 1046/18; 162wü02, 29wü03, 144wü03, 05wü08, 26wü08, 42wü08, 97wü09, 21wu11, 29wu11, 15wu14; UU23815 (paratype), 24,089 (holotype), 24,090 (paratype).

3.2. Sphenophyta

**Order:** Equisetales de Candolle ex Berchtold et J. Presl, 1820

**Family:** Equisetaceae Michaux ex de Candolle, 1804

**Genus:** Equisetites Sterenberg, 1833

**Diagnosis and discussion:** See Schenk (1865–1867), Waterson and Batten (1990), Pott et al. (2008).

*Type species:* Equisetites muensteri Sterenberg, 1833, from Strullendorf near Bamberg, Bavaria (Germany); this locality was first recorded as Rhaetian in age but is now considered to be Hettangian (see e.g., Van Konijnenburg-van Cittert et al., 2018a).

**Equisetites laevis Halle, 1908**

*Plate II, 1–4*

**Selected references:**

1908 Equisetites laevis—Halle, p. 13, pl. 5, figs. 1–11.

1926 Equisetites laevis Halle—Harris, p. 53, pl. 2, fig. 8; pl. 3, figs. 1–4.

1931 Equisetites laevis Halle—Harris, p. 14, pl. 3, figs. 7, 20; text-fig. 3A–E.

1950 Equisetites laevis Halle—Lundblad, p. 12, pl. 1, fig. 18.

1995 Equisetites sp.—Kelber and Hansch, p. 122, fig. 273.

1997 Equisetites laevis Halle—Schwertzel et al., p. 128, pl. 3, figs. 1, 2, 5–8; text-figs. 9, 11.

**Description:** In Wüstenwelsberg Equisetites laevis remains are mainly diaphragms (Plate II, 2, 6), sometimes with attached leaves (Q3/95, Q3/96, Q17/96, 141wü03; Plate II, 1), and uncommonly stem fragments occur (UU23230; Plate II, 3). Stems are almost smooth (Q262/03) or occasionally preserved as pith cast with imprints of vascular bundles (Q627/08, UU23230; Plate II, 4), varying in diameter between 2 and 4 cm. Each node commonly produced 24 leaves that are closely arranged and touching along the leaf sheaths for some 5 mm, while the free parts are up to 10 mm long with obtuse apices (Q3/96, 141wü03; Plate II, 5). Nodeal diaphragms are 3–4 cm in diameter, usually oval in shape owing to preservation (Q707/08; Plate II, 2). Nodes are commonly connected by internodia but none of those is complete. However, some shoot fragments show aberrant nodes separated by very short internodia (141wü03; Plate II, 1).

**Remarks:** The specimens from Wüstenwelsberg agree perfectly with this typically Rhaetian species as described and figured by, e.g., Halle (1908), Harris (1926) and Schweitzer et al. (1997). The type material comes from the Rhaetian of Bjuv (Sweden) (Halle, 1908), but the species is also found at other Rhaetian localities in the area such as Billesholm (Lundblad, 1950) and Rögl (Pott and McLoughlin, 2011). The latter is probably a diaphragm of E. laevis, even if left unassigned as Equisetites sp. by the authors. A diaphragm that might also be from E. laevis is recorded from the coeval and close-by locality of Heilgersdorf (Kelber and Van Konijnenburg-van Cittert, 1997). Equisetites laevis has also been recorded from the classical Rhaetian localities of Jameson Land (mainly as nodal diaphragms; Harris, 1926, 1931) and Iran (Schweitzer et al., 1997). The latter authors recorded larger stems, some of which with attached leaves.

A species very similar to Equisetites laevis is E. muensteri, which is the generic type. Equisetites muensteri is commonly found in Hettangian deposits, and occasionally has been recorded from the same Rhaetian localities as E. laevis (Jameson Land; Harris, 1931), but we question this identification because the remains he figured are far too fragmentary to make a specific assignment; this material should be referred to as Equisetites sp. Equisetites muensteri is distinguished from E. laevis by narrower stems, by fewer and narrower leaves per node, the latter even elongate and with acute apices (Harris, 1926, 1931; Schweitzer et al., 1997). Barth et al. (2014) wrote in their review of the Norian–Rhaetian flora from Seinstedt (Germany) that they never found the specimen of E. muensteri in the collections mentioned by Jüngst (1928), Pacyna (2014) mentioned Equisetum chalubinski Raciborski, 1890, from the Rhaetian of Poland (Tatra mountains), commenting that the species is very similar to Equisetites muensteri and should properly be referred to the genus Equisetites. He also stated that E. muensteri shoots have been recorded from Norian Polish sediments, however, without reference.

We consider Equisetites laevis a typically and purely Rhaetian species, whereas E. muensteri appears to be restricted to the Hettangian. Equisetites muensteri is a very common element in the Hettangian floras from Bavaria (its type area, Schenk (1865–1867); Weber, 1968; Hauptmann and Hauptmann, 1994). It has also been recorded from a number of other “Classic” localities such as Jameson Land (Harris, 1931), Hungary (Barbacka, 2009), Poland (Pacyna, 2013) and Sweden (Halle, 1908). There are records from older sediments, such as the Norian of Poland (Pacyna, 2014) and the Rhaetian of Jameson Land (Harris, 1926, 1931), but these records have either not been described and figured, or are fragmentary, so they should be referred to Equisetites sp. only.

*Material examined:* Q3/96, 4/96 (counterpart 5/96), 5/96 (counterpart 4/96), 6/96, 10/96, 11/96, 14/96, 16/96; 17/96, 35/96, 36/96, 161/02, 262/03, 263/03, 368/04, 391/04, 539/08, 603/08, 627/08, 628/08, 694/08, 707/08; 13wu02, 188wu02, 86wu03, 126wu03, 141wu03, 142wu03, 20wu05, 20wu08, 94wu08, 165wu08, 59wu09; UU23234, 23241, 23243, 23244, 23262, 23290, 23296B, 23307, 23320, 23820.
1968 Todites williamsonis (Brgt) Seward fvar. goeppertiana (Münster) Kilpper—Weber, p. 45.

Description: Todites roessertii is a rather common fern in the Wüstenwelsberg flora, but represented by small, not very well-preserved fragments only. Both sterile and fertile frond fragments with preserved in situ spores have been found.

The largest sterile specimen (Q941/13; Plate III, 1) shows a 62-mm-long pinna fragment. The rachis is 1.5 mm wide, with alternating pinnules that are attached by a broad base. The slightly falcate pinnules (Plate III, 1) are up to 12 mm long and 5 mm wide, and display a pecopterid venation with a central vein and secondary veins that only bifurcate in the basal portion of the pinnule. The vein concentration at the margin is 13 veins/cm. In other specimens (e.g., Q506/07, 507/07, 753/09), the pinnules are also suboppositely to alternately attached to the rachis by a broad base. Secondary venation often is indistinct, but when visible, only the basiscopic secondary veins commonly bifurcate.
once, which is clearly visible in 68wu08 (Plate III, 2) – a bipinnate, probably apical frond fragment. The pinnae alternate and the longest in 68wu08 is 45 mm long. The pinnule apex is commonly slightly rounded but acute ones occur.

Q501/07 (Plate III, 3) is a 6-cm-long and 1.2-cm-wide fertile fragment, with pinnules (6 mm long, 4 mm wide) arranged almost oppositely that are completely covered with sporangia rendering the venation invisible. In two other fertile specimens (Q502/07 and 505/07), venation is indistinctly visible (Plate III, 4). In situ spores were recovered from Q501/07; these are mainly clustered in contents of one sporangium (Plate VI, 1) but some single spores occur (Plate VI, 2, 3). Spores are spherical in shape, trilete, with a smooth surface and measure 40–45 μm in diameter.

Remarks: In the Rhaetian–Hettangian of Franconia, two quite similar osmundaceous ferns occurred at the same time, viz. T. roessertii and T. goeppertianus (Münster in Göppert) Krasser, 1922. Both names have been used for the same type of fern foliage and consequently, some authors consider them conspecific, while others claim that the difference lies in the venation: T. goeppertianus is regarded to have more of a neuropterid-type venation (similar to that of the Middle Jurassic type
species *T. williamsonii*), while *T. roessertii* has more of a pectocerid-type venation. However, both species are often reported from the same layers in a locality or area.

Schenk (1865–1867) described and figured *Acróstochitès goeperttianus* (Münster) Schenk from the Hettangian of Theta in Franconia, and *Asplenites roeseriti* (Göppert) Schenk from three localities around Nuremberg, including Theta. From the given description and figures, a range of leaf morphologies is obvious: compare the transitional forms of Schenk’s pl. 2, figs. 5, 5a (*Acróstochitès goeperttianus*) via pl. 7, fig. 2 (*Asplenites roeseriti*) to pl. 10, figs. 1–4 (also *A. roeseriti* but with a much larger variability in pinnule shape, size and venation). Gothan (1914) considered the two species as conspecific and assigned all specimens from the Liassic of Franconia to *Todites roeseriti* as that name has priority over *T. goeperttianus*, which was later agreed on by Weber (1968).

Harris (1926) described material from the Rhaetian of Jameson Land (Greenland) as *Cladophlebis roeseriti* (Schenk non Presl) Saporta and *Todites* cf. *williamsonii*. Later, Harris (1931) transferred the latter to *Todites goeperttianus* and placed the specimens earlier assigned to *C. roeseriti* in the new species *Cladophlebis scariosa* Harris, 1931, that is distinguished from *C. roeseriti* in having narrower, parallel-sided pinnules with a simpler venation and more delicate lamina. This differentiation was later confirmed (Harris, 1937), when evaluating other reported specimens. Harris (1937) recommended that many specimens identified as *T. roeseriti* should be assigned to *T. goeperttianus*, which also is the case for the original specimens of *C. roeseriti*.

Harris (1926) described material from the Rhaetian of Jameson Land described but only figured; due to the poor quality of the material, Harris (1937, p. 17) added the thinner rachis in *C. nebbensis* (c. 1 mm) and the obtuse pinnule apex. Bodor and Barbacka (2008) compared *Cladophlebis/Todites* specimens from the Hettangian of Hungary to *T. scariosa*. This differentiates the species from *Todites roeseriti* (Harris, 1926). In contrast, both 92wu08 and 93wu13 yield incomplete pinnules that are 23 mm long and 10 mm wide (*Plate III, 6*). The apical portions of the pinnules are tapering but no apices are preserved. The venation is katadromic with a clear midrib and secondary veins that arise at 45°–60°. These veins commonly bifurcate once near their point of emergence; the lowest pair may bifurcate twice (*Plate III, 5–7*). In two specimens (29wu10 and Q760/08), two veins on the basiscopic side of the pinnules bifurcate twice while they bifurcate once on the acroscopic side (*Plate III, 5, 7*). Vein concentration at the margin is 9–11 veins/cm. The pinnule margin is always smooth proximally but may show small dentations more distally with two veinlets ending there (*Q970/ 14; Plate III, 8*).

**Remarks:** The material from Wüstenwelsberg agrees in all aspects with the specimens from Jameson Land described by Harris (1926), including the variability in pinnule shape and size, and the character that, when present, small dentations occur only in the more apical part of the pinnules with two veins ending in a single tooth. Later, Harris (1931) described additional material including fertile frond portions, and transferred, therefore, the species to *Todites*, the genus used when fertile specimens are known in which the complete lower side of the pinnules is covered with sporangia. The material from Wüstenwelsberg yields only sterile fragments, thus necessitating the specimens to be assigned to *Cladophlebis*. Records of *Cladophlebis scariosa* from outside Greenland or Jameson Land are rare. Lundblad (1950) reported some sterile leaf fragments from the Rhaetian of Sweden. In a catalogue of material from Alborz (Iran) *Cladophlebis scariosa* appears (Sadvonikov, 1983, p. 10, pl. 11, figs. 3, 4), but the specimens are not described but only figured; due to the poor quality of the figures, we cannot say whether the material belongs to *C. scariosa*. Even Schweitzer et al. (1997) refrained from a definite identification of those specimens.

The by far most similar species is *Cladophlebis nebbensis* (Bronnigart) Nathorst, 1876. Harris (1926) stated the differences as (1) the greater size of the pinnules in *C. scariosa* and (2) the termination of two veins in a single tooth in *C. scariosa*. Schweitzer et al. (1997) added the thinner rachis in *C. nebbensis* (c. 1 mm) and the obtuse pinnule apex. Bodor and Barbacka (2008) compared *Cladophlebis/Todites* specimens from the Hettangian of Hungary to *T. scariosa*, which differ in the arising angle of the secondary veins and the morphology of the margin. Another similar species is *Cladophlebis denticulata* (Bronnigart) Nathorst, 1876, but this species differs by the distinctly dentate margin of the pinnules (see e.g., Harris, 1961).

Material examined: Q214/02, 215/02 + 216/02, 612/08, 668/08 + 670/08, 760/09, 892/12 (F) + 893/12, 939/13, 970/14; 92wu08, 117wu08, 11wu10, 29wu10, 10wu13, 13wu13; UU23721, 23872.

**Cladophlebis** sp.

*Plate IV, 1–3; Plate VI, 10–14*

**Description:** Three specimens yield small sterile fragments of a *Cladophlebis/Todites*-type frond morphology (*Q783/09, 03wu05, 27wu10*), but with a clear neoerupter venation that is different from that of the specimens assigned to *T. roeseriti* and *C. scariosa* as described above. The apical portion of *Q783/09* (*Plate IV, 1*) is only 14 mm long and up to 9 mm wide (3.9 mm at its apical part). It consists of six pairs of oppositely arranged pinnules, attached perpendicularly and almost with their whole base to a 0.8-mm-wide rachis. Pinnules vary in length between 4.8 (most basal one) and 2.5 mm (most apical one) but have an almost uniform width of 2.0–2.5 mm; apices are obtuse. The neoerupter venation is best visible in the lowermost pinnules (*Plate IV, 1*) and consists of a central vein arising at c. 45° from the basiscopic pinnule angle, and half way bending towards a horizontal plane proceeding to the apex. Secondary veins arise in a fan-shaped manner at regular distances from the central vein; they occasionally bifurcate once. Specimen 03wu05 (*Plate IV, 2*) yields a 36-mm-long
and 12-mm-wide fragment, consisting of a small number of oppositely arranged pinnules that are equal in size throughout the fragment, 8 mm long and 6 mm wide. Venation is clear as described above, with a central but less obvious vein arising from the basiscopic angle giving off fan-shaped secondary veins that commonly bifurcate once. Specimen 27wü10 (Plate IV, 3) provides the least preserved fragment with seven pairs of oppositely inserted pinnules, similar in size, shape and venation pattern to the other two specimens. Another specimen (part and counterpart Q529/07, Q530/07) is too poorly preserved to be assigned to this taxon without any doubt.

The fragment on Q783/09 (Plate IV, 1) unexpectedly yielded a thin cuticle providing some rare glimpses into the epidermal structure of this species: The upper cuticle (Plate VI, 11) is thicker than the lower one (Plate VI, 10, 14). The epidermal cells both on the upper and the lower cuticle are more or less isodiametric (Plate VI, 11, 12), commonly with straight anticlinal cell walls that occasionally might express slight sinuosity (Plate VI, 14); veins are indicated by more elongate epidermal cells. Trichomes and trichome bases are present, especially frequent on the adaxial cuticle (Plate VI, 12). Stomata occur sparsely on the abaxial cuticle only (Plate VI, 11; they consist of two slightly thickened guard
cells surrounded by a number of unspecialized subsidiary cells (Plate VI, 13).

Remarks: These specimens are small pinna fragments with tiny pinnules that exhibit typical characters such as an opposite and perpendicularly inserted pinnules on the rachis and the typical neuropterid, fan-shaped venation. Similar specimens have occasionally been described as Todites cf. williamsonii or Todites/Cladophlebis goeppertianus. However, due to the limited amount of material we keep it unassigned in Cladophlebis sp.

Antevs (1919, pl. 1, figs. 20–22) reported specimens from the Hettangian of Sweden as Todites williamsonii with bipinnate fronds with oppositely and perpendicularly inserted pinnules with a neuropterid venation consisting of a weak midrib and once-bifurcate secondary veins arising in a fan-shaped manner. The specimen of his pl. 1, fig. 22 is very similar to our Cladophlebis sp. specimens, both in size and shape. Harris (1926, p. 55, text-fig. 2F) described a similar specimen from the Rhätian of Jameson Land as Todites cf. williamsonii, which the author later included in Todites goeppertianus. We consider this species conspecific with T. roessertii (Harris, 1931, 1937). However, this particular specimen is more similar to our Cladophlebis sp. specimens in shape and venation than to the other T. roessertii-material from Jameson Land (see below).

Pott and McLoughlin (2011, p. 1029, text-fig. 3F) reported a specimen from the Rhätian of Kögl as Todites sp. cf. T. williamsonii. This specimen is also very similar in shape, size and venation to our Cladophlebis sp.

Material examined: Q529/07 +? Q530/07, 783/09; 03wü05, 27wü10.

Comparison of the osmundaceous species from Wüstenwelsberg

The three osmundaceous species from Wüstenwelsberg mainly differ in pinnule size and shape, and type of venation. Cladophlebis scoresbyensis has the largest pinnules (15–23 mm long have been found) and a definite pectocerid venation, with two veinlets ending in one small marginal dentation. Todites roessertii commonly has smaller pinnules (6–12 mm long), no marginal dentations and a venation that is intermediate between pectocerid and neuropterid. Finally, Cladophlebis sp. has even smaller pinnules (2.5–8 mm), with a completely fan-shaped, neuropterid venation, more of the type found in Todites/Cladophlebis goeppertianus.

However, some authors consider Todites/Cladophlebis goeppertianus and Todites/Cladophlebis roessertii as conspecific (e.g., Gothan, 1914; Harris, 1931) as there are intermediates between the two species. Poorly preserved specimens of C. scoresbyensis are also quite similar to those of Todites/Cladophlebis roessertii, especially those in which no marginal dentations have been preserved. Hence, it is possible that all the fragmentary specimens from Wüstenwelsberg in fact belong to one species only, which should be named Todites roessertii as that name has priority. However, as we do not have many intermediates between the three taxa described here, we prefer to separate them at the moment.

Order: Gleicheniales Schimper, 1869
Family: Matoniaeae Presl, 1847
Genus: Phlebopteris Bronniart, 1836
Diagnosis and discussion: See Bronniart (1828–1836), Hirmer and Hörhammer (1936) and Pott et al. (2018).
Type species: Phlebopteris polypondioideis Bronniart (1828–1836), from the Bathonian of Scarborough, Yorkshire (UK).

Phlebopteris angustiloba (Presl in Sternberg) Hirmer et Hörhammer, 1936

Plate IV, 4–6
Selected synonymy and references:
1838 Gutbiera angustiloba—Presl in Sternberg, p. 116, pl. 33 figs. 13a–e.
1843 Andrania baruthina—Braun, p. 42, pl. 9, figs. 3–12, pl. 10, figs. 1–3.
1867 Gutbiera angustiloba—Presl—Schken, p. 64, pl. 18, figs. 5–10.
1914 Gutbiera angustiloba—Presl—Gothan, p. 99, pl. 17, fig. 5.
1914 Andrania baruthina—Braun—Gothan, p. 102, pl. 17, fig. 8, pl. 18, figs. 1, 2.
1914 Andrania norimbergica n.sp.—Gothan, p. 102, pl. 17, figs. 6, 7.
1931 Laccopteris angustiloba (Presl) Raciborski—Harris, p. 74, pl. 14, figs. 6–17, text-fig. 26.
1936 Phlebopteris angustiloba (Presl)—Hirmer and Hörhammer, p. 26, pl. 6, text-fig. 5, 3.
1950 Phlebopteris angustiloba (Presl) Hirmer et Hörhammer—Lundblad, p. 23, pl. 2, fig. 14, pl. 3, figs. 1–6, pl. 13, fig. 2, text-fig. 4.
1968 Phlebopteris angustiloba (Presl) Hirmer et Hörhammer—Weber, p. 48, pl. 7, fig. 65.

Description: A few specimens assignable to Phlebopteris angustiloba have been found in Wüstenwelsberg. All of them appear to be fertile portions, however, without any preserved sori or sporangia apart from an indication of the receptaculum (Plate IV, 5). Most fragments of primary segments are 3–4.5 cm long (66wü02, 18wü04, 05wü04, Q181/02; Plate IV, 4–6), with a distinct but thin rachis (<500 µm wide) and up to 18 secondary segments (“pinnules”) preserved. Pinnules are attached at angles of 70°–90° to the rachis and are densely spaced (Plate IV, 4–6). None of the pinnules is complete and the largest reaches up to 4.5 mm in length by 2 mm in width (Plate IV, 4). Pinnules are tapering towards the [designated] apex, but apices are not preserved in any pinnule. The distinct pinnule central vein is thin and gives rise to several lateral veins at intervals of approximately 1 mm, thus producing a mesh consisting of hexagonal to roundish depressions (Plate IV, 5). These depressions represent the areas where sori were attached but details of sori or sporangia are not preserved; solely, an indication of the annuli is ascertainable but too poorly preserved to be illustrated.

Remarks: The material from Wüstenwelsberg assignable to Phlebopteris angustiloba is only fragmentary, but there is no doubt that specimens represent this species because of the typical mattress-like appearance of the pinnules, a feature that has not been recorded from any other species in Phlebopteris. All specimens from Wüstenwelsberg represent fertile frond portions, which is the case for many of the records worldwide (see e.g., Tralau, 1965), but sterile specimens occur occasionally in, e.g., Jameson Land (Harris, 1931) and Hungary (Barbacka et al., 2019). The secondary veins are often obscured, and sporangia are rarely preserved, thus in situ spores are known from a few specimens only (e.g., Harris, 1931; Van Konijnenburg-van Cittert, 1993). Spores of Phlebopteris angustiloba have further been described by Lundblad (1950) and Tralau (1965). All those descriptions have been based on light microscopy only; there has never been enough material preserved to study the spores under SEM and TEM.

Phlebopteris angustiloba is a very typical Rhätian–Hettangian fern, predominantly distributed in the Liassic of Europe, such as in Greenland (Jameson Land, Harris, 1931), Sweden (Lundblad, 1950; Tralau, 1965), Denmark (Möller, 1902), Poland (Pacyna, 2013, 2014), Germany (Bayaria; Gothan, 1914; Weber, 1968), Hungary (Barbacka et al., 2010, 2019) and Romania (Popa, 1997). Outside Europe, it has been recorded from, e.g., the Triassic floras of Mexico (Weber, 1997, 2008).

Material examined: Q181/02; 66wü02, 05wü04 + 18wü04, 91wü08, 159wü08; UU23272, 23825, 23923, 23924.

Phlebopteris muensteri (Schenk, 1865–1867) Hirmer et Hörhammer, 1936

Plate V, 1–6
Selected synonymy and references:
1867 Laccopteris muensteri—Schenk, p. 97, pl. 24, figs. 6–10, pl. 25, figs. 1, 2.
1914 Laccopteris sp.—Gothan, p. 98, pl. 18, fig. 3, 3a, pl. 39, fig. 5, 5a, text-fig. 1.
1931 Laccopteris braunii Göppert—Harris, p. 70, pl. 14, figs. 1, 2, text-figs. 24, 25.
1936 Phlebopteris muensteri (Schenk)—Hirmer et Hörhammer, p. 17, pls. 3, 4, figs. 1–6, pl. 5, text-fig. 5, 2A and 2B.
1968  *Phlebopteris muensteri* (Schenk) Hirmer et Hörhammer—Weber, p. 48, pl. 7, figs. 59–63.

**Description:** *Phlebopteris muensteri* is a relatively common species in the Wüstenwelsberg flora with more than 100 collected specimens. These comprise sterile and fertile specimens, varying from pinnule fragments to fairly complete fronds representing recognizable portions of the general architecture with a stipe branching into two axes (rachial arms) that themselves branch sympodially and catadromously, bearing few to many primary segments monopodial (e.g., 64wü03 and 66 wü03 (part and counterpart; Plate V, 1), 37wü08, 03wü13, Q334/03 (Plate V, 4)). The two largest frond fragments (64 and 66wü03 (Plate V, 1), Q334/03 (Plate V, 4) yield the basal portions of at least 10 primary segments. The stipe is ca. 1 mm wide; the largest primary-segment fragment in Q334/03 is 62 mm in length (Plate V, 4). The secondary segments ("pinnules") are densely arranged, attached at angles of 85°–90°, and commonly positioned sub-oppositely, with a few exceptions. The basalmost secondary segments are 3 × 2 mm in size, but their size rapidly increases and the largest are 11 mm long and 3 mm wide. Other primary-segment fragments are obviously from more distal segment portions as they yield much longer secondary segments that reach

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**Plate V.** Macroremains of Matoniaceae from the Rhaetian of Wüstenwelsberg with specimen numbers. 1. *Phlebopteris muensteri*, frond fragment showing a number of primary segments, 66wü03. 2. *Phlebopteris muensteri*, fragment with large pinnules, 59wü03. 3. *Phlebopteris muensteri*, fragment showing venation, Q302/03. 4. *Phlebopteris muensteri*, large frond fragment, Q334/03. 5. *Phlebopteris muensteri*, fertile specimen, Q875/11. 6. *Phlebopteris muensteri*, showing soral details, 100wü02. Scale bars 1, 2, 4, 5: 10 mm; 3, 6: 5 mm.
16–30 mm in length. (e.g., 147wü02, 59wü03; Plate V, 2). Adjacent secondary segments are connected through a narrow wing along the rachis; for most of their length, secondary segments keep the same width; solely at the apex, they taper rapidly forming a rounded apex. The venation is often difficult to recognise, but the central vein of the secondary segments is clearly ascertainable, and secondary veins arise at 70°–90° bifurcating at least once (Q302/03, Plate V, 3).

A number of isolated fertile primary-segment fragments have been also found (e.g., Q115/02, Q875/11, Q960/14, Plate V, 5, 6). These resemble the sterile fragments in size and shape. Complete secondary segments are up to 52 mm long (Q960/14), although a length of c. 15 mm is more common (Q875/11). On both sides of the central vein is a row of sori, with receptacula c. 1 mm apart. The sori reach up to 15 mm is more common (Q875/11). On both sides of the central vein width; solely at the apex, they taper rapidly forming a rounded apex. The tinct feature would be unique amongst Phlebopteris species but is usually very common in Thaumatopteris species; therefore, this species might belong to the latter genus instead.

Another species that is similar to Phlebopteris muensteri is Phlebopteris lunensis (Stur ex Krasser) Pott et Bomfleur, 2018 (in Pott et al., 2018), from the Carnian of Lunz (Austria) (Pott et al., 2018). Hirmer and Höhrammer (1936) considered P. lunensis to be conspecific with P. muensteri, but Pott et al. (2018) regarded it to be a separate species based on the possible occurrence of an indumentum on the primary-segment bases and the secondary-segment veins, the wider distances between the secondary segments and the widely separated individual sori. Pott et al. (2018) also briefly described and figured a specimen tentatively assigned to Phlebopteris sp., which resembles specimens of Phlebopteris muensteri, figured by Schweitzer et al. (2009) from Iran (their pl. 4, figs. 1, 2).

Phlebopteris muensteri is known from the Late Triassic to the Early Cretaceous, mainly from Europe, but has also been recorded from, e.g., Iran (Schweitzer et al., 2009). It was described from Carnian sediments on Svalbard as Phlebopteris sp. cf. P. muensteri by Pott (2014), which, if it is P. muensteri, is besides the above-mentioned specimen from Lunz, another pre-Rhaetian record. Apart from Wüstenwelsberg, there is a Rhaetian occurrence from Jameson Land, originally described as Laccopteris groenlandica Harris, 1926 by Harris (1926), but later, Harris (1931) placed it in the synonymy of Laccopteris braunii Göppert, 1841 (a species mainly known from the Hettangian sediments of Jameson Land). Another Rhaetian occurrence is at Röga in southern Sweden (Pott and McLoughlin, 2011). Lundblad (1950) briefly described and figured small primary-segment fragments as Phlebopteris sp. from the Hettangian of Sweden, which might represent P. muensteri. Popa (1997) reported specimens from the Hettangian of Romania as Matonia braunii but did not discuss, why the specimens were attributed to that species rather than to P. muensteri as identification, as the latter might be more logical. Kerp and Bomfleur (2011) figured fertile specimens of P. muensteri reported from the Middle Jurassic of Sardinia. Scano et al. (2016) reported P. muensteri from the Middle Jurassic of Sardinia.

Material examined: Q1/96, 2/96, 7/96, 8/96, 9/96, 12/96, 13/96, 15/96, 36/96, 49/99, 50/99, 92/02, 111/02–115/02, 151/02, 152/02, 204/03, 302/03, 303/03, 334/03, 366/04, 367/04, 394/04, 437/06, 463/06, 464/06, 465/06, 536/08, 568/08, 569/08, 582/08, 654/08, 682/08, 738/09, 875/11, 891/12, 960/14; 07wü02, 08wü02, 10wü02, 36wü02, 53wü02, 66wü02, 70wü02, 79wü02, 81wü02, 90wü02, 97wü02, 100wü02, 117wü02, 147wü02, 177wü02, 183wü02, 186wü02, 02wü03, 11wü03, 20wü03, 33wü03, 47wü03, 49wü03, 59wü03, 63-65wü03, 69wü03, 75wü03, 92wü03, 97wü03, 110wü03, 119wü03, 33wü04, 55wü04, 01wü05, 09wü05, 12wü05, 15wü05, 18wü05, 01wü06, 06wü06, 15wü08, 33wü08, 36wü08, 37wü08, 84wü08, 90wü08, 103wü08, 169wü08, 173wü08, 07wü09, 05wü09, 05wü10, 35wü10, 06wü11, 21wü12, 03wü13, 05wü13, 08wü14; UU23222, 23224, 23225, 23230, 23232, 23266, 23268, 23271, 23273, 23275, 23280, 23281, 23286, 23289, 23315, 23323, 23335, 23347, 23519, 23819.

Family: DIPTERIDACEAE (Diels) Seward et Dale, 1901
Genus: Clathropteris Bronnignt, 1828
Diagnosis and discussion: See Bronnignt (1828), Ōishi and Yamasita (1936), Choo et al. (2016) and Pott et al. (2018).
Type species: Clathropteris meniscioides (Bronnignt) Bronnignt, 1828, from the Hettangian of Scania.

Clathropteris meniscioides (Brongniart) Bronnignt, 1828
Plate VII, 1–4
Selected synonymy and references:
1825 Filicites meniscioides—Bronnignt, p. 200, pls. 11, 12.
1828 Clathropteris meniscioides (Bronnignt)—Bronnignt, p. 62, 194.
1836 Clathropteris meniscioides (Bronnignt)—Göppert, p. 520, 15, fig. 7.
1867 Clathropteris platyphylla (Göppert)—Schenk, p. 81, pl. 16, figs. 2–9, pl. 17.
1914 cf. Clathropteris platyphylla Göppert—Gothen, p. 107.
1936 Clathropteris meniscioides (Bronnignt)—Ōishi and Yamasita, p. 289.
1995 Clathropteris meniscioides (Bronnignt)—Kelber and Hansch, p. 122, figs. 257, 260.
2016 Clathropteris meniscioides (Bronnignt)—Choo et al., sum syn., p. 89, pls. 1–6.
Clathropteris meniscioides (Brongniart) Brongniart—Choo and Escapa, p. 10.

Description: More than 30 specimens Clathropteris meniscioides have so far been collected from the quarry at Wüstenwelsberg. The best-preserved specimen is Q449/06 (Plate VII, 1) with three almost entire, sterile primary segments preserved, arranged in the typical dipteridacean matter converging towards the (not preserved) racinal arm. The primary segments are up to 10 cm long; none of them has its apex preserved. Segment margins are hardly preserved, but are, when preserved, shallowly serrate, with the acute lobes 7–8 mm apart from each other (Plate VII, 3). Teeth are asymmetrical and acutely pointed. The central primary veins are 2 mm wide at the base and decreasing in robustness towards the primary segment apex. The secondary veins are predominantly sub-oppositely arranged, arise at c. 60° at regular intervals of 8–13 mm and project into the lobes of the crenate margin. Anastomosing tertiary and quaternary veins arise in a very regular pattern at angles of 90°, forming commonly rectangular meshes, but polygonal ones occur occasionally (Plate VII, 2). About half of the specimens are fertile, but often the sporangia have fallen off and only the imprints of the sori are visible. In few specimens (e.g., Q156/02; Plate VII, 4), sori remains are visible within the rectangular meshes. They are c. 1.5 mm in diameter and contain probably only a few sporangia. Tight spore masses (diameter up to 500 μm) were recovered from Q156/06 probably representing the contents of a sporangium. On the outside of the spore masses, outlines of individual spores can be seen; these appear to be 50–80 μm in diameter and show a granulate surface (Plate VI, 4, 5).

Remarks: Although some authors (e.g., Seward and Dale, 1901; Herbst, 1992) consider Clathropteris as a subgenus of Dictyophyllum, Choo and Escapa (2018) in their phylogenetic study of the Dipteridaceae, found that Clathropteris always appeared as a highly distinctive monophyletic clade, recognizing that Clathropteris as separate genus is justified.

Clathropteris meniscioides is a very common species in Rhaetian–Early Jurassic localities throughout Europe (see e.g., Gothan, 1914; Johansson, 1922; Harris, 1931; Lundblad, 1950; Janichen and Kahlert, 1996; Pacyna, 2014; Barbacca et al., 2019), Asia (Stanislavski, 1971, 1976; Kimura and Tsjui, 1981; Zhou, 1984; Schweitzer et al., 2009; Zhou et al., 2016), North and South America (Choo et al., 2016; Bodnar et al., 2018) and Antarctica (Bomfleur and Kerp, 2010).

The earliest records are reported from the Ladonian of Thale, Germany (Kustatscher and Van Konijnenburg-van Cittert, 2011, p. 226), but the attribution of those specimens to Clathropteris meniscioides is questionable as only based on “typical venation,” which is not a reliable character here (see Choo et al., 2016; Pott et al., 2018), and segment margins are not preserved. An assignment to C. reticulata is consequently suggested after the re-investigation of the original specimens by Pott et al. (2018). Carnian records are, e.g., from Germany (Frentzen, 1922) and Malaysia (Kon’no, 1972), Clathropteris platyphylla (Göppert) Brongniart, 1849 and C. meniostera Lindley et Hutton, 1834, from the Middle Jurassic of Yorkshire.

More than 20 Clathropteris species have been described in the past, but ambiguous features, incomplete preservation and high morphological variability render the delimitation of many species difficult (Choo et al., 2016). As a result, many species have been merged into one of the two common and broadly defined species, viz. C. meniscioides and C. obovata Ôishi, 1932. Clathropteris obovata is distinguished from C. meniscioides by its typical (and smaller) obovate primary segments with sub-acutely and deeply lobed margins and secondary veins arising at lower angles of c. 45° (Harris, 1961; Schweitzer et al., 2009). Moreover, the primary vein is often much wider in C. meniscioides than in C. obovata (c. 2.0 mm versus 0.5–1.0 mm) (Schweitzer et al., 2009).

Another rather common species is the Ladonian–Carnian Clathropteris reticulata Kurr ex Heer, 1877 (Pott et al., 2018). Clathropteris reticulata is distinguished from C. meniscioides by its symmetrical teeth with evenly rounded to slightly acute tips, while in C. meniscioides teeth are asymmetrical and acutely pointed (Pott et al., 2018). Additionally, venation of C. reticulata appears to produce even more regularly square areoles than C. meniscioides where the areoles are more often polygonal than regularly square (Choo et al., 2016; Pott et al., 2018).

Material examined: Q86/02, 87/02, 94/02, 156/02 + 157/02, 196/02, 211/02, 212/02, 270/02, 279/03, 280/03, 440/06, 449/06, 901/12; 01wü02, 06wü02, 74wü02, 168wü02, 187wü02, 19wü03, 31wü03, 98wü03, 105wü03, 109wü03, 03wü06, 22wü06, 23wü06, 66wü08, 166wü08, 01wü10, 01wü12; UU23288, 23325.

Genus: Dictyophyllum Lindley et Hutton, 1834
Diagnosis and discussion: See Lindley and Hutton (1833-1835), Ôishi and Yasumita (1936), Harris (1961); Pott et al. (2018).

Type species: Dictyophyllum rugosum Lindley et Hutton, 1834, from the Middle Jurassic of Yorkshire.

Dictyophyllum exile (Brauns) Nathorst, 1878
Plate VII, 5–8

Selected synonymy and references:
1862 Canopteris exile—Brauns, p. 54, pl. 13, figs. 11a–c.
1878 Dictyophyllum exile (Brauns)—Nathorst, p. 39, pl. 5, fig. 7.
1922 Dictyophyllum cf. exile (Brauns)—Nathorst—Johansson, p. 8, pl. 1, figs. 1–6, pl. 5, figs. 45–52.
1926 Dictyophyllum exile (Brauns) Nathorst—Harris, p. 64, pl. 1 figs. 1–2, text-fig. 7b.
1931 Dictyophyllum exile (Brauns) Nathorst—Harris, p. 80, pl. 18, figs. 15, 16.
1950 Dictyophyllum exile (Brauns) Nathorst—Lundblad, p. 28, pl. 3 fig. 12.
1995 Dictyophyllum acutilobum—Kelber and Hansch, p. 128, fig. 280.
1997 Dictyophyllum acutilobum—Kelber and Van Konijnenburg-van Cittert, p. 107, pl. 2 fig. 9.

Description: Dictyophyllum exile is one of the most common ferns in the flora. Some 90 specimens have been found so far. Most of them are primary segment fragments, but a few yield primary segments attached to the racinal arm (64wü08, 195wü08, Q615/08; Plate VII, 5) that appear to be connate for less than 1 cm. Both 64wü08 (Plate VII, 7) and 195wü08 have at least six primary segments and especially 195wü08, these are clearly free almost to their base and partly overlap each other. Primary segments are usually 18–28 mm wide in their presumed middle portion (see e.g., Q616/08, 97wü08). Specimen 98wü02 yields an apical primary segment fragment where the width tapers from 20 to 10 mm without the exact apex preserved. The central primary vein is distinct and 1 mm wide. Segment margins are strongly lobed (almost dentate) with sometimes almost falcate lobes. The lobes are predominantly sub-oppositely arranged, with a prominent secondary vein entering from the primary segment that gives off a complex reticulum of tertiary and quaternary veins (Plate VII, 7). The apices of the lobes are rather variable, but are usually acutely rounded (e.g., Q616/08, Plate VII, 6).

Almost all preserved specimens represent sterile frond fragments, but a few show remains of sori or sporangia, viz. 81wü02, 178wü02 (Plate VII, 8), 97wü08, 110wü08, Q437/06 and Q914/13. These show the same morphology as the sterile fragments but with small, ill-defined sori between the tertiary veins, possibly constituting 3–5 sporangia. Groups of in situ sporangia (c. 500 μm in diameter; Plate VI, 6, 7) were retrieved from Q437/06, probably representing the contents of a sporangium. Spores are immature, but some could be separated from the spore masses. These are slightly folded, trilette, smooth and c. 50–60 μm in diameter (Plate VI, 8, 9).

Remarks: In their phylogenetic study on the Dipteridaceae, Choo and Escapa (2018) did not recognize Dictyophyllum as a separate clade, but assigned some Dictyophyllum species (including, e.g., D. exile and
D. nathorstii) to the new genus Sewardalea Choo et Escapa, 2018, that also included many Camptopteris species. The main difference to other fossil genera in the Dipteridaceae lies in the number of primary segments attached to a single rachial arm (12, but up to 100). However, we doubt if this is a feature diagnostic for a genus and prefer to identify the present material as Dictyophyllum exile. The remaining Dictyophyllum spp. were kept by Choo and Escapa (2018) in the unresolved group “Dictyophyllum” together with Kenderlykia (Turutanova-Ketova, 1962).

Many Dictyophyllum species are known from Upper Triassic to Lower Cretaceous sediments from all over the world. The species most similar to D. exile is D. nathorstii Zeiller, 1903, from the Triassic Tonkin flora (Vietnam; Zeiller, 1903). The differences between the two species are minor, and they sometimes occur together in Triassic floras such as

**Plate VI.** In situ spores (Figs. 1–9) and cuticle remains (Figs. 10–13) from the Rhaetian of Wüstenwelsberg with specimen numbers from which they were derived. 1. Todites roesserti, spore cluster, Q501/04. 2 and 3. Todites roesserti, single spore in different focus, Q501/04. 4. Clathropteris meniscioides, spore cluster, Q156/02. 5. Clathropteris meniscioides, detail of another spore cluster showing spore ornamentation, Q156/02. 6. Dictyophyllum exile, spore cluster, Q437/06. 7. Detail from Fig. 6. 8. Dictyophyllum exile, two spores, Q437/06. 9. Dictyophyllum exile, one spore, Q437/06. 10. Cladophlebis sp., lower cuticle with stomata indicated by arrows, Q783/06. 11. Cladophlebis sp., upper cuticle, Q783/06. 12. Cladophlebis sp., lower cuticle with numerous trichome bases (arrows), Q783/06. 13. Cladophlebis sp., single stoma, Q783/06. 14. Cladophlebis sp., part of lower cuticle with slightly sinuous epidermal cells, Q783/06. Scale bars 1–4, 10–12, 14: 20 μm, 5–9, 13: 50 μm.
in Iran (Schweitzer et al., 2009) and China (Zhou et al., 2016). The lobes of the primary segments of \textit{D. exile} are more densely arranged than in \textit{D. nathorstii} and have more acute apices. The species are best distinguished by the extent in which neighbouring primary segments are basally connate. This is up to 1 cm or even less in \textit{D. exile}, while in \textit{D. nathorstii}, the area of adnation can be up to 4 cm long.

The primary segments in the specimens from Wüstenwelsberg are always basally connate to a maximum length of 1 cm, hence we attribute this material to \textit{D. exile}. Webb (1982) mentioned that sori in \textit{D. exile} are round, arranged very crowded over the whole lower surface and c. 0.5 mm in diameter, while those of \textit{D. nathorstii} are more variable in outline, less densely scattered on the lower surface but more concentrated near the veins, and smaller, only up to 0.2 mm in diameter.

\textit{Dictyophyllum exile} was first described from the Upper Triassic of Seinstedt (Germany; Brauns, 1862; Barth et al., 2014). It was also recorded from some other localities in Germany, such as Mecklenburg (Jänichen and Kahlert, 1996). Kelber and Hansch (1995) and Kelber and Van Konijnenburg-van Cittert (1997) described Dictyophyllum...
Dictyophyllum exile was also reported from the Upper Triassic (Carnian) of Svalbard (Pott, 2014), and the Hettangian–Pliensbachian but not the Rhaetian of Poland (Pacyna, 2013, 2014). Stanislavski, 1976 described a primary segment fragment from the Upper Triassic of the Donets Basin as Dictyophyllum sp. 1, which resembles D. exile. Dictyophyllum exile has been described from a couple of Russian localities (Dobruskina, 1994) and from Iran (Schweitzer et al., 2009) and China (Zhou et al., 2016).

Material examined: Q90/02, 110/02, 131/02, 154/02, 163/02, 250/02, 258/03, 257/03, 357/03, 379/04, 415/05, 423/05, 437/06, 489/07, 570/08, 574/08, 615/08, 616/08, 676/08, 806/11, 809/12, 914/13, 1051/14, 05wu02, 19wu02, 39wu02, 49wu02, 64wu02, 67wu02, 76wu02, 81wu02, 88 + 89wu02, 98wu02, 106wu02, 113wu02, 143wu02, 164wu02, 165wu02, 171wu02, 176wu02, 178wu02, 179wu02, 180wu02, 13wu03, 18wu03, 24wu03, 25wu03, 34wu03, 56wu03, 67wu03, 68wu03, 72wu03, 72-74wu03, 94wu03, 101wu03, 04wu04, 26wu04, 30wu04, 41wu04, 42wu04, 05wu06, 23wu06, 01wu08, 32wu08, 64wu08, 69wu08, 78wu08, 96wu08, 97wu08, 99wu08, 110wu08, 135wu08, 146wu08, 169wu08, 195wu08, UU23264, 23265, 23266, 23287, 23319, 23336, 23817, 23828.

Genus: Thaumatopteris Popp, 1863
Diagnosis and discussion: See Popp (1863), Schenk (1865–1867), Nathorst (1907), Schweitzer (1978), Pott et al. (2018) and Zijlstra and Van Konijnenburg-van Cittert (2019).

Type species: Thaumatopteris brauniana Popp, 1863 nom. cons., Zijlstra and Van Konijnenburg-van Cittert, 2019, from the Hettangian of the Bayreuth area (Germany).

Plate VIII. Macroremains of Dipteridaceae and incertae sedis from the Rhaetian of Wüstenwelsberg with specimen numbers. 1. Thaumatopteris brauniana, long secondary segments showing venation, Q428/06. 2. Thaumatopteris brauniana, venation, 02wu04. 3. Thaumatopteris brauniana, fertile specimen, Q230/02. 4. Spiropteris sp., Q426/05. Scale bars 1, 3: 10 mm; 2, 4: 5 mm.

acutilobum from Heilgersdorf, which is readily identified as D. exile. Extensive material is reported from the Rhaetian of Scania, (Nathorst, 1878; Johansson, 1922; Lundblad, 1950; Pott and McLoughlin, 2011) and Jameson Land (Harris, 1926, 1931). Dictyophyllum exile was also reported from the Upper Triassic (Carnian) of Svalbard (Pott, 2014), and the Hettangian–Plänsbachian but not the Rhaetian of Poland (Pacyna, 2013, 2014). Stanislavski, 1976 described a primary segment fragment from the Upper Triassic of the Donets Basin as Dictyophyllum sp. 1, which resembles D. exile. Dictyophyllum exile has been described from a couple of Russian localities (Dobruskina, 1994) and from Iran (Schweitzer et al., 2009) and China (Zhou et al., 2016).

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1914 Thaumatopteris schenkii Nathorst—Gothen, p. 16, pl. 19, fig. 3, 3a.
1926 Thaumatopteris brauniana Popp—Harris, text-fig. 7c.
1931 Thaumatopteris schenkii Nathorst—Harris, p. 93, pl. 17, figs. 6–8, figs. 1, 2, text-fig. 35.
1931 Thaumatopteris brauniana Popp—Harris, p. 94, pl. 17, fig. 5, pl. 18, figs. 4–6, text-fig. 36.
1950 Thaumatopteris brauniana Popp—Lundblad, p. 27, pl. 4, figs. 10, 11, pl. 4, fig. 1.
1950 Thaumatopteris schenkii Nathorst—Lundblad, p. 28, pl. 3, figs. 1, 2.
1964 Thaumatopteris bipinnata Kilpper—Kilpper, p. 34, pl. 5, figs. 8, 9.
1968 Thaumatopteris bipinnata Kilpper—Weber, p. 49, pl. 8, fig. 74.
1968 Thaumatopteris schenkii Nathorst—Weber, p. 49.
1968 Thaumatopteris brauniana Popp—Weber, p. 49.
2019 Thaumatopteris brauniana Popp—Barbacka et al., figs. 7c–e, 8a.

Description: Thaumatopteris brauniana is the third representative of the Dictyophyllaceae in the Wüstenwelsberg flora with 16 specimens found so far. These are only small primary segment fragments up to 5.2 cm long (Q230/02) or detached fragments. The central primary vein is 1.5–2.5 mm wide and longitudinally striate (Plate VIII, 3). Lobes (or secondary segments) are attached at angles of 80°–90° and are almost free up to the base with a narrow wing along the central vein (“rachis”) connecting neighboring secondary segments. The secondary segments are inserted oppositely to sub-oppositely (Q230/02; Plate VIII, 3) and, although, none is complete, they probably reached a considerable length of at least 4.1 cm (Q428/06; Plate VIII, 1); secondary segments taper in width from basally 11 mm to 4 mm distally. The secondary-segment margin is basally almost straight while it is strongly lobed distally (Plate VIII, 1); no apex was preserved. The secondary segment’s central vein (secondary veins) is conspicuous but the tertiary (and quaternary) veins are commonly indistinct (Plate VIII, 1). When visible (Q428/06; Plate VIII, 2), they form a network of irregular, often elongate, hexagonal meshes. All specimens represent sterile fragments, except for one (Q230/02) that appears fertile, but no details of sori, sporangia or spores are visible, only some imprints of possible sporangia could be observed.

Remarks: Thaumatopteris was published by Göppert (1841–1846) with T. muensteri as the only and consequently type species. However, Thaumatopteris muensteri has been allocated to Dictyophyllum (Nathorst, 1876; Harris, 1931), thus rendering Thaumatopteris illegitimate. The genus was, however, continuously in use and new species were added (e.g., Harris, 1931; Lundblad, 1950; Weber, 1968), while others used one specific name for particular material (e.g., Gothan, 1914 used T. schenkii, while Popa et al., 2003 used T. brauniana). Next to T. schenkii, Kilpper (1964) described Thaumatopteris bipinnata Kilpper, 1964 from the Hettangian of Iran differing only in the fact that a few secondary segments were so deeply lobed in their apical part that they were almost bipinnate. However, nowadays, most authors (e.g., Schweitzer et al., 2009, and references therein) consider the three species conspecific and use the name T. brauniana that deserves priority, as we also do with the specimens from Wüstenwelsberg. Stanislavski (1976, pl. 3, text-fig. 6) reported T. variabilis Stanislavski (1976), from the Upper Triassic of the Donets Basin, which shows all three secondary-segment shapes in one frond), comparing it with T. brauniana, T. schenkii and T. bipinnata, and with a few of Oishi’s (1932) Rhetaian species such as T. elongata Oishi, 1932 (with relatively long secondary segments) and T. nipponica Oishi, 1932 (with relatively short secondary segments). In our opinion, it is very likely that all these species fall within the natural variability of one species, viz. T. brauniana.

Material examined: Q191/02, 197/02, 198/02, 230/02, 265/03, 378/04, 427/06, 428/06, 571/08; 123wu02, 137wu03, 02wu0, 24wu06, 141wu08, 143wu08, 162wu08.

Genus: Spiropteris Schimper, 1869
Spiropteris sp.
Plate VIII, 4

Description: Some specimens yield curled fern fronds that have been embedded before they were fully developed. Commonly, such fossils are assigned to the form genus Spiropteris. The specimens from Wüstenwelsberg are relatively small with a diameter of c. 10 mm (e.g., Q426/05, Plate VIII, 4).

Remarks: Circinate vernation is typical for most if not all fern fronds. At this stage of development of the fern frond, it is impossible to say, which fern species a leaf belongs to if found isolated. This applies especially to fossil fronds and therefore, these fronds are commonly assigned to the fossil-genus Spiropteris. Consequently, it is impossible to assign these specimens to any species. Therefore, we keep the specimens unassigned as Spiropteris sp.

Material examined: Q315/03, 426/05; 21wu05, 178wu08.

4. Discussion
4.1. Composition of the flora

The Rhetaian flora from Wüstenwelsberg is currently under detailed study by the authors (see Van Konijnenburg-van Cittert et al., 2018b, lunuensis by Pott et al., 2018] and extended up to the Hettangian with its heyday in the latter period (e.g., the indexed Thaumatopteris zone in Jameson Land; Harris, 1931, 1937). Other Hettangian occurrences include Poland (Pacyna, 2013), Hungary (Barbacka et al., 2019), Romania (Popa et al., 2003) and Iran (Kilpper, 1964; Schweitzer, 1978). Although in Germany, the abundance of Thaumatopteris is much higher in the Hettangian (Schenk, 1865–1867; Gothan, 1914; Weber, 1968), the species occurs, as documented here, also in the Rhetaian.

Nathorst (1878) described Thaumatopteris schenkii Nathorst, 1878, from the Hettangian flora of Scania. The species resembled T. brauniana closely, differing only in the almost straight to slightly sinuous secondary segment margin in T. brauniana and the more lobed margin in T. schenkii. Nathorst (1907) included part of the Bavarian material described by Schenk (1865–1867) as T. brauniana in T. schenkii. Schenk (1867, pl. 18, fig. 1) figured both secondary-segment types in the discussion of T. brauniana, stating that the secondary-segment margin is entire near the primary-segment rachis and more lobed near the apex. Schenk (1865–1867) was of the opinion that these morphologies belonged to the natural variability of one species. After Nathorst’s work, several scholars distinguished between both species, thereby agreeing with Nathorst (1907), even from the same localities (e.g., Harris, 1931; Lundblad, 1950; Weber, 1968), while others used one specific name for particular material (e.g., Gothan, 1914 used T. schenkii, while Popa et al., 2003 used T. brauniana). Therefore, we keep the species T. brauniana that deserves priority, as we also do with the specimens from Wüstenwelsberg. Stanislavski (1976, pl. 3, text-fig. 6) reported T. variabilis Stanislavski (1976), from the Upper Triassic of the Donets Basin, which shows all three secondary-segment shapes in one frond), comparing it with T. brauniana, T. schenkii and T. bipinnata, and with a few of Oishi’s (1932) Rhetaian species such as T. elongata Oishi, 1932 (with relatively long secondary segments) and T. nipponica Oishi, 1932 (with relatively short secondary segments). In our opinion, it is very likely that all these species fall within the natural variability of one species, viz. T. brauniana.

Material examined: Q191/02, 197/02, 198/02, 230/02, 265/03, 378/04, 427/06, 428/06, 571/08; 123wu02, 137wu03, 02wu0, 24wu06, 141wu08, 143wu08, 162wu08.

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Material examined: Q315/03, 426/05; 21wu05, 178wu08.

4. Discussion
4.1. Composition of the flora

The Rhetaian flora from Wüstenwelsberg is currently under detailed study by the authors (see Van Konijnenburg-van Cittert et al., 2018b,
and references therein). Here, we discuss the ferns and fern allies (sphenophytes and lycophytes) of this assemblage. Especially the ferns also constitute an abundant portion of the flora, just as the seed ferns, the cycads and the Bennettitales (Pott et al., 2016; Van Koninjenburg-van Cittert et al., 2018a, 2018b). As the entire composition of the flora is not yet entirely known, we can only compare the fern portion of the flora with that of contemporary and adjacent floras of the Northern Hemisphere.

Lycophytes are rare; two species of two different orders, Isoetales and Selaginellales, have been recorded. One specimen of the isoeulatean Lepacyclotes sp. has been found, a genus that is commonly recorded from Upper Triassic–Lower Jurassic outcrops in the Germanic Basin, but records form the Rhaetian were unknown until to date. The spikemoss Selaginellites coburgensis is quite well known from Wüstenwelsberg (Van Koninjenburg-van Cittert et al., 2014, 2016); both sterile and fertile material with in situ spores has been described in detail previously. Equisettes laevis is the only horsetail recorded so far from the assemblage.

Ferns are represented by three families. The Osmundaceae are rare with three species of Cladophlebus/Todites, all of which occur only with small fragments in low numbers. Matoniaceae occur in much higher numbers of fossil remains and thus were more common; two species of Phlebopteris have been identified, of which especially P. muensteri is very abundant and reflected by the presence of more or less complete fronds. Dpteridaceae also represent a large portion among the cryptogams from Wüstenwelsberg, especially in terms of abundance of specimens. Three species have been identified, one each of the genera Clathropteris, Dictyophyllum and Thaumatopteris. Thaumatopteris is the least common, while Clathropteris and Dictyophyllum are abundant. It is interesting to note that no marattialean species has so far been recorded from the flora, while representatives of these families have been recorded from other Rhaetian–Hettangian floras (see below).

4.2. Comparisons

4.2.1. Comparison with other Rhaetian floras

Comparison of the ferns found at Wüstenwelsberg with those of the Rhaetian floras of Jameson Land, Scania, Franconia and, to a lesser degree, southern Poland have several of the mentioned key Rhaetian taxa in common (Table 1). Floras further to the east such as those from the Donets Basin and Alborz in Iran share less taxa with the central European Rhaetian floras (Table 1), although the Alborz floras have 5 (or possibly 6) taxa in common with the Rhaetian flora from Franconia (Schweitzer et al., 1997, 2009). The flora from the Donets Basin (Stanislavski, 1971) shares only one species with all the other floras, viz. Clathropteris meniscioides. The Rhaetian–Hettangian flora from the Cheljabinsk Basin (eastern Ural) does not even have one species in common with the Wüstenwelsberg flora (Kryštofová and Prinada, 1933).

Clathropteris meniscioides is the only species that apparently occurred in all Rhaetian floras. Most other species occur in at least three or four floras, viz. Equisettes laevis, Todites roessertii, Phlebopteris muensteri, P. angustiloba, Dictyophyllum exile and Thaumatopteris brauniana (Table 1). Solely, Todites (Cladophlebus) scoresbyensis has been recorded from Franconia, Jameson Land and Scania only. Consequently, the fern flora of Wüstenwelsberg lacks any species with remarkable features, except for piina fragments assigned to Cladophlebus sp. that yield small fragments of cuticle that are described here, a feature that is very rare in ferns.

4.2.2. Comparison with the Hettangian flora of Franconia

The Rhaetian flora from Wüstenwelsberg shows some differences with the Hettangian flora from adjacent areas in Franconia (see Van Koninjenburg-van Cittert et al., 2014, 2018b; Pott et al., 2016, and references therein). All major plant groups are present, but the species and even genera within the two floras vary considerably; for details on other groups than the ferns and fern allies, see Pott et al. (2016) and Van Koninjenburg-van Cittert et al. (2018b). In the Hettangian flora of Franconia, a Lepacyclotes species occurs as well, viz. L. kirchneri, although it is rare and only known from one locality (Bauer et al., 2015) while spikemosses (Selaginellales) have not been recorded so far in the Hettangian flora of Franconia. The number of equisetalean genera and species is higher in the Hettangian flora; not only is there a different Equisettes species: E. muensteri instead of E. laevis in the Rhaetian flora. Representatives of two additional genera occur in the Hettangian flora, viz. Neocalamites lehmannianus (Göppert, 1841-1846) Weber, 1968, and Schizoneura carcinoides (Harris) Weber, 1968 (Weber, 1968). Ferns are also more abundant and more diverse in the Hettangian than in the Rhaetian flora of Franconia (see e.g., Schenk, 1865–1867; Gothan, 1914; Weber, 1968). Representatives of several

| Rhaetian taxa            | Jameson Land | Franconia | Scania    | S. Poland | Donets Basin | Alborz       |
|--------------------------|--------------|-----------|-----------|-----------|--------------|--------------|
| Equisettes laevis        | X            | X         | X         | X         |              |              |
| Todites goeppertianus    | X            | ?Cladophlebus sp. | X |       | X            | ?Todites williamsoni |
| Todites roessertii       | ?X           | X         | ?X        | X         |              |              |
| Todites scoresbyensis    | X            | Cladophlebus scoresbyensis | X |       | X            | ?            |
| Phlebopteris muensteri   | X            | X         | X         | X         |              | X            |
| Phlebopteris angustiloba | X            | X         | X         | X         |              | X            |
| Clathropteris meniscioides| X          | X         | X         | X         |              | X            |
| Dictyophyllum exile      | X            | X         | X         | X         |              | X            |
| Thaumatopteris brauniana | X            | X         | X         | X         |              | X            |

Sources for the taxa: Harris (1937); This study; Pott and McLaughlin (2011), Pacyna (2014), Barbacka et al. (2014a, 2014b), Stanislavski (1971), Schweitzer et al. (1997, 2009).
families, not yet present in the Rhaetian, occur in the Hettangian flora, such as the mastarellian *Marattia intermedia* (Münster) Kilpper, 1964, and the schizaeacean *Phialopteris heterophylla* (Sternberg ex Göppert) Van Konijnenburg-van Cittert et al., 2018a. The fern family already present in the Rhaetian flora of Wüstenwelsberg have different and/or more species in the Hettangian flora. While the osmundaceous *Todites* roesertii still occurs in the Hettangian, *Todites princeps* (Presl in Sternberg) Gothan, 1914 is the more abundant species in the latter flora. The two matoniaciate families from Wüstenwelsberg, *Phlebopteris muenstери* and *P. angustiloba*, occur in the Hettangian flora as well, but with *Selenocarpus muelleri* (Presl in Sternberg) Schenk, 1866, there is an additional but rare Hettangian species. This species was long thought to be endemic to Franconia (Harris', 1961 record from Yorkshire was a misidentification), but Czeir (1999) described the species from the Liassic of Romania and this was confirmed by Popa and Van Konijnenburg-van Cittert (2006). In contrast to its very abundant occurrence in the Rhaetian flora, the dipteraceaeous *Clathropteris meniscioides* is comparatively rare in Hettangian floras, but *Thaumatopteris brauniana*, in turn, is again more common in the Hettangian than in the Rhaetian. *Dictyophyllum exle* is not known from the Hettangian of Franconia at all, whereas a different species, viz. *Dictyophyllum nissenii* (Brongniart) Göppert, 1841–1846, is quite abundant then. Another dipteraceaeous species, the bipinnate *Goepertella microloba* (Schenk, 1866) Ōishi et Yamasita, 1936, has been found in Hettangian sediments only, albeit being uncommon.

The fern and fern ally genera found in the Wüstenwelsberg flora are all common genera found throughout most of the Mesozoic. *Equisetites* and *Cladophlebis/Todites* have been recorded from all over the world with large numbers of species (Tidwell and Ash, 1994; Collinson, 1996; Skog, 2001; Kustatscher et al., 2018). *Phlebopteris* has been known from the Late Triassic onwards and became widespread during the Jurassic but has only a few Cretaceous representatives (Van Konijnenburg-van Cittert, 1993; Tidwell and Ash, 1994; Collinson, 1996). It was especially widely distributed in the Northern Hemisphere but taxa from, e.g., South America and Australia are known as well (Tidwell and Ash, 1994). From the Late Jurassic onwards, *Phlebopteris* tends to disappear from the northern regions, and to date the family only occurs in the Malesian Archipelago. The same applies for the representatives of the Dicteridaceae in the Wüstenwelsberg flora. All three genera have their first occurrences in the Middle Triassic to early Late Triassic. *Thaumatopteris* is mainly known from Late Triassic–Early Jurassic localities, while *Clathropteris* and *Dictyophyllum* are well-known in the Middle Jurassic but decline during the Late Jurassic and only one species of *Dictyophyllum* is still known from the Wealden (Skog, 2001).

For Jameson Land, Harris (1931) established the *Lepidopteris* zone for the Rhaetian beds (with *Lepidopteris ottonis* as index fossil) and the *Thaumatopteris* zone for the Hettangian beds (with *Thaumatopteris brauniana* and *Phlebopteris angustiloba* as index fossils). Although these zones have been in general use since then, *Thaumatopteris brauniana* and *Phlebopteris angustiloba* occur in Rhaetian sediments as well, albeit in much lower numbers than in Hettangian floras (Table 1; see e.g., Lundblad, 1959; Pacyna, 2014). The characterization of these zones thus should be only used carefully nowadays.

### 4.3. Paleoecolgical and paleogeographical implications

Climate conditions during the Rhaetian in Europe are generally re-constructed as hot and arid (Preto et al., 2010), but more humid conditions may have prevailed locally and for short periods of time (Bonis et al., 2010). In Wüstenwelsberg, this hypothesis is supported in the palynomorphs by a spike in horsetail, lycophyte and fern spores, and remains of aquatic algae (e.g., representatives of the genera *Borycococcus*, *Cymatosphaera* and *Tasmanites*) in some of the layers (Bonis et al., 2010), indicating that bodies of stagnant or slowly running water existed in the Wüstenwelsberg area during the latest Rhaetian (Van Konijnenburg-van Cittert et al., 2014, 2016, 2018b).

The diverse and abundant flora, rich in hygrophytic elements, which in many cases are dependent on the presence of water for their reproduction cycles, supports this. *Selaginellites coburgiensis*, a small and delicate lycophyte, would have grown near water bodies in the more humid understorey, just as the sphenophyte *Equisetites laevis* and possibly the lycophyte *Lepacyclotes* sp.; the latter might also have grown on more open and disturbed habitats (see e.g., Kustatscher et al., 2010). The osmundaceous ferns *Todites* and *Cladophlebis* could have been small arborescent plants with slender stems (Schenk, 1865–1867; Schweitzer, 1978; Taylor et al., 2009; Barbacka et al., 2019) – similar somewhat to modern tree ferns – preferring warm and humid environments, such as riverbanks, lake shores, fresh-water marshes, or brackish near-coast environments (Harris, 1961; Vakhrameev, 1991; Van Konijnenburg-van Cittert and Van der Burg, 1996; Deng, 2002; Van Konijnenburg-van Cittert, 2002; Wang, 2002; Sun et al., 2010). They could have lived also in slightly more disturbed and wetter environments although these plants probably had high adaptation to moderately disturbed and relatively dry environments (Barbacka, 2011; Bodor and Barbacka, 2012).

The ecology of matoniaciate ferns during the Mesozoic is variable. They are known both as arborescent ferns as with short stems and an extended rhizome system (Schweitzer, 1978), *Phlebopteris angustiloba* and *Phlebopteris muenstери* could have had a similar morphology. They are considered herbaceous plants with large fronds that grew in humid environments under low light conditions (understorey: Schweitzer, 1978; Wang, 2002; Bomfleur and Kerp, 2010). They could have been also pioneer plants that *colonized* disturbed, short-lived, moderately wet areas formed by alluvial deposits (Barbacka et al., 2010, 2019; Barbacka, 2011).

Dipterid ferns occupied during the Mesozoic mainly humid and warm–temperate to subtropical climate zones. They are considered opportunistic plants colonizing disturbed habitats like riverbanks, exposed ridges and clearings (Cantrill, 1995; Van Konijnenburg-van Cittert, 2002; Bomfleur and Kerp, 2010; Pott et al., 2018; Barbacka et al., 2019). Representatives of *Clathropteris, Dictyophyllum* and *Thaumatopteris* are commonly considered herbaceous plants (Schweitzer, 1978; Wang, 2002; Bomfleur and Kerp, 2010). Wang (2002) suggested that *Dictyophyllum* species with large fronds could be dwellers in humid environments under reduced light conditions (understorey). *Thaumatopteris brauniana* has been reconstructed with several metres long, horizontally growing rhizomes (Schweitzer, 1978) based on its resemblance with the modern analog *Dipteris reinwardtii*, 1825. Barbacka (2011) considered this species a plant colonizing highly disturbed and moderately wet habitats, whereas later, Barbacka et al. (2019) assigned it to the wettest and most disturbed habitats. *Clathropteris meniscioides* apparently formed also large monotypic stands in large areas along floodplains in environments, where light and water availability were not limiting factors for growth and thriving (Choo et al., 2016). In Antarctica, the plants were reconstructed as herbaceous members of open vegetation dominated by bennettitaleans that became a dominant element during the colonization phase of disturbed sites after catastrophic volcanic events (Bomfleur and Kerp, 2010).

The fern remais were collected from fossil-rich levels yielding also other abundant plant remains, including seed ferns, bennettitaleans and conifers. Considering that most plant remains co-occur in the same horizons, this suggests that both the xerophytic (such as some seed ferns and conifers) and hygrophytic (such as the ferns and fern allies) forms lived during the same period of time. This would suggest that the plants lived together in the same area and/or environment, but in different microhabitats. This would enforce the hypothesis that this area represented a complex environment with highly disturbed and rapidly changing conditions (Pott et al., 2016; Van Konijnenburg-van Cittert et al., 2018b), such as perhaps due to the rise and fall of the sea level, which also could explain locally very abundant algae in the succession.
5. Conclusions

The ferns remain from the Rhaetian of Wüstenwelsberg, Franconia, southern Germany, show a high diversity: two lycophytes (Lepacyclotes sp. and Selaginellites coburgiensis) and one sphenophyte species (Equisetites laevis) and nine fern species have been identified, all with sterile and fertile fragments. Three fern families represent the ferns. For Osmundaceae, three species (Osmunda sp.) with rare occurrences in the assemblage.

Author declaration

None.

Declaration of Competing Interests

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

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