



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., Gothan, 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), Zavalova 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 coburgensis* Van Konijnenburg-van Cittert et al., 2014, (Selaginellales, see Van Konijnenburg-van Cittert et al., 2014, 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 Bennettitales (Van Konijnenburg-van Cittert et al., 2018b, and references therein). The diverse fern flora includes *Todites roessertii* (Presl) Kryštofovich, 1912, *Cladophlebis scoresbyensis* Harris, 1926, *Cladophlebis* sp. (with a cuticle), *Phlebopteris muensteri* (Schenk) Hirmer and Hörhammer, 1936, *Phlebopteris angustiloba*, *Clathropteris*

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meniscioides (Brongniart) Brongniart, 1828, *Dictyophyllum exile* (Brauns) Nathorst, 1878, *Thaumatopteris brauniana* Popp, 1863 and *Spiropteris* sp.

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 Düttsch (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). The

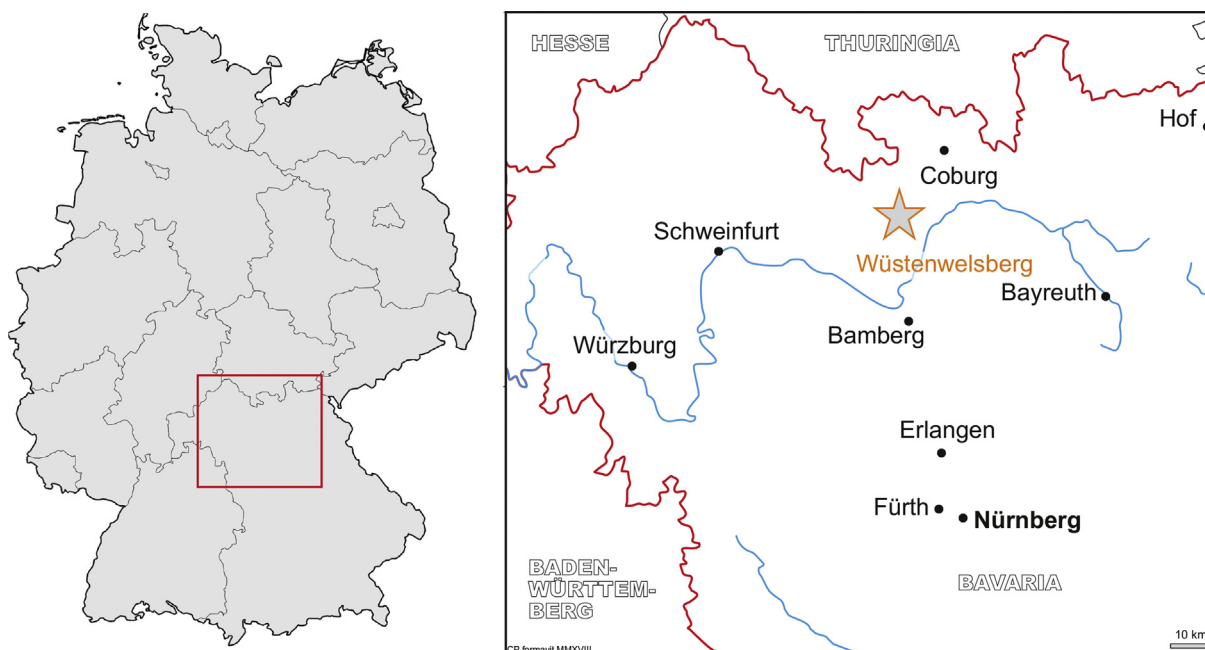


Fig. 1. Map of Germany indicating the position of the locality Wüstenwelsberg in Franconia.

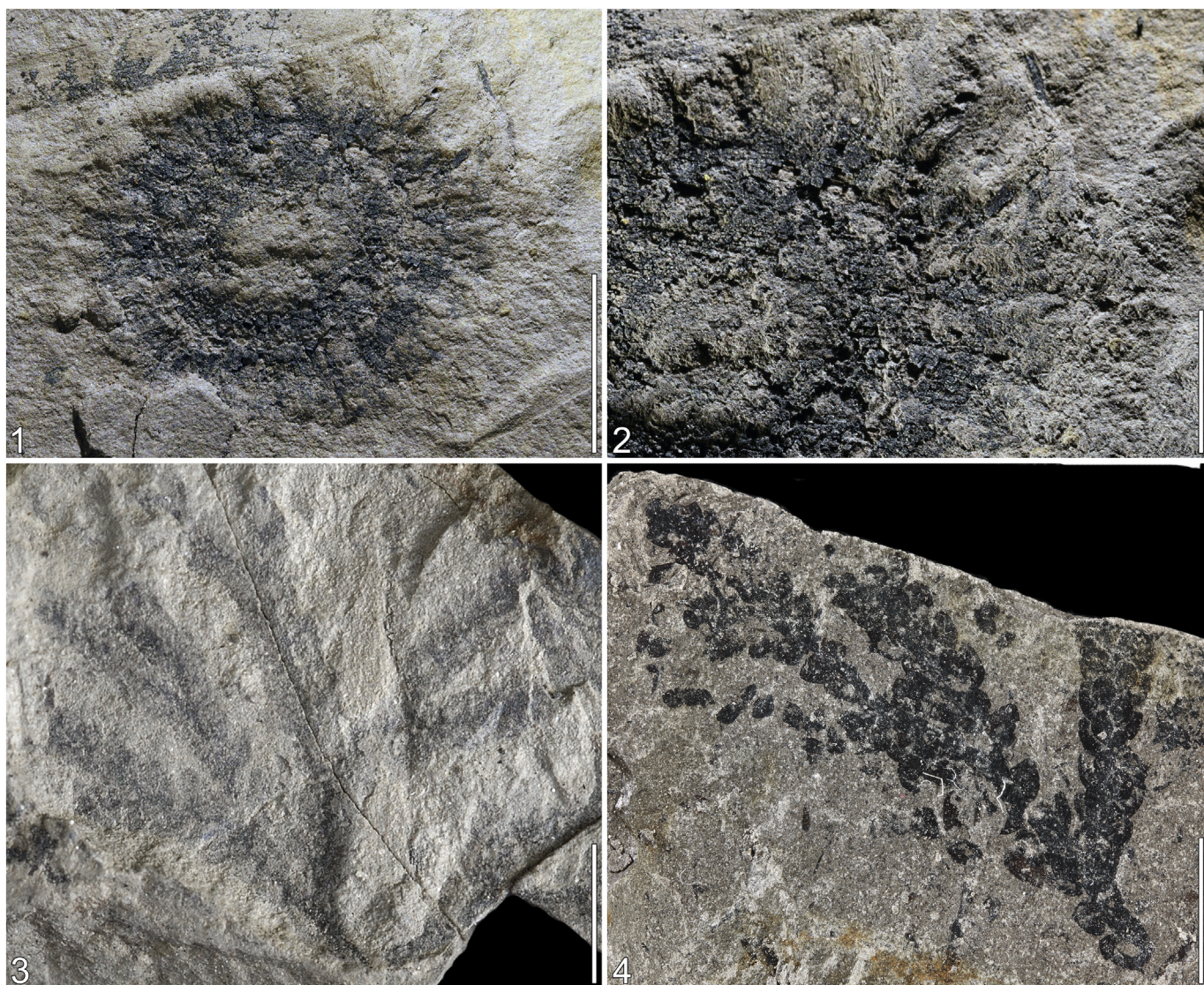


Plate I. Lycophyte macroremains from the Rhaetian of Wüstenwelsberg with specimen numbers. 1. *Lepacyclotes* sp., several superimposed circles of sporophylls, 20wü04. 2. *Lepacyclotes* sp., detail from Fig. 2, 1, showing sporophylls. 3. *Selaginellites coburgensis*, showing pattern of bifurcations, Q121/02. 4. *Selaginellites coburgensis*, showing details of leaf arrangement, Q897/12. Scale bars 1: 10 mm; 2–4: 5 mm.

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 Düringer, 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) (Pott 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 suissei* (Zeiller) Zeiller, 1906 from the Late Carboniferous (Stephanian) of Blanzky, France.

Selaginellites coburgensis Van Konijnenburg-van Cittert et al., 2014, Plate I, 3–4

Selected references:

2014 *Selaginellites coburgensis*—Van Konijnenburg-van Cittert et al., p. 117, Figs. 2, 3.

2016 *Selaginellites coburgensis* Van Konijnenburg-van Cittert et al.—Van Konijnenburg-van Cittert et al., p. 178, figs. 1, 2.

Remarks: *Selaginellites coburgensis* is a small spikemoss that has been described, figured and discussed previously in so much detail that a re-prise is unnecessary, and the reader is referred to Van Konijnenburg-van Cittert et al. (2014, 2016). However, for the complete picture of

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, 21wü11, 29wü11, 15wü14; UU23815 (paratype), 24,089 (holotype), 24,090 (paratype).

3.2. Sphenophyta

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

Family: EUISETACEAE Michaux ex de Candolle, 1804

Genus: *Equisetites* Sternberg, 1833

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

Type species: *Equisetites muensteri* Sternberg, 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—Schweitzer 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 (Q3/96, Q5/96, 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). Nodal 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 Rögla (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 chalubinskii* 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 typical 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 “Liassic” 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; 13wü02, 188wü02, 86wü03, 126wü03, 141wü03, 142wü03, 20wü05, 20wü08, 94wü08, 165wü08, 59wü09; UU23234, 23241, 23243, 23244, 23262, 23290, 23296B, 23307, 23320, 23820.

3.3. Pterophyta

Order: OSMUNDALES Bromhead, 1838

Family: OSMUNDACEAE Berchtold and Presl, 1820

Genus: *Todites* Seward, 1900

Diagnosis and discussion: See Seward (1900), Harris (1961).

Type species: *Todites williamsonii* (Brongniart) Seward, 1900, from the Middle Jurassic (Bajocian) of Yorkshire, UK.

Todites roessertii (Presl in Sternberg) Krystofovich, 1912

Plate III, 1–4

Selected synonymy and references:

- 1838 *Alethopteris roesserti*—Presl in Sternberg, p. 145, pl. 33, figs. 14a, b.
 1867 *Asplenites roesserti* (Presl)—Schenk, p. 49, pl. 7 figs. 6, 7, 7a, pl. 10, figs. 1–4.
 ?1867 *Acrostichites goeppertianus* (Münster) Göppert—Schenk, p. 44, pl. 5, figs. 5, 5a, pl. 7 figs. 2, 2a.
 1873 *Cladophlebis roesserti* (Presl)—Saporta, p. 301, pl. 31 fig. 4.
 1912 *Todites roesserti* (Presl)—Kryshtofovich, p. 492, pl. 15, figs. 4, 4a.
 1914 *Todites roesserti* (Presl) Kryshtofovich—Gothan, p. 9, pl. 17, figs. 9, 9a.
 1919 *Cladophlebis roesserti* (Presl) Saporta—Antevs, p. 18, pl. 2, fig. 1, text-fig. 2.
 1926 *Cladophlebis roesserti* (Schenk non Presl) Saporta—Harris, p. 57, text-fig. 3A–D.
 1931 *Todites goeppertianus* (Münster) Krasser—Harris, p. 31, pl. 11 figs. 3, 8, text-figs. 6, 7.
 1937 *Todites goeppertinus* (Münster) Krasser—Harris, p. 15.
 1950 *Todites goeppertianus* (Münster) Krasser—Lundblad, p. 18, pl. 2, figs. 8–11.
 1968 *Todites roesserti* (Presl) Kryshtofovich—Weber, p. 45, pl. 4, figs. 41, 42.

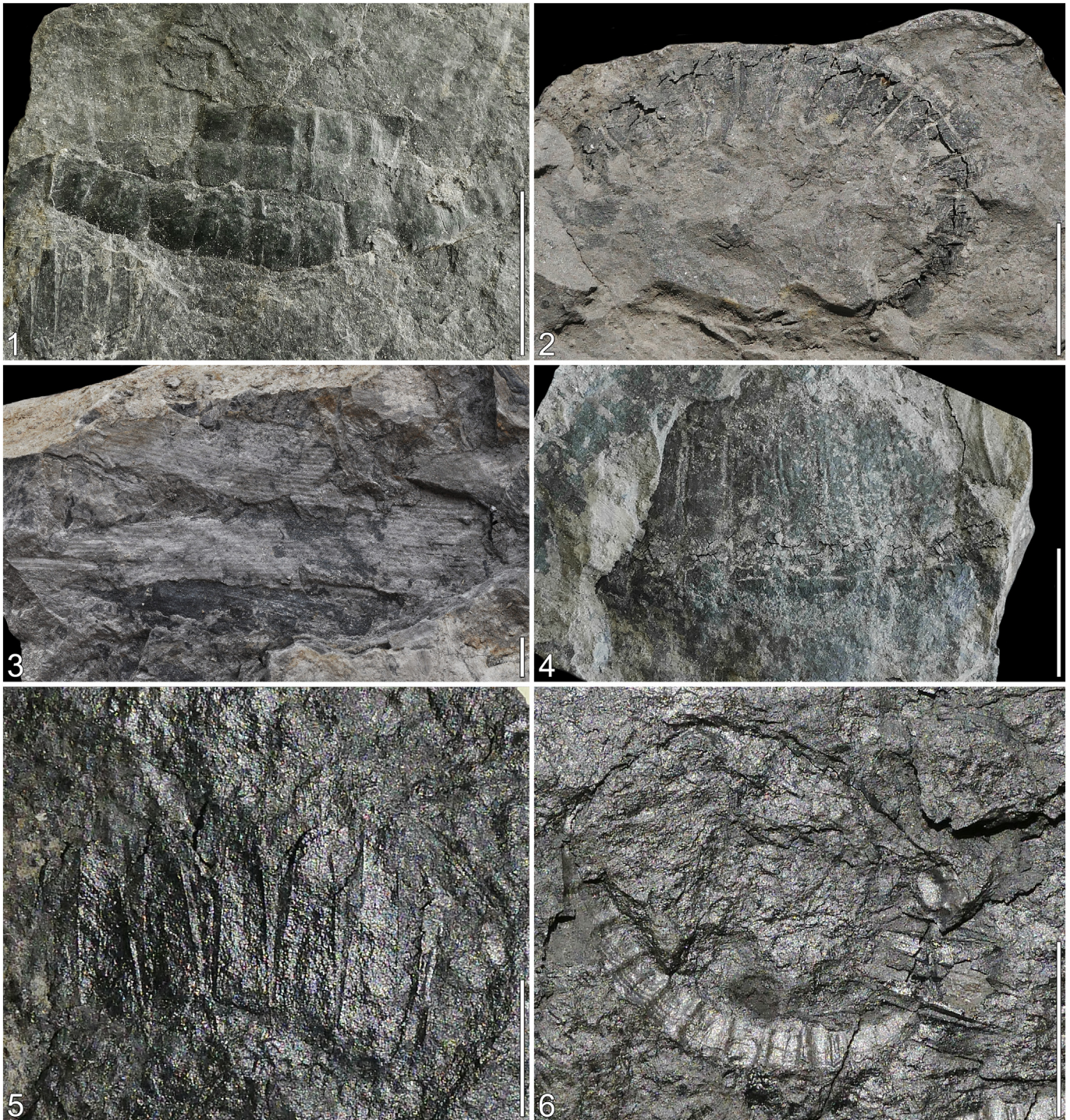


Plate II. Macroremains of Equisetales from the Rhaetian of Wüstenwelsberg with specimen numbers. 1. *Equisetites laevis*, shoot fragment with short internodia, 141wü03. 2. *Equisetites laevis*, nodal diaphragm with leaf remains, Q707/08. 3. *Equisetites laevis*, stem fragment, UU23320. 4. *Equisetites laevis*, stem fragment with node and leaf remains, Q627/08. 5. *Equisetites laevis*, node with attached leaves, Q03/96. 6. *Equisetites laevis*, diaphragm with leaf remains, Q04/96. Scale bars 1–4, 6: 10 mm; 5: 5 mm.

?1968 *Todites williamsonis* (Brغت) Seward fvar. *goepfertiana* (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 pectopterid 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 basicopic secondary veins commonly bifurcate

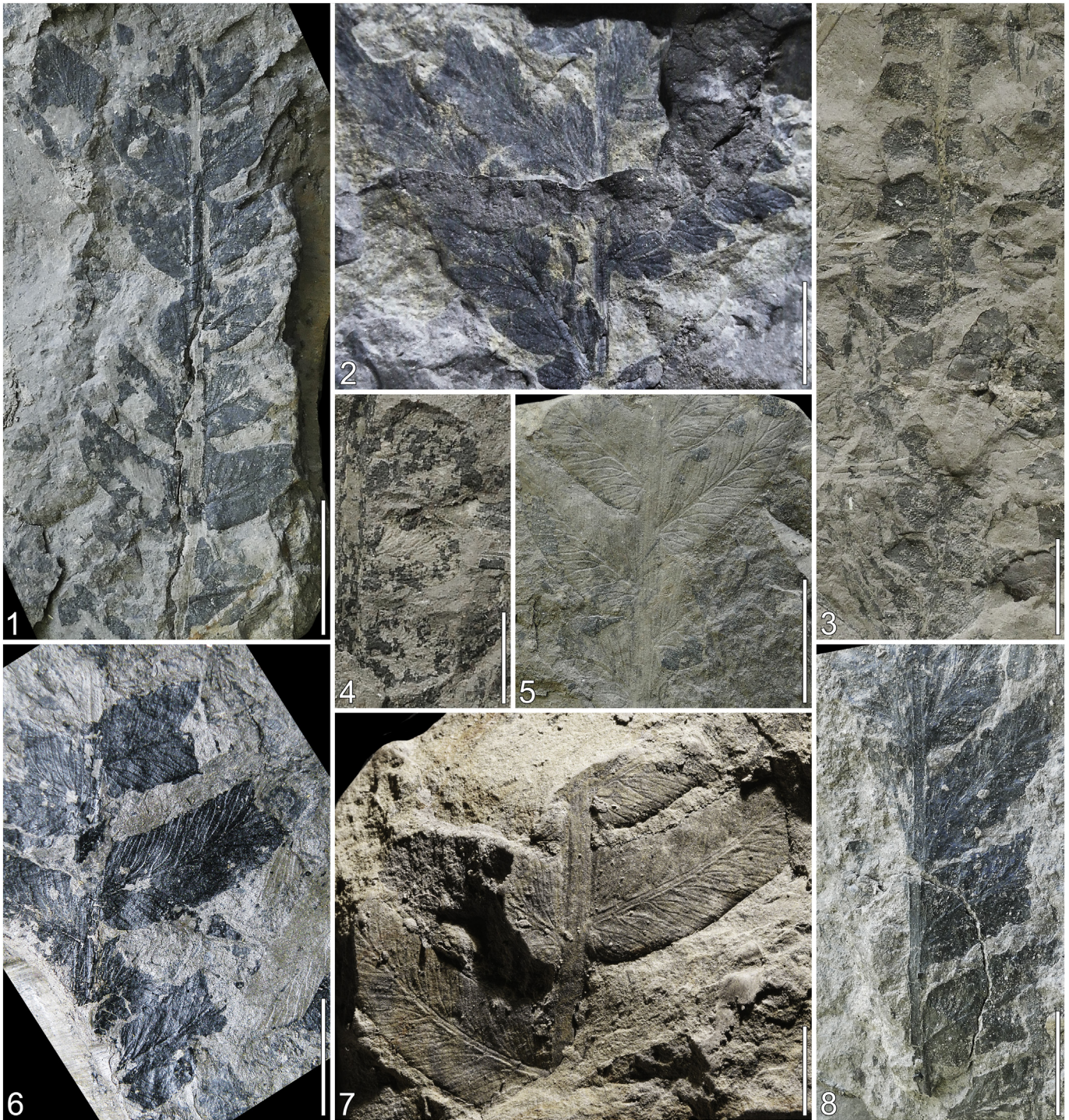


Plate III. Macroremains of Osmundaceae from the Rhaetian of Wüstenwelsberg with specimen numbers. 1. *Todites roessertii*, Q941/13. 2. *Todites roessertii*, 68wü08. 3. *Todites roessertii*, fertile specimen, Q501/07. 4. *Todites roessertii*, fertile specimen showing venation, Q502/07. 5. *Cladophlebis scoresbyensis*, with clear venation, Q670/08. 6. *Cladophlebis scoresbyensis*, 92wü08. 7. *Cladophlebis scoresbyensis*, 29wü10. 8. *Cladophlebis scoresbyensis*, small marginal dentations with two veinlets ending there, Q970/14. Scale bars 1–3, 5–6: 10 mm; 4, 7: 5 mm.

once, which is clearly visible in 68wü08 (Plate III, 2) – a bipinnate, probably apical frond fragment. The pinnae alternate and the longest in 68wü08 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 pectopterid-type venation. However, both species are often reported from the same layers in a locality or area.

Schenk (1865–1867) described and figured *Acrostichites goeppertianus* (Münster) Schenk from the Hettangian of Theta in Franconia, and *Asplenites roesserti* (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 (*Acrostichites goeppertianus*) via pl. 7, fig. 2 (*Asplenites roesserti*) to pl. 10, figs. 1–4 (also *A. roesserti* 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 roessertii* as that name has priority over *T. goeppertianus*, which was later agreed on by Weber (1968).

Harris (1926) described material from the Rhaetian of Jameson Land (Greenland) as *Cladophlebis roessertii* (Schenk non Presl) Saporta and *Todites cf. williamsonii*. Later, Harris (1931) transferred the latter to *Todites goeppertianus* and placed the specimens earlier assigned to *C. roessertii* in the new species *Cladophlebis scariosa* Harris, 1931, that is distinguished from *C. roessertii* 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. roessertii* should be assigned to *T. goeppertianus*, which also is the case for the original specimens of *Alethopteris roessertii*. *Cladophlebis scariosa* is difficult to be clearly distinguished from what others described as *C. roessertii* and *C. nebbensis* (Harris, 1937, p. 17).

Lundblad (1950) reported frond fragments from the Rhaetian/Hettangian of Scania, Sweden, including specimens from Nathorst (1878) and possibly Antevs (1919), as *T. goeppertianus* without considering *T. roessertii*. The Antevs material is discussed below together with *T. williamsonii* from the Rhaetian of Rögla, Sweden (Pott and McLoughlin, 2011).

Todites roessertii is originally reported from Franconia, but has been recorded from all over the world, mainly from Rhaetian–Hettangian strata (see e.g., Möller, 1902; Zeiller, 1903; Ôishi, 1932; Barbacka and Bodor, 2008; Pacyna, 2014; Barbacka et al., 2019).

Material examined: Q501/07, 502/07, 503/07, 504/07, 505/07, 506/07, 507/07, 521/07, 617/08, 641/08, 657/08, 658/08, 684/08, 702/08, 715/08, 753/09, 789/09, 851/11, 890/12, 894/12, 903/12, 914/13, 915/13, 941/13, 973/14, 1048/18; 82wü02, 102wü02, 145wü02, 08wü03, 97wü03, 28wü06, 30wü06, 17wü07, 18wü07, 14wü08, 33wü08, 61wü08, 68wü08, 74wü08, 76wü08, 86wü08, 109wü08, 176wü08, 14wü09, 26wü10, 57wü10, 09wü11, 20wü11; UU23823.

Genus: *Cladophlebis* Brongniart, 1849

Diagnosis and discussion: See Brongniart (1849), Seward (1910), Bodor and Barbacka (2008).

Type species: *Pecopteris defrancei* Brongniart, 1834 = *Cladophlebis defrancei* (Brongniart) Brongniart, 1849, from the Carboniferous of Saarbrücken, Germany.

Cladophlebis scoresbyensis Harris, 1926

Plate III, 5–8

Synonymy and references:

1926 *Cladophlebis scoresbyensis*—Harris, p. 59, pl. 2, fig. 4, text-fig. 4A–D.

1931 *Todites scoresbyensis* (Harris) sterile leaves—Harris, p. 42, text-fig. 12.

1950 *Cladophlebis scoresbyensis* Harris—Lundblad, p. 20, text-fig. 3.

Description: *Cladophlebis scoresbyensis* is a rare fern in Wüstenwelsberg. All are small fragments, sometimes consisting of a secondary (pinna) rachis with a few attached pinnules, sometimes even of isolated pinnules only. The secondary rachis is between 1.5 mm (apically) and 2.5 mm wide (proximal; with larger attached pinnules), and shows longitudinal striae (92wü08, Q670/08, Q892/12,

Q970/14; Plate III, 5, 6, 8). Only a few pinnules are complete; the smallest is 15 mm long and 6 mm wide with a rounded apex (Q215/02). In contrast, both 92wü08 and Q939/13 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 (29wü10 and Q670/08), two veins on the basiscopic side of the pinnules bifurcate twice while they bifurcate once on the acrosopic 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 scoresbyensis* 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 scoresbyensis* appears (Sadovnikov, 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. scoresbyensis*. Even Schweitzer et al. (1997) refrained from a definite identification of those specimens.

The by far most similar species is *Cladophlebis nebbensis* (Brongniart) Nathorst, 1876. Harris (1926) stated the differences as (1) the greater size of the pinnules in *C. scoresbyensis* and (2) the termination of two veins in a single tooth in *C. scoresbyensis*. 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. scoresbyensis*, which differ in the arising angle of the secondary veins and the morphology of the margin. Another similar species is *Cladophlebis denticulata* (Brongniart) 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; 92wü08, 117wü08, 11wü10, 29wü10, 10wü13, 13wü13; UU23271, 23827.

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, 03wü05, 27wü10), but with a clear neuropterid venation that is different from that of the specimens assigned to *T. roessertii* and *C. scoresbyensis* 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 neuropterid 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 03wü05 (Plate IV, 2) yields a 36-mm-long

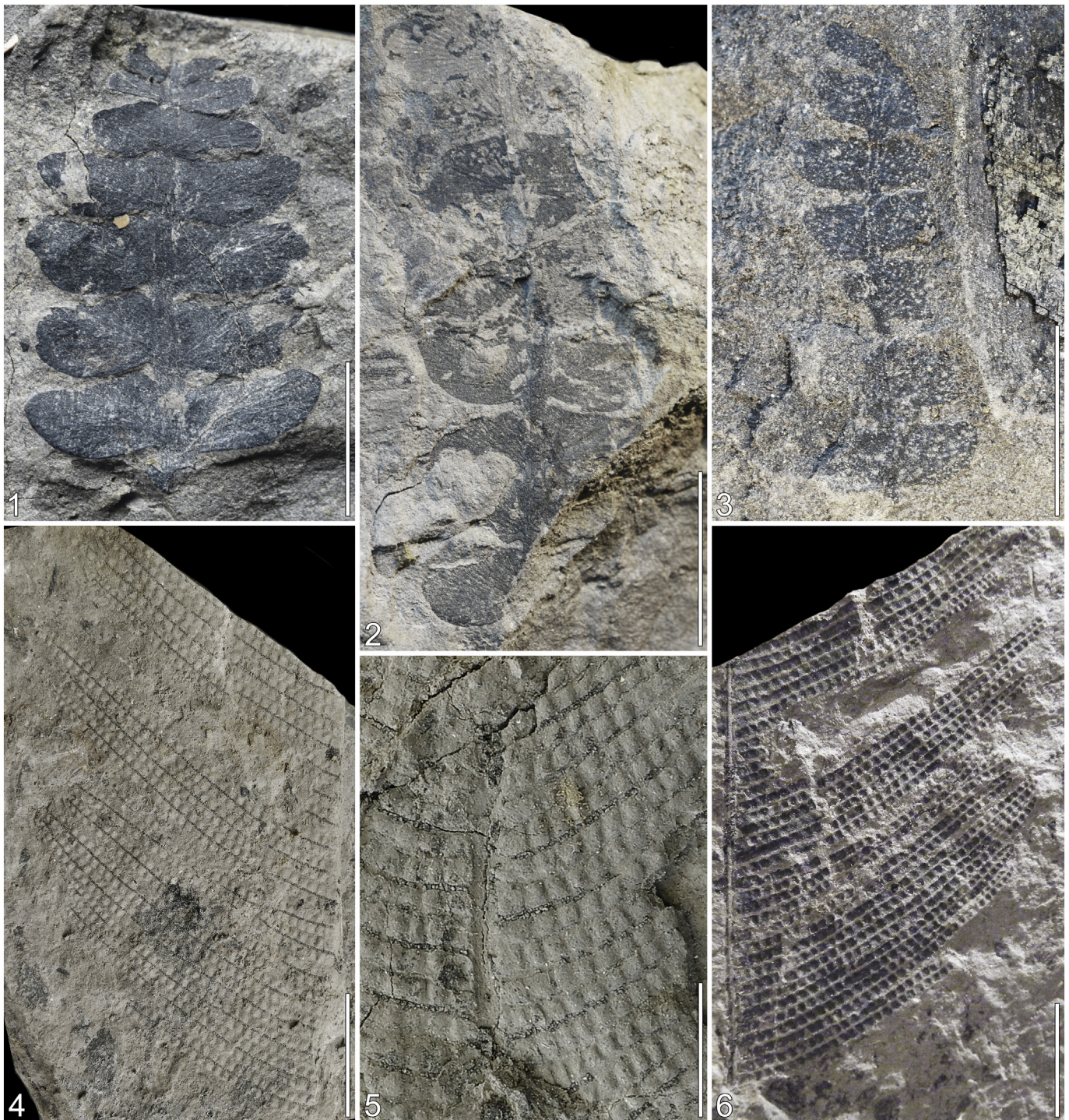


Plate IV. Macroremains of Osmundaceae (Figs. 1–3) and Matoniaceae (Figs. 4–6) from the Rhaetian of Wüstenwelsberg with specimen numbers. 1. *Cladophlebis* sp., specimen showing venation and yielding cuticle fragments, Q783/09. 2. *Cladophlebis* sp., showing venation, 03wü05. 3. *Cladophlebis* sp., 27wü10. 4. *Phlebopteris angustiloba*, largest specimen, 66wü02. 5. *Phlebopteris angustiloba*, 05wü04. 6. *Phlebopteris angustiloba*, Q181/02. Scale bars 2, 4, 6: 10 mm; 1, 3, 5: 5 mm.

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 basicopic 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 pinnales that exhibit typical characters such as an opposite and perpendicular insertion of the pinnales 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.

Anteus (1919, pl. 1, figs. 20–22) reported specimens from the Hettangian of Sweden as *Todites williamsonii* with bipinnate fronds with oppositely and perpendicularly inserted pinnales 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 Rhaetian 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 Rhaetian of Rögla 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 + ? 530/07, 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 pectopterid 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 pectopterid 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: MATONIACEAE **Presl, 1847**

Genus: *Phlebopteris* **Brongniart, 1836**

Diagnosis and discussion: See **Brongniart (1828–1836), Hirmer and Hörhammer (1936)** and **Pott et al. (2018)**.

Type species: *Phlebopteris polypodioides* **Brongniart (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 *Andriana baruthina*—**Braun**, p. 42, pl. 9, figs. 3–12, pl. 10, figs. 1–3.

1867 *Gutbiera angustiloba* **Presl—Schenk**, p. 64, pl. 18, figs. 5–10.

1914 *Gutbiera angustiloba* **Presl—Gothan**, p. 99, pl. 17, fig. 5.

1914 *Andriana baruthina* **Braun—Gothan**, p. 102, pl. 17, fig. 8, pl. 18, figs. 1, 2.

1914 *Andriana 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 Rhaetian–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 (Bavaria; **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 and Hörhammer**, p. 17, pls. 3, 4, figs. 1–6, pl. 5, text-fig. 5, 2A and 2B.

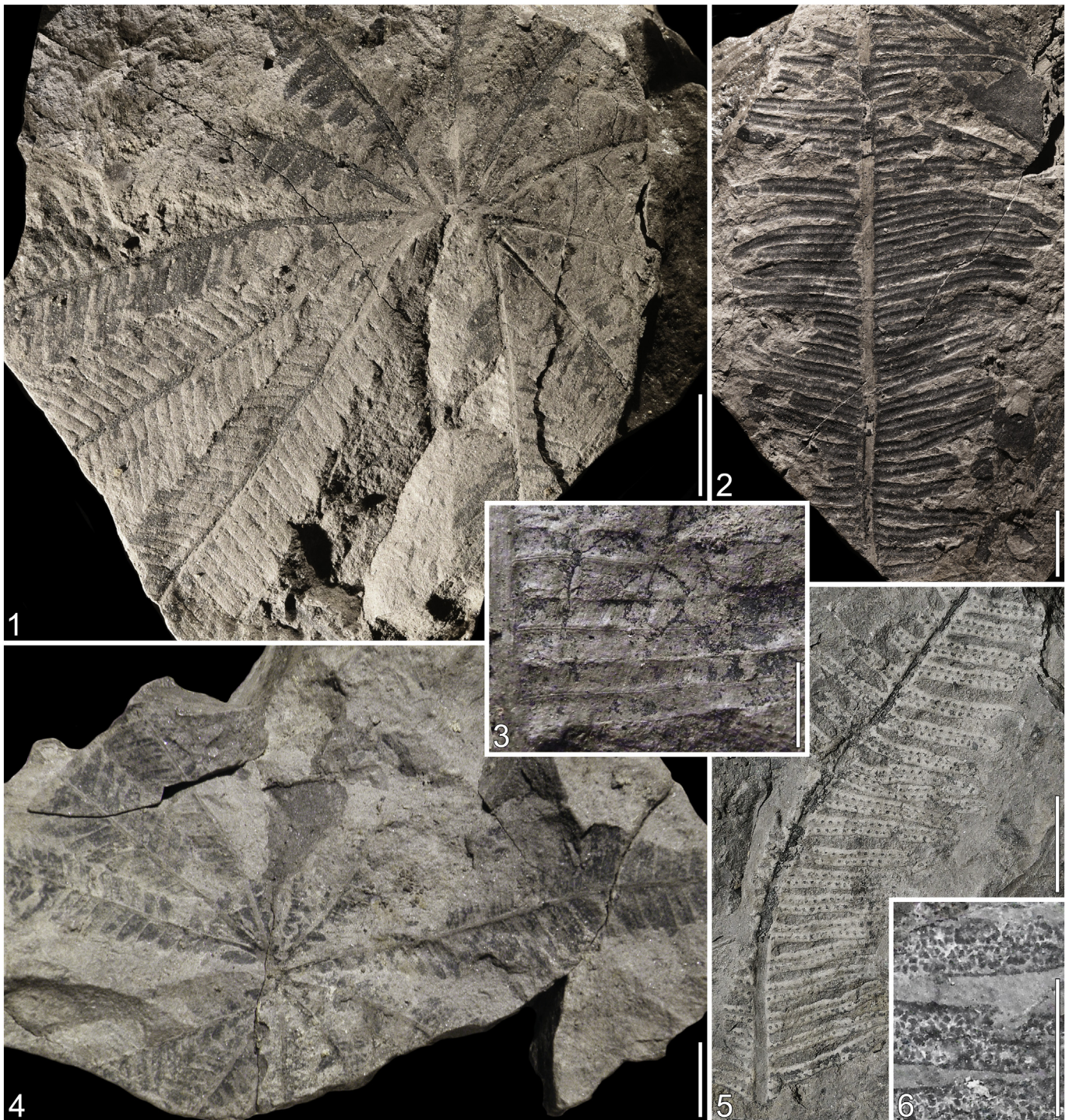


Plate V. Macroremains of Matoniaceae from the Rhaetian of Wüstenwelsberg with specimen numbers. 1. *Phlebopteris muensteri*, frond fragment showing a number of primary segments, 66wü03. 2. *Phlebopteris muensteri*, fragment with large pinnules, 59wü03. 3. *Phlebopteris muensteri*, fragment showing venation, 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.

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

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 1 mm in diameter and consist of 6–8 sporangia (100wü02; Plate V, 6), but these have often fallen off and as a consequence, only the receptaculum is left/preserved (Plate V, 5). Although coaly material has been preserved occasionally, no *in situ* spores could be isolated from the material at hand.

Remarks: *Phlebopteris muensteri* was first described as *Laccopteris muensteri* by Schenk (1865–1867) from the Hettangian flora of Bavaria (from the type locality Theta) in detail including *in situ* spores. The latter is remarkable because *in situ* spores are commonly not preserved in any fossils of this species; in fact, they are only known from a few German specimens (Van Konijnenburg-van Cittert, 1993). Gothan (1914) described sterile and fertile material from a number of Hettangian Bavarian localities as *Laccopteris* sp.; Weber (1968) reported specimens from a number of additional Hettangian localities from Germany; Weber (1968) also reported descriptions and illustrations of complete juvenile fronds (Weber, 1968, pl. 7, figs. 60, 61). Hirmer and Hörhammer (1936) gave the most elaborate description of *Phlebopteris muensteri* in their revision of the Matoniaceae. Spores were first described in detail by Van Konijnenburg-van Cittert (1993). Hirmer and Hörhammer (1936) included specimens in *Phlebopteris muensteri* that have later been recognized as a different species, viz. *Phlebopteris lunzensis* by Pott et al. (2018).

Harris (1931, 1980) considered *Phlebopteris muensteri* and *Phlebopteris braunii* (Göppert) Hirmer et Hörhammer as conspecific, as he was of the opinion that they were sun (*P. muensteri*) and shade (*P. braunii*) fronds of the same species, as both species were usually reported as occurring together in the same localities. Harris (1980) merged them into a single species and named it *Matonia braunii* Harris, 1980. Barbacka et al. (2016) followed Harris' (1980) hypothesis when describing specimens from the Jurassic of Poland. Van Konijnenburg-van Cittert (1993) in contrast separated the two species, because the sori in *Phlebopteris muensteri* are larger (diameter c. 1 mm), covering a prominent part of the lamina, than those of *Phlebopteris (Matonia) braunii* (diameter c. 500 µm). In addition, the spores of both species differ considerably in size (60–70 µm in *P. muensteri* and c. 50 µm in *P. (M.) braunii*). The latter view is supported by localities were only one of the two species has been reported, such as Wüstenwelsberg and a number of Iranian/Afghan localities (Schweitzer et al., 2009).

Barbacka et al. (2019) described *Phlebopteris kirchneri* from the Hettangian of Hungary. On first view, it appears to be similar to *P. muensteri* but in well-preserved specimens, the delicate secondary venation is visible, which consists of oval to hexagonal meshes. This distinct 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 lunzensis* (Stur ex Krasser) Pott et Bomfleur, 2018 (in Pott et al., 2018), from the Carnian of Lunz (Austria) (Pott et al., 2018). Hirmer and Hörhammer (1936) considered *P. lunzensis* 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 Rögla 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* from the Hettangian of Bornholm (Denmark). Scanu 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, 264/03, 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, 105wü09, 05wü10, 35wü10, 06wü11, 21wü12, 03wü13, 05wü13, 08wü14; UU23222, 23224, 23225, 23230, 23232, 23259, 23266, 23268, 23271, 23273, 23275, 23280, 23281, 23286, 23289, 23315, 23323, 23335, 23819.

Family: DIPTERIDACEAE (Diels) Seward et Dale, 1901

Genus: *Clathropteris* Brongniart, 1828

Diagnosis and discussion: See Brongniart (1828), Ôishi and Yamasita (1936), Choo et al. (2016) and Pott et al. (2018).

Type species: *Clathropteris meniscioides* (Brongniart) Brongniart, 1828, from the Hettangian of Scania.

Clathropteris meniscioides (Brongniart) Brongniart, 1828

Plate VII, 1–4

Selected synonymy and references:

1825 *Filicites meniscioides*—Brongniart, p. 200, pls. 11, 12.

1828 *Clathropteris meniscioides* (Brongniart)—Brongniart, p. 62, 194.

1836 *Clathropteris meniscioides* (Brongniart) Brongniart—Göppert, p. 290, pl. 15, fig. 7.

1867 *Clathropteris platyphylla* (Göppert)—Schenk, p. 81, pl. 16, figs. 2–9, pl. 17.

1914 cf. *Clathropteris platyphylla* Göppert—Gothan, p. 107.

1936 *Clathropteris meniscioides* (Brongniart) Brongniart—Ôishi and Yamasita, p. 289.

1995 *Clathropteris meniscioides* (Brongniart) Brongniart—Kelber and Hansch, p. 122, figs. 257, 260.

2016 *Clathropteris meniscioides* (Brongniart) Brongniart—Choo et al., *cum syn.*, p. 89, pls. 1–6.

2018 *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 dipteridaceous matter converging towards the (not preserved) rachial 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 50–60 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; Jänichen and Kahlert, 1996; Pacyna, 2014; Barbacka et al., 2019), Asia (Stanislavski, 1971, 1976; Kimura and Tsujii, 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 Ladinian 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. muensteriana* Schenk, 1865–1867 are nowadays considered to be conspecific with *C. meniscioides* (see, e.g., Pott et al., 2018).

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 Ladinian–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 Yamasita (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 *Camptopteris exilis*—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 rachial arm (64wü08, 195wü08, Q615/08; Plate VII, 5, 7). Q615/08 shows at least eight attached primary segments (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 in 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* spores (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, trilete, 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

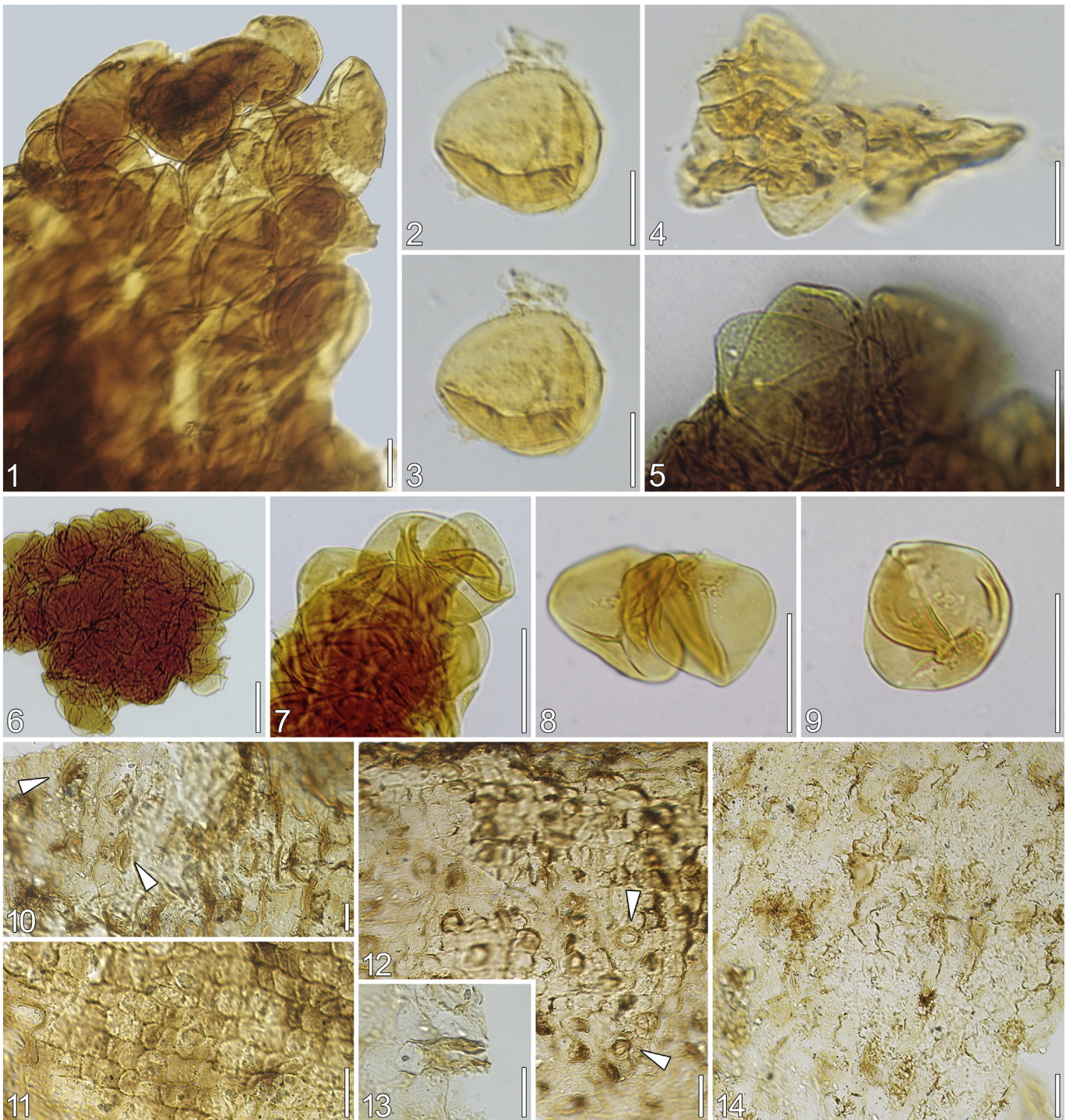


Plate VI. *In situ* spores (Figs. 1–9) and cuticle remains (Figs. 10–13) from the Rhaetian of Wüstenwelsberg with specimen numbers from which they were derived. 1. *Todites roessertii*, spore cluster, Q501/04. 2 and 3. *Todites roessertii*, single spore in different focus, Q501/04. 4. *Clathropteris 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 μ m, 5–9, 13: 50 μ m.

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 VII. Macroremains of Dipteridaceae from the Rhaetian of Wüstenwelsberg with specimen numbers. 1. *Clathropteris meniscioides*, most complete frond fragment, Q449/06. 2. *Clathropteris meniscioides*, detail of venation, 98wü03. 3. *Clathropteris meniscioides*, serrate margin, Q440/06. 4. *Clathropteris meniscioides*, fertile specimen, Q.156/02. 5. *Dictyophyllum exile*, largest frond fragment, Q615/08. 6. *Dictyophyllum exile*, 4 primary segments, Q616/08. 7. *Dictyophyllum exile*, 64wü08. 8. *Dictyophyllum exile*, fertile specimen, 178wü02. Scale bars 1, 3–8: 10 mm; 2: 5 mm.

in Iran (Schweitzer et al., 2009) and China (Zhou et al., 2016). The lobes of the primary segments of *D. exile* are more densely arranged than in *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 *D. exile*, while in *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 *D. exile*. Webb (1982) mentioned that sori in

D. exile are round, arranged very crowded over the whole lower surface and c. 0.5 mm in diameter, while those of *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.

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*



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, 02wü04. 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–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, 111/02, 153/02, 154/02, 163/02, 250/02, 328/03, 357/03, 358/03, 379/04, 415/05, 422/05, 423/05, 437/06, 489/07, 570/08, 574/08, 615/08, 616/08, 676/08, 866/11, 890/12, 914/13, 1051/18; 05wü02, 19wü02, 39wü02, 49wü02, 64wü02, 67wü02, 76wü02, 81wü02, 88 + 89wü02, 98wü02, 106wü02, 113wü02, 143wü02, 164wü02, 165wü02, 171wü02, 176wü02, 178wü02, 179wü02, 180wü02, 13wü03, 18wü03, 24wü03, 25wü03, 34wü03, 56wü03, 67wü03, 68wü03, 70wü03, 72–74wü03, 94wü03, 101wü03, 04wü04, 26wü04, 30wü04, 41wü04, 42wü04, 05wü06, 23wü06, 01wü08, 32wü08, 64wü08, 69wü08, 78wü08, 96wü08,

97wü08, 99wü08, 110wü08, 135wü08, 146wü08, 169wü08, 195wü08; 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).

Thaumatopteris brauniana Popp, 1863

Plate VIII, 1–3

Selected synonymy and references:

1863 *Thaumatopteris brauniana*—Popp, p. 409.

1867 *Thaumatopteris brauniana* Popp—Schenk, p. 73, pl. 18, figs. 1–3, pl. 19, fig. 1.

1878 *Thaumatopteris schenkii*—Nathorst, p. 46, pl. 6, fig. 1, pl. 8, fig. 4.

1907 *Thaumatopteris schenkii* Nathorst—Nathorst, p. 1, pls. 1, 2.

- 1914 *Thaumatopteris schenkii* Nathorst—Gothan, 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, pl. 18, figs. 1, 2, text-fig. 35.
 1931 *Thaumatopteris brauniana* Popp—Harris, p. 94, pl. 17, fig. 5, pl. 18, figs. 4, 6–11, 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, 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 Dipteridaceae 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 neighbouring 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; Schweitzer, 1978; Schweitzer et al., 2009). Nathorst (1907) identified the two most important differences between *Thaumatopteris* and *Dictyophyllum* (see below) and defined an updated generic diagnosis with *T. brauniana* as type species. Nomenclatorially, this is illegitimate, but the genus has been continuously used in this way until to date (e.g., Harris, 1931, as index fossil for the *Thaumatopteris* zone in Jameson Land). Zijlstra and Van Konijnenburg-van Cittert (2019) submitted a proposal to conserve the generic name *Thaumatopteris* with the conserved type *T. brauniana* considering it distinct from *Dictyophyllum*. The characters distinguishing *Thaumatopteris* from *Dictyophyllum* given by Nathorst (1907) are the almost perpendicular insertion of the basally constricted secondary segments to the central vein (‘rachis’) of the primary segments in *Thaumatopteris* versus the more obliquely and basally broadly inserting secondary segments in *Dictyophyllum*. Schweitzer (1978) added differences in sori (fewer but larger in *Thaumatopteris* than in *Dictyophyllum*) and sporangial size (smaller in *Dictyophyllum* than in *Thaumatopteris*). Choo and Escapa (2018) recognized *Thaumatopteris* as a separate clade in the Dipteridaceae based on laminal dissection, arrangement of primary segments and sporangial diameter.

Thaumatopteris first occurred in the Anisian of Argentina (*T. barrealensis* Bodnar et al., 2018) and late Ladinian of the Dolomites (*Thaumatopteris* sp.; Kustatscher et al., 2014). It became more abundant during the Carnian of Australia (*T. shirleyi* Herbst, 1979) and Lunz, Austria (*T. lunzensis* Stur ex Krasser, 1909 [attributed to *Dictyophyllum*

lunzensis 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 Rhaetian.

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*). 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 Ôishi’s (1932) Rhaetian species such as *T. elongata* Ôishi, 1932 (with relatively long secondary segments) and *T. nipponica* Ôishi, 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; 123wü02, 10wü03, 137wü03, 02wü0, 24wü06, 141wü08, 143wü08, 162wü08.

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: Circinnate 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; 21wü05, 178wü08.

4. Discussion

4.1. Composition of the flora

The Rhaetian 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 Konijnenburg-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 isoetalean *Lepacyclotes* sp. has been found, a genus that is commonly recorded from Upper Triassic–Lower Jurassic outcrops in the Germanic Basin, but records from the Rhaetian were unknown until to date. The spikemoss *Selaginellites coburgensis* is quite well known from Wüstenwelsberg (Van Konijnenburg-van Cittert et al., 2014, 2016); both sterile and fertile material with *in situ* spores has been described in detail previously. *Equisetites 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 *Cladophlebis/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. Dipteridaceae 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 marattiacean 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 from the Northern Hemisphere

The flora from Wüstenwelsberg is a typical Rhaetian flora yielding key pteridophyte taxa such as *Equisetites laevis*, *Phlebopteris angustiloba*, *Phlebopteris muensteri*, *Dictyophyllum exile*, *Clathropteris meniscioides* and *Thaumatopteris brauniana*, although some of these taxa also extend into Jurassic floras. These species place the Wüstenwelsberg flora in line with the renowned Rhaetian floras from Jameson Land (Greenland, Harris, 1926, 1937), Scania (Sweden, Nathorst, 1876, 1878, 1907; Lundblad, 1950; Pott and McLoughlin, 2011), southern Poland

(Pacyna, 2014; Barbacka et al., 2014a, 2014b), the Donets Basin (e.g., Stanislavski, 1971) and Alborz, Iran (Schweitzer et al., 1997, 2009). Especially the floras from 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 Cheliabinsk Basin (eastern Ural) does not even have one species in common with the Wüstenwelsberg flora (Kryštofovich 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. *Equisetites laevis*, *Todites roessertii*, *Phlebopteris muensteri*, *P. angustiloba*, *Dictyophyllum exile* and *Thaumatopteris brauniana* (Table 1). Solely, *Todites (Cladophlebis) 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 pinna fragments assigned to *Cladophlebis* 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 Konijnenburg-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 Konijnenburg-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 *Equisetites* 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

Table 1

Comparison of the ferns found at Wüstenwelsberg with those of the Rhaetian floras of Jameson Land, Scania, Poland, Donets Basin and Iran.

Rhaetian taxa	Jameson Land	Franconia	Scania	S. Poland	Donets	Alborz
<i>Equisetites laevis</i>	X	X	X			X
<i>Todites goeppertianus</i>	X	? <i>Cladophlebis</i> sp.	X			? <i>Todites williamsonii</i>
<i>Todites roessertii</i>	?X	X	?X	X		
<i>Todites scoresbyensis</i>	X	<i>Cladophlebis scoresbyensis</i>	X			?
<i>Phlebopteris muensteri</i>	X	X				X
<i>Phlebopteris angustiloba</i>	X	X	X			
<i>Clathropteris meniscioides</i>	X	X	X	X	X	X
<i>Dictyophyllum exile</i>	X	X	X			X
<i>Thaumatopteris brauniana</i>	X	X	X			X
Sources for the taxa	Harris (1937)	This study	Pott and McLoughlin (2011), Lundblad (1950)	Pacyna (2014), Barbacka et al. (2014b)	Stanislavski (1971)	Schweitzer et al. (1997, 2009)

families, not yet present in the Rhaetian, occur in the Hettangian flora, such as the marattialean *Marattia intermedia* (Münster) Kilpper, 1964, and the schizaeacean *Phialopteris heterophylla* (Sternberg ex Göppert) Van Konijnenburg-van Cittert et al., 2018a. The fern families already present in the Rhaetian flora of Wüstenwelsberg have different and/or more species in the Hettangian flora. While the osmundaceous *Todites roessertii* still occurs in the Hettangian, *Todites princeps* (Presl in Sternberg) Gothan, 1914 is the more abundant species in the latter flora. The two matoniacean species from Wüstenwelsberg, *Phlebopteris muensteri* and *P. angustiloba*, occur in the Hettangian flora as well, but with *Selenocarpus muensterianus* (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 dipteridaceous *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 exile* is not known from the Hettangian of Franconia at all, whereas a different species, viz. *Dictyophyllum nilssonii* (Brongniart) Göppert, 1841–1846, is quite abundant then. Another dipteridaceous species, the bipinnate *Goepfertella microloba* (Schenk, 1866) Ôishi 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 Dipteridaceae 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 the zones thus should be only used carefully nowadays.

4.3. Paleocological and paleogeographical implications

Climate conditions during the Rhaetian in Europe are generally reconstructed 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 *Botryococcus*, *Cymatiosphaera* 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 coburgensis*, 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, freshwater 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 matoniacean 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 muensteri* 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 Reinwardt*, 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 remains 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 fern remains from the Rhaetian of Wüstenwelsberg, Franconia, southern Germany, show a high diversity: two lycophytes (*Lepacyclotes* sp. and *Selaginellites coburgensis*) 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 (*Todites roessertii*, *Cladophlebis scoresbyensis*, *Cladophlebis* sp.) with rare occurrences in the assemblage are reported; fossils of Matoniaceae are more abundant, representing two species (*Phlebopteris muensteri*, *Phlebopteris angustiloba*). Dipterid remains are very common, assignable to three species of each another genus (*Clathropteris meniscioides*, *Dictyophyllum exile*, *Thaumatopteris brauniana*). Frond fragments preserved in the developing stage showing circinnate venation (*Spiropteris* sp.) could not be assigned to any of the species.

The cryptogams of Wüstenwelsberg include key Rhaetian taxa such as *Equisetites laevis*, *Phlebopteris muensteri*, *Dictyophyllum exile*, and *Clathropteris meniscioides*. These are represented in most coeval Rhaetian floras of Central Europe such as Jameson Land, Scania, Franconia and southern Poland. However, taxa that are considered as key taxa for Hettangian floras, e.g., *Phlebopteris angustiloba* and *Thaumatopteris brauniana*, are present in Wüstenwelsberg, albeit not in large numbers. The comparison with the Jurassic floras of Germany shows, on the other hand, that the latter plant assemblages are much more diverse.

The lycophytes and sphenophytes from Wüstenwelsberg were probably part of the more humid or wetter environments of the understoreys. The ferns too possibly colonized the understorey of humid environments but were also pioneer plants of disturbed, short-living, wet areas in the alluvial plains, just as the lycophyte *Lepacyclotes* sp. might have been.

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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