Research papers

The Rhaetian flora of Wüstenwelsberg, Bavaria, Germany: Description of selected gymnosperms (Ginkgoales, Cycadales, Coniferales) together with an ecological assessment of the locally prevailing vegetation

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ABSTRACT

This paper describes the ginkgoaleans (Ginkgoites) and conifers (Palissya, Stachyotaxus, Schizolepis) of the Rhaetian flora from Wüstenwelsberg, as well as a new species of the cycad Becklesia. The ginkgophyte leaf fragments are very abundant in certain levels ('Blätterkohle') whereas conifers are common in the main fossiliferous bed. The Wüstenwelsberg specimens extend the range for Ginkgoites taeniatus from the Hettangian to the Rhaetian and for the genus Becklesia from the Cretaceous to the Rhaetian. The other elements are typical for the Rhaetian floras of Bavaria and often also of the Northern Hemisphere. A comparison with other Northern Hemisphere plant assemblages demonstrates a high similarity with the Rhaetian floras from Jameson Land (Greenland) and Scania (Sweden) but significant differences to the Hettangian floras from adjacent areas in Franconia, especially at species and sometimes at generic level. A comparison with the microflora from the same sections shows a hidden diversity that is highest in small herbaceous plants (mosses, lycophytes, ferns) and in the conifers. Wüstenwelsberg reflects, thus, an articulated landscape with a high water and nutrients availability (stagnant water bodies and/or river systems) covered by a complex and multi-storeyed vegetation shown, among others, by the general abundance in hygrophytic spores and high diversity among the various plant groups. This must have corresponded to one of the humid episodes that characterized the generally warm and arid climate of the Rhaetian of Europe.

1. Introduction

The fossil flora from the uppermost Triassic and Lower Jurassic strata of Upper Franconia (Bavaria, Germany), the "Rhaeto–Liassic flora" of Franconia, has received considerable scholarly attention recently (for references see Van Konijnenburg-van Cittert et al., 2014, 2016, 2017, 2018a, 2018b, 2019, 2020; Pott et al., 2016a). Most 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, in a few localities around the town of Coburg the sediments are Rhaetian (Upper Triassic) in age instead (see e.g., Kelber and

Van Konijnenburg-van Cittert, 1997; Van Konijnenburg-van Cittert et al., 2014; Pott et al., 2016a), including a quarry near Wüstenwelsberg. Systematic sampling in the last three decades uncovered more than 40 different fossil plants species, which are currently thoroughly studied (Bonis et al., 2010; Zavialova and Van Konijnenburg-van Cittert, 2011; Van Konijnenburg-van Cittert et al., 2014, 2016, 2017, 2018a, 2020; Pott et al., 2016a).

This paper is the last of a series, and here we describe some gymnosperm remains including two representatives of the Ginkgoales [viz. Ginkgoites taeniatus (Braun, 1843) Harris, 1935, and Ginkgoites sp.], three different conifer taxa [Palissya sphenolepis (Braun, 1843) Nathorst, 1908, Stachyotaxus septentrionalis (Agardh, 1823) Nathorst, 1886, and Schizolepis liasokeuperianus (Braun, 1846) Schenk, 1867] and sterile cycadalean foliage attributable to the genus Becklesia, which is recognized as a species new to science, viz. Becklesia franconica

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sp. nov. The latter was earlier sorted into the coniferalean genus *Pityophyllum* due to its long, single-veined needle fragments. Later, a pinnate specimen was discovered with such 'needles' attached to a rachis, the material was re-evaluated and identified as cycadalean instead of coniferous.

Palynological data and ecological aspects, the environment and the habitat in which the flora and the individual species thrived in, are included in a comparison with the composition of the Rhaetian flora of Franconia, with the Hettangian flora of the same region, and with the Rhaetian floras of East Greenland (Jameson Land), Sweden (Scania), Poland, Ukraine (Donets Basin) and Iran (Alborz); herein we also 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 and elaborate sedimentological data see Bonis et al., 2010; Pott et al., 2016a; Van Konijnenburg-van Cittert et al., 2018a, 2020, and Fig. 2). 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 (see Bonis et al., 2010 and Fig. 2). Almost all layers in the section are Rhaetian in age, only the uppermost one (barren of 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 preserved as compressions; some of the better-preserved specimens yielded cuticles and so contributed to our knowledge of some of the species in this Rhaetian flora.

2.3. Methods

Cuticles were picked directly from the rock surface. These were macerated following the standard procedure using Schulze's reagent (30% HNO_3 with a few crystals of $KClO_3$) and subsequently treated with 5–10% ammonia (NH_4OH) or potassium hydroxide (KOH). Macerated cuticles were rinsed with water and dehydrated in glycerine. The upper and lower cuticle surfaces were separated, 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 stored in the private collections of SS and GD 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 and an Objective Leica DC Vario-Elmarit 1:2.8–4.0/9.1–146. Oblique lightning and polarizing filters in front of the camera lenses and the lights were used to enhance contrast and fine details.

3. Systematic palaeobotany

Order: GINKGOALES Gorozhankin, 1904
Family: GINKGOACEAE Engler in Engler and Prantl, 1897
Genus: **Ginkgoites** Seward, 1919
Diagnosis and discussion: See Seward (1919), Harris (1935), Florin (1936), Pott et al. (2016b).
Type species: Ginkgoites obovatus (Nathorst, 1886) Seward, 1919 from the Rhaetian of Bjuv, Scania, Sweden.

Ginkgoites taeniatus (Braun, 1843) Harris, 1935

Plate I, 1; V, 1–3
Selected references
1843 *Baiera taeniata* — Braun, p. 21.
1867 *Baiera taeniata* Braun — Schenk, p. 26, pl. 5, figs. 1–4; pl. 6, figs. 1, 2.
1914 *Baiera taeniata* Braun — Gothan, p. 150, pl. 29, fig. 2; pl. 31–32, fig. 1.
1935 *Ginkgoites taeniata* (Braun) — Harris, cum syn., p. 19, pl. 1, figs. 1, 2, 9; pl. 2, figs. 3, 4; text-figs. 9–11.
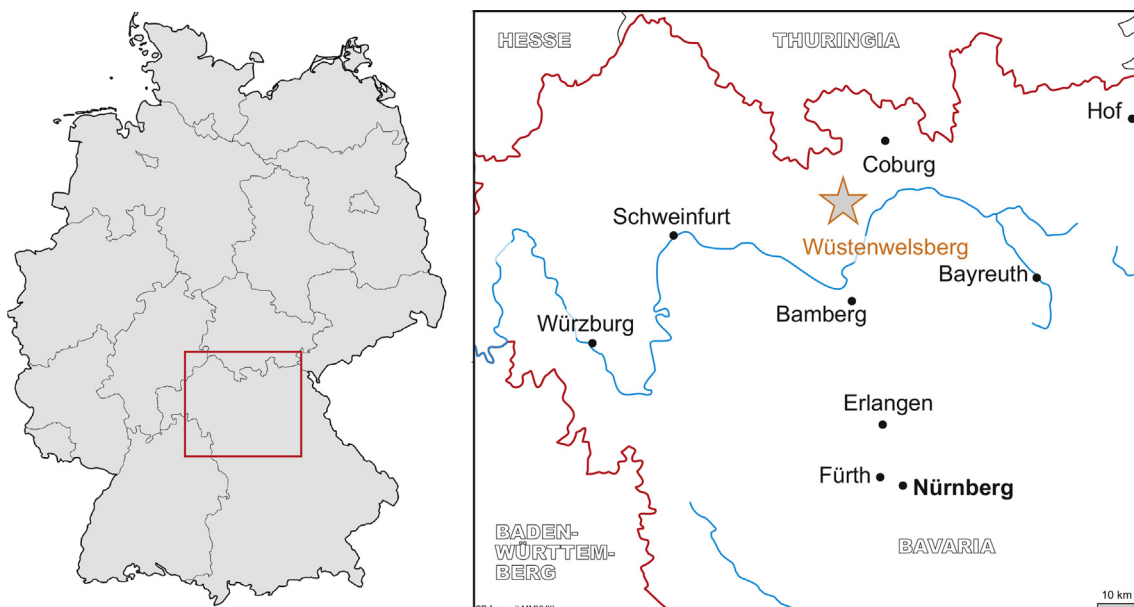

Fig. 1. Map of Germany indicating the position of the locality Wüstenwelsberg in Franconia (Bavaria).
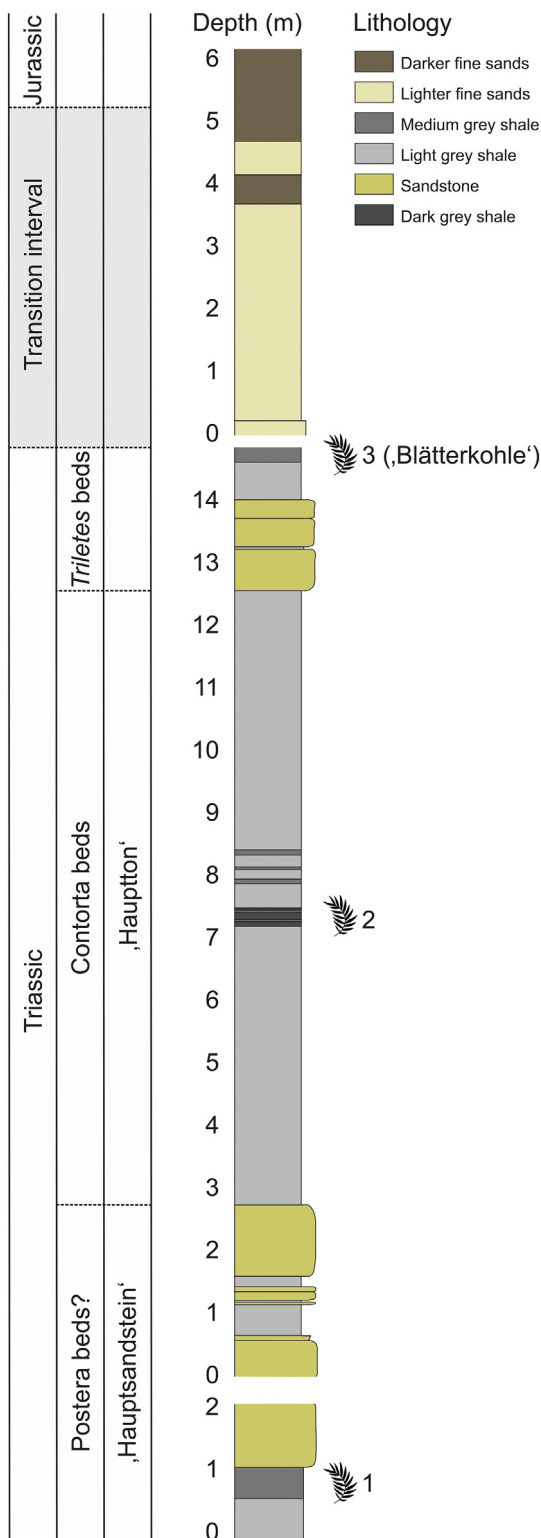
Fig. 2. Lithological column of the quarry Wüstenwelsberg with indication of the plant beds named in the text (modified from Bonis et al., 2010).

1959 *Ginkgoites taeniata* (Braun) Harris — Kräusel, p. 101, pl. 4, fig. 2; text-fig. 2.

2010 *Ginkgoites taeniata* (Braun) Harris — Bonis et al., p. 148, figs. 3B, D, F.

Description: In the uppermost layers at Wüstenwelsberg, we find a so-called 'Blätterkohle' (= paper shale or paper coal) with numerous dispersed leaf segments (no complete leaves found so far) assignable to *Ginkgoites taeniatus* yielding well-preserved cuticles. The individual leaf segments vary in width between 2.5 mm and 5.0 mm; occasionally they show a rounded apex and they are rarely forked (Plate I, 1). One cuticle fragment (C. 4694 from UU23330) provides connected adaxial and abaxial cuticles, 5.0 mm wide, in which the apical part is not attached anymore and decreases to 3.5 mm although no apex has been preserved. Stomata are present on both cuticles rendering the leaves amphistomatic. The cuticles are moderately thick (3–4 μm), and slightly thicker on what is presumed the adaxial side. Epidermal cells are isodiametric with bands of more elongate cells in between, the latter indicating veins (Plate V, 1, 2). The haplocheilic, monocyclic to imperfectly dicyclic stomata occur in irregular rows in bands between the veins; commonly not more than 2–4 rows of cells per band. Stomata have a small stomatal pit (10–15 μm in diameter) surrounded by 5–7 subsidiary cells. The latter either form a thickened ring around the stomatal pit (Plate V, 1, 2) or produce papillae (Plate V, 2, 3). The stomata are interconnected by epicuticular striae forming a microrelief characteristic for ginkgophytes (see Pott et al., 2007) (Plate V, 3).

Remarks: *Ginkgoites taeniatus* was first mentioned as *Baiera taeniata* by Braun (in Braun, 1843) from the Hettangian of Strullendorf (Bavaria). Braun separated it from *Baiera dichotoma* Braun, 1843, from the same locality due to its wider segments. The number of six veins per segment led Harris (1935) to transfer the species to *Ginkgoites* because *Baiera* includes leaves with only up to four veins per segment. *Ginkgoites taeniatus* has been recorded from various Hettangian localities in Bavaria (Schenk, 1867; Gothan, 1914; Kräusel, 1959; Weber, 1968; Kirchner, 1992), partly still as *Baiera taeniata*.

The dispersed segments are up to 5.0 mm wide justifying an assignment to *Ginkgoites taeniatus* because those of *Baiera muensteriana* are at maximum 3.0 mm wide (see, e.g., Harris, 1926, 1935; Florin, 1936, 1937). The cuticle of both species is rather similar (Florin, 1936, 1937; Kirchner, 1992) differing only in a few details, one of which is the common occurrence of slightly undulating anticlinal cell walls in *B. muensteriana* (see, e.g., Schenk, 1867; Kirchner, 1992) that are absent in *G. taeniatus*. The sunken stomata of *G. taeniatus* either lack or have only occasionally prominent papillae, but they exhibit thickened rings (Florin rings?) around the stomatal pit (Harris, 1935). Here, some cuticle portions have subsidiary cells with papillae, in others, there is only a thickened ring around the stomatal pit, but this is even sometimes occurring in the same portion of cuticle and might reflect environmental circumstances rather than interspecific variation.

Typical specimens of *G. taeniatus* and *B. muensteriana* can easily be distinguished by the width of their segments, and whose number per leaf is higher the latter. However, there are specimens, especially in the larger collections of Hettangian plant fossils from Bavaria, in which the difference is sometimes ambiguous. Given the variety of leaves of the extant *Ginkgo biloba* L., it might be possible that there is only one natural taxon of which both species are the extreme outliers, especially as they often occur in the same Hettangian localities, not only in Bavaria (Schenk, 1867; Gothan, 1914; Kräusel, 1959), but also in, e.g., Sassendorf (Germany, Kräusel, 1959), Poland (Pacyna, 2013; Barbacka et al., 2014) and Greenland (Jameson Land, Harris, 1935). In other areas, only either species has been recorded, e.g., *G. taeniatus* (as *Baiera taeniata*) in the eastern Urals (Kryshtofovich and Prinada, 1933), or *B. muensteriana* from Iran (Kilpper, 1971; Schweitzer and Kirchner, 1995). These outliers might also reflect environmental effects on leaf shape and size given climatic influences. Interestingly, neither species has been recorded in the renowned Rhaetian–Hettangian floras of Scania in southern Sweden (Lundblad, 1959; Pott et al., 2016b). In the (unlikely) case that both taxa belong to one natural species, *Baiera muensteriana* (Presl) Heer, 1867, has nomenclatural priority.

The fact that all the dispersed segment fragments were found in the uppermost 'Blätterkohle' layer more or less concurs with the fact that so far, all specimens of *G. taeniatus* (and of *B. muensteriana*) have been found exclusively in Hettangian sediments. This 'Blätterkohle' layer is
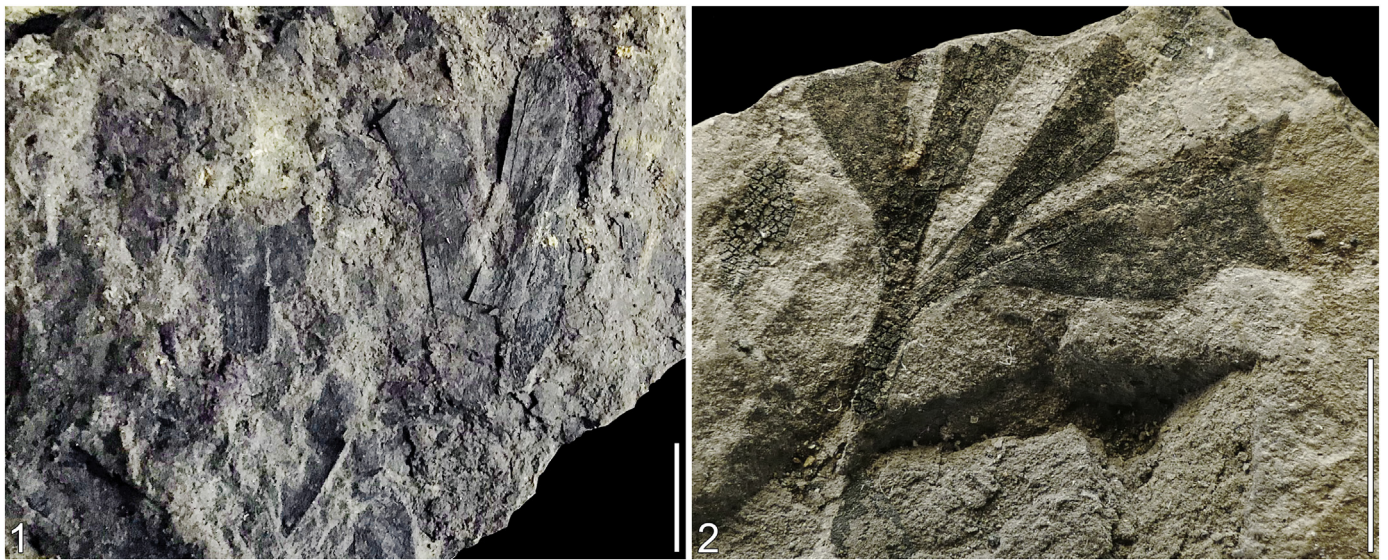
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Plate I. Gingkophytes from the Rhaetian of Wüstenwelsberg with specimen numbers. 1. Bifurcate segment of *Ginkgoites taeniatus* with rounded apex from the 'Blätterkohle" layer, UU23330. 2. *Ginkgoites* sp., leaf fragment with two orders of segments, Q375/04. Scale bars 1: 10 mm; 2: 5 mm.

the boundary layer between Rhaetian and Hettangian sediments, and belongs to the uppermost Rhaetian *Triletes* beds (Bonis et al., 2010), extending the stratigraphic range of *G. taeniatus* slightly. The mass occurrence of leaf fragments in this layer suggests that *G. taeniatus* was a deciduous tree similar to its extant representative.

A number of somewhat similar species have been described from various Rhaetian–Hettangian localities in Europe (see Lundblad, 1959, for an overview). *Ginkgoites acosmius* Harris, 1935, was described from the Rhaetian of Jameson Land and has also been recorded from the Rhaetian of Poland (Barbacka and Wcislo-Luraniec, 2002). It differs from *G. taeniatus* in having much wider segments and an upper cuticle with almost no stomata and obscure papillae on the epidermal cells. *Ginkgoites troedsonii* Lundblad, 1959, was described from the Rhaetian of Billesholm (Scania; Lundblad, 1959). The dissected segments can arise from the petiole at an angle (sinus) of up to 180°. Although the leaf is amphistomatic, the aspects of the upper and lower cuticle are rather different, in contrast to *G. taeniatus*, in which both cuticles are relatively similar. The presumed upper cuticle of *G. troedsonii* has heavily papillate epidermal cells and irregularly scattered stomata throughout the whole lamina without differentiation into stomatal and stomata-free zones. The presumed lower cuticle shows such differentiation clearly. Epidermal cells are less heavily papillate; the stomata have subsidiary cells that commonly form a thickened ring around the stomatal pit or bear papillae. Pott and McLoughlin (2011) recorded the species also from the Rhaetian of Rögla (Scania, Sweden).

Harris (1935) described *Ginkgoites minutus* (Nathorst, 1878) Harris, 1935, from the Rhaetian of Jameson Land. Earlier, Harris (1926) identified the material still as *Baiera muensteriana*, but described it as *G. minutus* later (Harris, 1935). The species was originally erected as *Baiera minuta* by Nathorst (1878a); that name has also been used by, e.g., Volynets and Shorokhova (2007) for material from the Late Triassic of Primorye (Russia). The species has relatively small leaves, in which dissected lobes arise from the petiole with a sinus of 120°–180°. The epidermal cell walls of the upper cuticle have undulating cell walls and a few stomata scattered between the epidermal cells, the lower cuticle is divided into stomata-free and stomatal zones, with stomata in irregular rows and less heavily cutinized than in *G. taeniatus*. *Ginkgoites hermelini* (Hartz) Harris, 1926, was included by Lundblad (1959) in *Ginkgoites marginatus* (Nathorst, 1878) Florin, 1936. It was recorded from the Hettangian of Jameson Land and Scania (Harris, 1935; Florin, 1936; Lundblad, 1959). The macromorphology is rather similar to that of *G. taeniatus*, but it differs in its cuticle; the upper cuticle has very few, sparsely distributed stomata,

the lower cuticle has numerous stomata with heavily papillate subsidiary cells. *Ginkgoites baieraeformis* Kilpper, 1971, and *Ginkgoites* sp. cf. *G. baieraeformis* were described by Kilpper (1971) from the Liassic of Iran. Both taxa were united by Schweitzer and Kirchner (1995) into *Baiera baieraeformis* (Kilpper) Schweitzer et Kirchner, 1995; the species macromorphologically resembles *G. taeniatus*, but is distinguished by its amphistomatic leaves with much thinner cuticles with clearly distinguishable stomatal and stomata-free zones on both sides; the stomata are always heavily cutinized carrying papillae, while the epidermis cells are much less cutinized with sometimes very thin, almost indistinct cell walls (Kilpper, 1971; Schweitzer and Kirchner, 1995).

Material examined: Schmeißner slide collection nrs. 478, 479, 496a, 558, ?559, 560–566 755, 758, 761. UU23301(C.4663), 23302 (C.4664), 23304 (C.4666, 4667), 23305 (C.4668), 23314 (C.4669), 23317 (C.4670–4773), 23330 (C.4693, 4694), 23338 (C.4701), 23342 (C.4708).

Ginkgoites sp.
Plate I, 2
Description: In the layer just below the 'Blätterkohle', a typical *Ginkgo*-type leaf fragment (Q375/04; Plate I, 2) was found showing a typical *Ginkgo*-type shape and outline. The broadly fan-shaped fragment, with a distinct petiole, is 11.0 mm long and 13.0 mm wide. The preserved portion of the petiole is 4.0 mm long and 1.0 mm wide (the base is not preserved). The transition from the petiole to the leaf lamina (sinus) is about 100°. The outer margin of the lamina is straight, with almost no curvature. The lamina is deeply dissected into two orders of tongue-shaped, slender lobes; the incisions reach almost down to the leaf base. The segments widen from their base and none of them is complete; apices have not been preserved. Two first-order lobes are preserved that are irregularly incised, the lateral lobes being much wider than the central lobes. First-order lobes are incised until c. 90–100% of their length. The venation is obscured due to poor preservation of the specimen, but a few bifurcating veins are observable in each segment with incident illumination. Vein density is, therefore, not to ascertain.

Discussion: We have some reservation in identifying the specimen as *Ginkgoites taeniatus* because it is comparatively small, not well preserved and we do not have a cuticle sample. The specimen was obtained from the layer just below the uppermost 'Blätterkohle'and consequently is definitely Rhaetian in age (see e.g., Bonis et al., 2010). As so far *G. taeniatus* has only been found in Hettangian outcrops, the identification of this leaf as *G. taeniatus* would represent the first Rhaetian record.

Material examined: Q375/04.

Order: CONIFERALES Engler et Prantl, 1889
Family: PALISSYACEAE Florin, 1958
Genus: **Palissya** Endlicher, 1847
Diagnosis and discussion: See Schenk (1867), Nathorst (1908), Pott and McLoughlin (2011), Pattemore et al. (2014).
Type species: Palissya sphenolepis (Braun, 1843) Nathorst, 1908, from the Hettangian of Hart near Bayreuth (Bavaria, Germany).

Palissya sphenolepis (Braun, 1843) Nathorst, 1908

Plate II, 1–5, V, 4
Selected references
1843 *Cunninghamites sphenolepis* — Braun, p. 24; pl. 13 figs. 19, 20.
1867 *Palissya braunii* Endlicher — Schenk, p. 175; pl. 41, figs. 2–14.
1908 *Palissya sphenolepis* (Braun) — Nathorst, p. 1; pl. 1, figs. 1–18; text-figs. 1–6.
1914 cf. *Palissya sphenolepis* Braun — Gothan, p. 159; pl. 25, figs. 3, 4.
1926 Conifer B — Harris, p. 124; no illustration.
1935 *Ontheodendron sternbergi* (Nilsson) — Harris, p. 78; pl. 11, figs. 5, 12–15, 18; pl. 15, figs. 1, 4–11; text-figs. 31A–D.
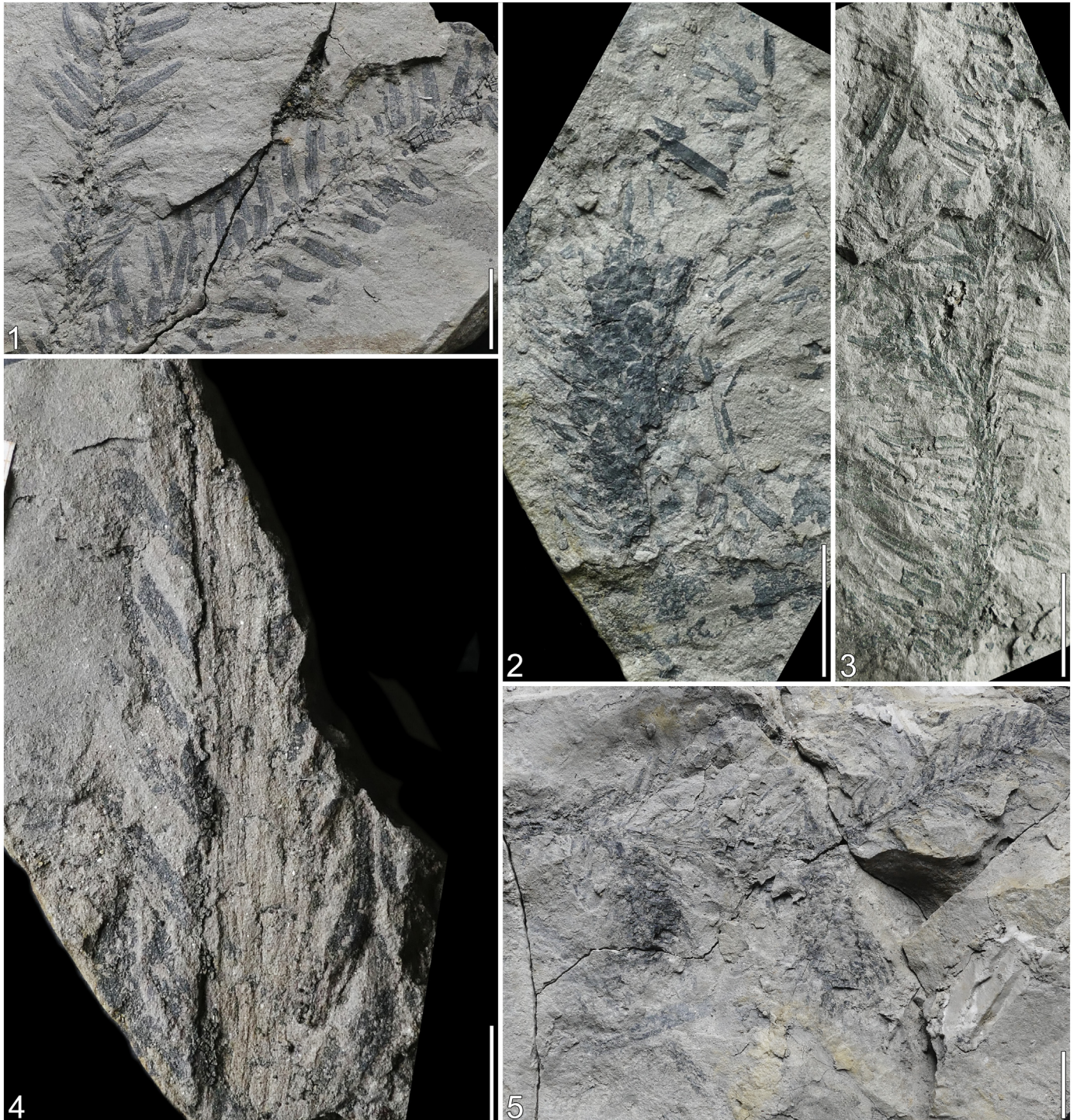
Plate II. *Palissya sphenolepis* from the Rhaetian of Wüstenwelsberg with specimen numbers. 1. *Palissya sphenolepis*, branched shoot fragment, Q124/02. 2. *Palissya sphenolepis,* cone, Q949/13. 3. *Palissya sphenolepis*, branched shoot fragment, Q686/08. 4. *Palissya sphenolepis*, fragment of an old stem with leaf scars, Q206/03. 5. *Palissya sphenolepis*, long-shoot fragment with two short-shoots, each carrying a cone, Q688/08. Scale bars 1–3, 5: 10 mm; 4: 5 mm.

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1958 *Palissya sphenolepis* (Braun) Nathorst — Florin, p. 270; pl. 1, figs. 1–6; pl. 2, figs. 1–3; text-fig. 1.

1959 *Palissya sphenolepis* (Braun) Nathorst — Kräusel, p. 133, pl. 6, figs. 36, 37.

1968 *Palissya sphenolepis* (Braun) Nathorst — Weber, p. 65; pl. 15, figs. 155–157; pl. 16, fig. 176.

2011 *Elatocladus* sp. cf. *Palissya sphenolepis* (Braun) Nathorst — Pott and McLoughlin, p. 1042; text-fig. 9M.

2014 *Palissya sphenolepis* (Braun) Nathorst — Pattemore et al., p. 51; text-figs. 1A, B.

Description: There are some 60 specimens of *Palissya sphenolepis* in the Wüstenwelsberg assemblage. Specimens include vegetative shoots and seed cones. Some specimens only yield small fragments of vegetative shoots, others yield densely foliated vegetative short shoots with helically arranged but pseudo-distichous leaves; some shoots represent long shoots that occasionally produce short shoots (e.g., Q304/03, 686/08; Plate II, 3). Cones are found isolated or terminally attached to vegetative shoots (e.g., Q688/08, 949/13; Plate II, 5). Q688/08 displays the longest long-shoot fragment (113.0 mm long) with two short shoots carrying cones (Plate II, 5). Other shoot fragments are commonly shorter (35.0–97.0 mm) (e.g., Q124/02, 613/08; Plate II, 1). Leaves are persistent, bifacial and helically arranged. They are lanceolate, slightly contracted at their base and tapering to a more or less acute apex (Plate II, 1, 3). Leaves are 8.0–13.0 mm long and 0.9–1.4 mm wide; they are inserted at angles of 30°–70°. The ovulate cones in Q688/08 measure 17.0 × 8.5 mm and 22.0 × 11.0 mm respectively; the cone in Q949/13 (Plate II, 2) is 20.5 × 14.7 mm in size and that of 95wü08 is 35.0 × 15.5 mm in dimensions.

Leaves are hypostomatic. Cuticles are thin and difficult to prepare; we only obtained small fragments. Epidermal cells vary in shape between elongate rectangular (over the vein and near the margins) to irregularly isodiametric; cells sometimes bear short papillae. The abaxial epidermis has two narrow stomatal bands, one on each side of the midvein; stomata are irregularly arranged or forming short rows within the bands (Q686/08; Plate V, 4). Stomata are haplocheilic and monocyclic, consisting of two slightly sunken guard cells (commonly not preserved) and 5–7 subsidiary cells, sometimes displaying papillae overhanging the stomatal pit.

A number of detached ovulate cones similar to *Palissya* cones are among the fossils, such as Q205/02, Q699/08, Q949/13 (Plate II, 2), none of which is complete and well-preserved; they measure 40.0–50.0 × 17.0–26.0 mm in dimensions. Details cannot be observed although bracts seem to be spirally arranged and carrying axillary seed-scales; however, details such as the number of seeds per seed scale are not discernable.

Some thicker, probably older shoot/stem fragments with only a few leaves attached show leaf scars on naked areas (e.g., Q206/03, Plate II, 4); the figured shoot fragment is only 40.3 mm long and 15.0 mm wide, consisting of a 4.5-mm-wide axis with some attached leaves, the longest of which is 12.0 mm long and 1.5 mm wide. The denuded part of the shoot displays spirally arranged leaf scars up to 1.3 mm wide (Plate II, 4).

Remarks: *Palissya* plants are characterized by their ovulate cones with characteristic cone scales consisting of a seed–scale-complex and a slightly longer subtending bract. The seed–scale-complex adaxially yields of two rows of very short seed scales, each carrying an orthotropous seed distally that is basally surrounded by a cup-shaped aril (Pattemore et al., 2014; Pattemore and Rozefelds, 2019). The original material of *Palissya sphenolepis* was described as *Cunninghamites sphenolepis* from the Hettangian of Bavaria (Braun in Münster, 1843; Schenk, 1867), based on foliage and attached ovulate cones, while pollen cones remained unknown. Later, the species was recorded also from the Rhaetian–Hettangian strata of Scania (Nathorst, 1878, 1886, 1908).

Nathorst (1908) recognized that the name *Palissya braunii* Endlicher, 1847 was illegitimate and recombined it into *Palissya sphenolepis*. However, Nathorst (1908) was unable to reveal the exact nature of the ovulate cones. Florin (1958) improved Nathort's description of the morphology of the ovulate cones. Schweitzer and Kirchner (1996) published a renewed concept of the reproductive structures of *Palissya* inferred from *Palissya oleschinkskii* Schweitzer et Kirchner, 1996 from the Hettangian of Zangerud, Iran. They re-interpreted the hitherto ovulate cones of *Palissya* as male ones; what was interpreted as seeds were in fact pollen sacs. They also described ovulate cones attached to shoots with *Elatocladus* foliage as *Compsostrobus brevirostratus* Schweitzer et Kirchner, 1996, the ovuliferous scales of which only comprise two seeds per seed-scale-complex, leading them to emend the diagnosis of the family Palissyaceae and the genus *Palissya*. This interpretation has since then seriously been debated by e.g., Parris et al. (1995), Pattemore et al. (2014) and Pattemore and Rozefelds (2019) in their elaborate papers on *Palissya* including a re-study of the holotype of *Palissya oleschinkskii*. The authors revealed that the specimen lacked seed-scale pairs and ovules, and thus an assignment to *Palissya* was not warranted, rendering the Iranian record of *Palissya* doubtful. Based on permineralized specimens of *Palissya tillackiorum* Pattemore et Rozefelds, 2019 from Australia, Pattemore and Rozefelds (2019) concluded that the ovulate cones of *Palissya* have helically arranged bract/scale complexes, each comprising a bract with an adaxial ovule/scale unit, ovules placed in two parallel rows. Each ovule/scale unit has an ovule mounted terminally on a vascular trace and is subtended by a pair of scales that surround the ovule (but are not fused), forming a cup-like structure. So far, the authors did not find pollen cones either.

The material from Wüstenwelsberg neither yields details of the ovulate bract/scale complexes nor good cuticles, but in all other aspects (size, leaf morphology, cone grossmorphology), the specimens are similar to *Palissya sphenolepis* material as known from elsewhere. Hence, we identify our material as *P. sphenolepis*.

Palissya sphenolepis was widely documented from the Rhaetian–Hettangian of Germany (Braun, 1843; Schenk, 1867; Gothan, 1914; Weber, 1968; Kräusel, 1959) and southern Sweden (Scania; Nathorst, 1878, 1886, 1908; Pott and McLoughlin, 2011). From the Rhaetian–Hettangian flora of Jameson Land, Harris, 1926 recorded 'Conifer B' being reminiscent of a *Palissya* shoot, according to the description. Later, Harris (1935) proved the presence of *P. braunii* by including it and the identical *P. sternbergii* (Nilsson, 1831) Nathorst, 1886, from Scania in the synonymy of *Ontheodendron sternbergii* (Nilsson, 1831) Harris, 1935, but omitting the earlier 'Conifer B'. The type material of *Ontheodendron* Sahni and Rao, 1933 was subsequently identified as a cycadophyte (Rao and Bose, 1959) rendering the genus *Ontheodendron* illegitimate. The coniferalean specimens from Jameson Land should be considered as *Palissya* as well.

Apart from Germany, Sweden and Greenland, *Palissya sphenolepis* has also been recorded from Rhaetian–Hettangian localities of Poland (Pacyna, 2013, 2014) and Canada (Vavrek et al., 2007). Outside Europe, another *Palissya* species has been recorded from the Rhaetian of Hunan, China, viz., *Palissya hunanensis* Wang, 2012 by Wang (2012). From younger (Toarcian–Aptian) strata, several species have been described from the UK, New Zealand and Australia (Parris et al., 1995, Pattemore et al., 2014, Pattemore and Rozefelds, 2019).

Material examined: Q76/01, 85/01, 124/02, 203/02, 213/02, 304/03, 327/03, 345/03, 479/06, 484/07, 491/07, 495/07, 513/07, 522/07, 613/08, 621/08, 667/08, 686/06, 688/08 + cone, 697/08, 733/09 + cone fragment, 787/09, 852 + 853/11, 855/11, 860/11, ?905/12, 948/13, 949 + 950/13 cones; 12wü01, 24wü02, 31wü02 + cone, 136wü02 + cone, 154wü02, 182wü02, 04wü03, 09wü03, 96wü03, 107wü03 + cone, 13wü06, 40wü06, ?48wü06, 08wü08, 09wü08, 70wü08 + cone, 73wü08, 95wü08 (shoot plus cone), 106wü08, 131wü08, 10wü09, 81wü09 + cone,

86wü09, 34wü10, 39wü10 + female cone, 42wü10, 45wü10; UU 23321 (C.4683), 23349 (C. 4715), 23826 (C. 7455).

Detached female cones: Q204 + 205/02, 442/06, 527/07, 665/08, 699/08, 705/08, 706/08, 716/08, 742/09, 784/09, 785/09, 786/09; 112wü02, 136wü03, 34wü06, 11wü08, 95wü08, 109wü09, 09wü12, 16wü13, 05wü18.

Old almost denuded twigs: Q206/06, Q225/02 (C.440), 857/11, 153wü08 (stem), 32wü09, 02wü12, UU23263.

Genus: **Stachyotaxus** Nathorst, 1886

Diagnosis and discussion: See Nathorst (1886), Harris (1935), Arndt (2002), Pott and McLoughlin (2011), Pattemore et al. (2014).

Plate III. *Stachyotaxus septentrionalis* from the Rhaetian of Wüstenwelsberg with specimen numbers. 1. *Stachyotaxus septentrionalis*, typical shoot fragment, Q1078/18. 2. *Stachyotaxus septentrionalis*, shoot fragment with some leaves showing more acute apices, Q758/09. 3. *Stachyotaxus septentrionalis*, shoot fragment showing the pseudodistichous arrangement of the leaves clearly, Q713/08. 4. *Stachyotaxus septentrionalis*, female cone, Q253/02. 5. *Stachyotaxus septentrionalis*, branched shoot fragment, Q611/11. 6. *Stachyotaxus septentrionalis*, small apical shoot fragment, Q701/08. Scale bars 1–3: 10 mm; 4–6: 5 mm.

Type species: Stachyotaxus septentrionalis (Agardh, 1823) Nathorst, 1886, from the Rhaetian of Bjuv, Scania (Sweden).

Stachyotaxus septentrionalis (Agardh, 1823) Nathorst, 1886.

Plate III, 1–6, V, 5

Selected references

1823 *Caulerpa septentrionalis* — Agardh, p. 110; pl. 2, fig. 7.

1886 *Stachyotaxus septentrionalis* (Agardh) — Nathorst, p. 98; pl. 22, figs. 20–23, 33, 34; pl. 23, fig. 6; pl. 25, fig. 9.

1908 *Stachyotaxus elegans* — Nathorst, p. 11; pl. 2, figs. 1–24, 27; pl. 3, figs. 10–12.

1922 *Stachyotaxus elegans* Nathorst — Johansson, p.51; pl. 1, figs. 30–31; pl. 6, figs. 18–19.

1926 *Stachyotaxus elegans* Nathorst — Harris, p. 119; pl. 10, figs. 2–4; pl. 12, figs. 1, 2, 6; pl. 13, fig. 5; text–figs. 30E, F, I, J.

1935 *Stachyotaxus elegans* Nathorst — Harris, p. 52; pl. 10, figs. 1–3, 6–9, 11; pl. 21, figs. 1–3; pl. 27, fig. 7; text-fig. 23.

1935 *Stachyotaxus septentrionalis* (?non Agardh) Nathorst — Harris, p. 56; pl. 9, figs. 11, 12, 14–17; pl. 10, figs. 4, 5, 10, 12, 13.

1995 *Stachyotaxus elegans* Nathorst — Kelber and Hansch, p. 128, fig. 264.

1997 *Stachyotaxus elegans* Nathorst — Kelber and Van Konijnenburg-van Cittert, p. 107; pl. 2, fig. 2.

2002 *Stachyotaxus septentrionalis* (Agardh) Nathorst — Arndt, p. 13; pl. 3, figs. 1–6; text-figs. 5, 6. (and references therein).

2011 *Stachyotaxus septentrionalis* (Agardh) Nathorst — Pott and McLoughlin, p. 1044; text-figs. 9K–L, P–Q. (and references therein).

Description: More than 60 specimens of *Stachyotaxus septentrionalis* were recorded; all specimens yield only small leafy shoot fragments, the largest ones being around 50 mm long (e.g., Q1078/18; Plate III, 1). One specimen (Q666/11; Plate III, 5) includes a branched apical fragment, 38.6 mm long and consisting of 4 terminal young short shoots with spirally arranged leaves. Leaves are 2.0–3.5 mm long and 0.7–1.1 mm wide; they are inserted at angles of 45°–60°. Another apical fragment (Q701/08; Plate III, 6) is only 21.1 mm long and has 2.2–4.5 mm long leaves that are 0.8–1.1 mm wide. Most other leafy shoots have longer and slightly wider leaves, up to 7.7 mm long and 1.5 mm wide. All leaves are inserted spirally at angles of 70°–90°, but appear pseudodistichous, thus are twisted basally to be confined to one plane (Plate III, 1–3, 6), never overlapping. Leaves are single-veined, strongly decurrent basally and commonly with an obtuse apex (Q634/08, Q713/08; Plate III, 3), although some leaves may have more acute apices (Q758/09; Plate III, 2).

Cuticles are thin and difficult to prepare; separating adaxial and abaxial cuticle is often impossible. The adaxial cuticle reflects polygonal cells that are more elongate over the vein and near the margins (UU23321, Q758/08, Q1078/18; Plate V, 5). The abaxial cuticle has the same type of epidermal cells, but on each side of the midrib, there is narrow stomatal band with smaller, almost isodiametric epidermal cells. Stomata are more or less arbitrarily scattered in the bands, or forming short, irregular rows. Stomata are hard to observe (Plate V, 5) and consequently, their orientation within the bands is not always discernible. Guard cells are always lacking; the 4–6 subsidiary cells are mainly unspecialized with occasional thickenings around the stomatal pit. No papillae, trichomes or hairs have been observed. The obtained small cuticle fragments (Plate V, 5) are identical with those described by Harris (1935).

A number of female cones has been collected, but most are poorly preserved. The best one is Q253/02 (Plate III, 4), a laterally embedded cone fragment, only 26.0 mm long and 10.0 mm wide. The female scales are about 6.0 mm long. They bear seeds (4.5 mm long) at their base. Cuticles were extremely difficult to prepare; we only got one very small portion from a female scale showing a single type of isodiametric polygonal epidermal cells. The cones are similar to those described by Nathorst (1886), Harris (1926, 1935), Arndt (2002) and Pott and McLoughlin (2011).

Remarks: *Stachyotaxus septentrionalis* is a taxon characteristic for the Rhaetian, identified by the features of its cones (see below) and its leafy shoots with leaves that are inserted spirally, but are twisted basally to be confined to one plane (Plate III, 1–3, 6), almost never overlapping. The apices are commonly obtuse (Q634/08, Q713/08), although sometimes more acute apices occur (Q758/09).

Initially, such vegetative shoot fragments and cones were described as *Caulerpa septentrionalis* Agardh, 1823. They were transferred to *Cyparissidium septentrionale* (Agardh) by Nathorst (1878b) and subsequently to the new genus *Stachyotaxus* Nathorst, 1886, as *Stachyotaxus septentrionalis* (Agardh) Nathorst, 1886, based on material from the Rhaetian of Bjuv (Scania, Sweden; Nathorst, 1886). Later, Nathorst (1908) identified a second species, viz. *Stachyotaxus elegans* Nathorst, 1908, also from Bjuv. The species was differentiated from *S. septentrionalis* by minimal size differences. After elaborate studies of Rhaetian material from Scania (Bjuv and Rögla), Arndt (2002) as well as Pott and McLoughlin (2011) came to the conclusion that the material falls well into the variability of a single species, of which *Stachyotaxus septentrionalis* had priority. In the Wüstenwelsberg material we also found shoots with leaves of quite variable size. Despite of this variability, and in agreement with Arndt (2002) and Pott and McLoughlin (2011), we believe that all fragments from Wüstenwelsberg belong to a single species as well, viz. *S. septentrionalis*.

Stachyotaxus septentrionalis (and material described under the junior synonym *S. elegans*) has been recorded from the Rhaetian of Scania (Nathorst, 1886, 1908; Johansson, 1922; Arndt, 2002; Pott and McLoughlin, 2011), Jameson Land (Harris, 1935, 1937) and Heilgersdorf (Bavaria, Germany) (Kelber and Van Konijnenburg-van Cittert (1997). Doubtful or records in need of revision include the specimens described as *S. elegans* by Boersma and Van Konijnenburg-van Cittert (1991) from the Rhaetian of Aghdarband (Iran), *S. septentrionalis* from the Rhaetian and Hettangian of Poland (Pacyna, 2013, 2014) and two small fragments from the Lower Jurassic of Bornholm (Möller, 1903). Volynets and Shorokhova (2007) mention *Stachyotaxus gracilis* from the Late Triassic flora of Primorye (Russia), but without description or discussion.

Material examined: Q67/01, 68/01, 234/02, 254/02, 345/03, 346/03, 365/04, 481/06, 482/06, 512/07, 577/08, 578/08, 634/08, 635/08, 666/08, 674/08, 679/08, 693/08, 697/08, 701/08, 713/08, 728/09, 758 + 759/09, 948/13, 1078/18, 1079/18, 1080/18, 1081/18, 1082/18; 73wü02, 103wü02, 159wü02, 163wü02, 21wü03, 32wü03, 42wü03, 102wü03, 132wü03, 29wü06, 10wü08, 52wü08, 181wü08, 184wü08, 87wü09 (C.), 106wü09, 34wü10, 42wü10, 45wü10 + cone, 01wü18, 02wü18, 03wü18, 04wü18, 06wü18, 09wü18, 10wü18; UU23244, 23249, 23262, 23276, 23278, 23284, 23313, 23343.

Cones: Q253/02, 344/03 found together with 345/03 and 346/03, 887/11 and its counterpart 888/11; 58wü08, 08wü18.

Comparison to Palissya: *Palissya sphenolepis* and *Stachyotaxus septentrionalis* occur in more or less the same quantities in the Wüstenwelsberg flora and are both relatively common species in the flora. Both belong to the Palissyaceae and appear to be closely related, but they are distinguished by foliage and female cone features (Florin, 1958; Pattemore et al., 2014). These include genuinely helically arranged leaves in *P. sphenolepis*, while those of *S. septentrionalis* are helically arranged but are disposed distichously (cf. extant *Sequoia* or *Taxodium*)., and epidermal cells and stomata that appear to be slightly larger in *S. septentrionalis* than in *P. sphenolepis* [compare e.g., Florin, 1958 pl. 1, figs. 1–3 (*P. sphenolepis*) to pl. 2 fig. 4 (*S. septentrionalis*)]. The ovulate cones are overall similar in general bract–/cone-scale morphology, but differ in the number of ovules/seeds per scale: whereas *S. septentrionalis* produced only 2 ovules/seeds per scale, the number is up to 10 in *P. sphenolepis* (see Pattemore et al., 2014, fig. 1 for the latest reconstruction).

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Stratigraphically, the first appearance of both genera is in the Rhaetian. *Stachyotaxus* is so far restricted to Rhaetian assemblages only, whereas *Palissya* has a longer stratigraphic range with a number of species occurring from the Rhaetian up to the Aptian (Pattemore and Rozefelds, 2019).

Family: INCERTAE SEDIS
Genus: **Schizolepis** Braun, 1847

Diagnosis and discussion: See Braun (1847), Schenk (1867), Kirchner (1992).

Type species: Schizolepis liasokeuperianus (Braun, 1846) Schenk, 1867, from the Rhaetian–Hettangian of Veitlahm near Kulmbach (Bavaria, Germany).

Schizolepis liasokeuperianus (Braun, 1847) Schenk, 1867
Plate IV, 1–3, Plate V, 6–9.
Selected references
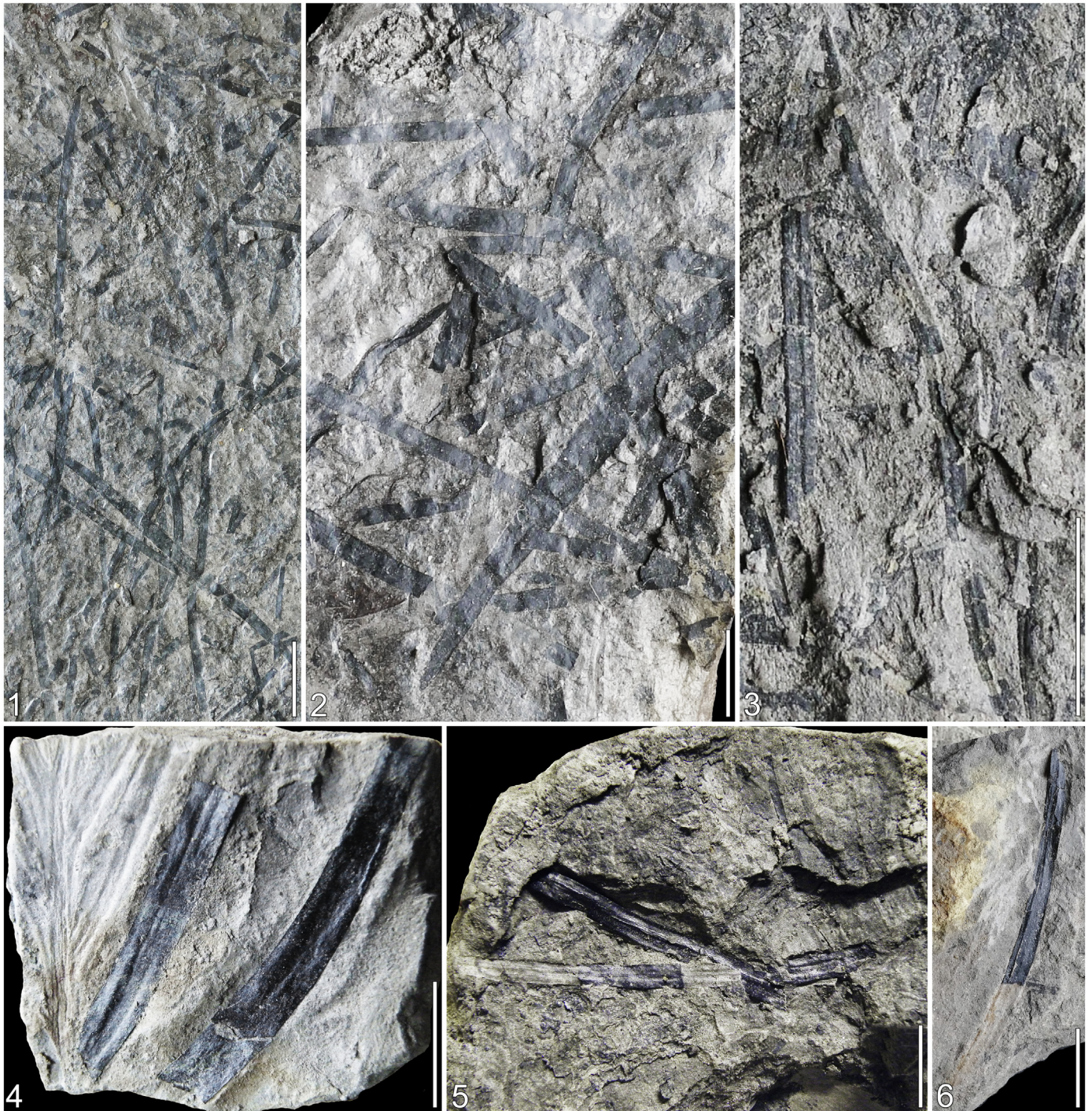
Plate IV. *Schizolepis liasokeuperianus* (Figs. 1–3) and *Becklesia franconica* sp. nov. (Figs. 4–6) from the Rhaetian of Wüstenwelsberg with specimen numbers. 1. *Schizolepis liasokeuperianus*, part of a slab covered with needles, Q961/14a. 2. *Schizolepis liasokeuperianus*, part of a slab covered with needles, one of which is showing an obtuse apex, Q963/14. 3. *Schizolepis liasokeuperianus*, some needles showing the midrib, Q495/07. 4. Segmented frond fragment of *Becklesia franconica* sp. nov., holotype, UU27000. 5. *Becklesia franconica* sp. nov., two isolated leaflets showing the central sunken portion flanked by a bulging zone on each side, 09wü09. 6. *Becklesia franconica* sp. nov., apical part of a leaflet with margins converging to an obtusely rounded apex, Q182/02. Scale bars 1, 3–6: 10 mm; 2: 5 mm.

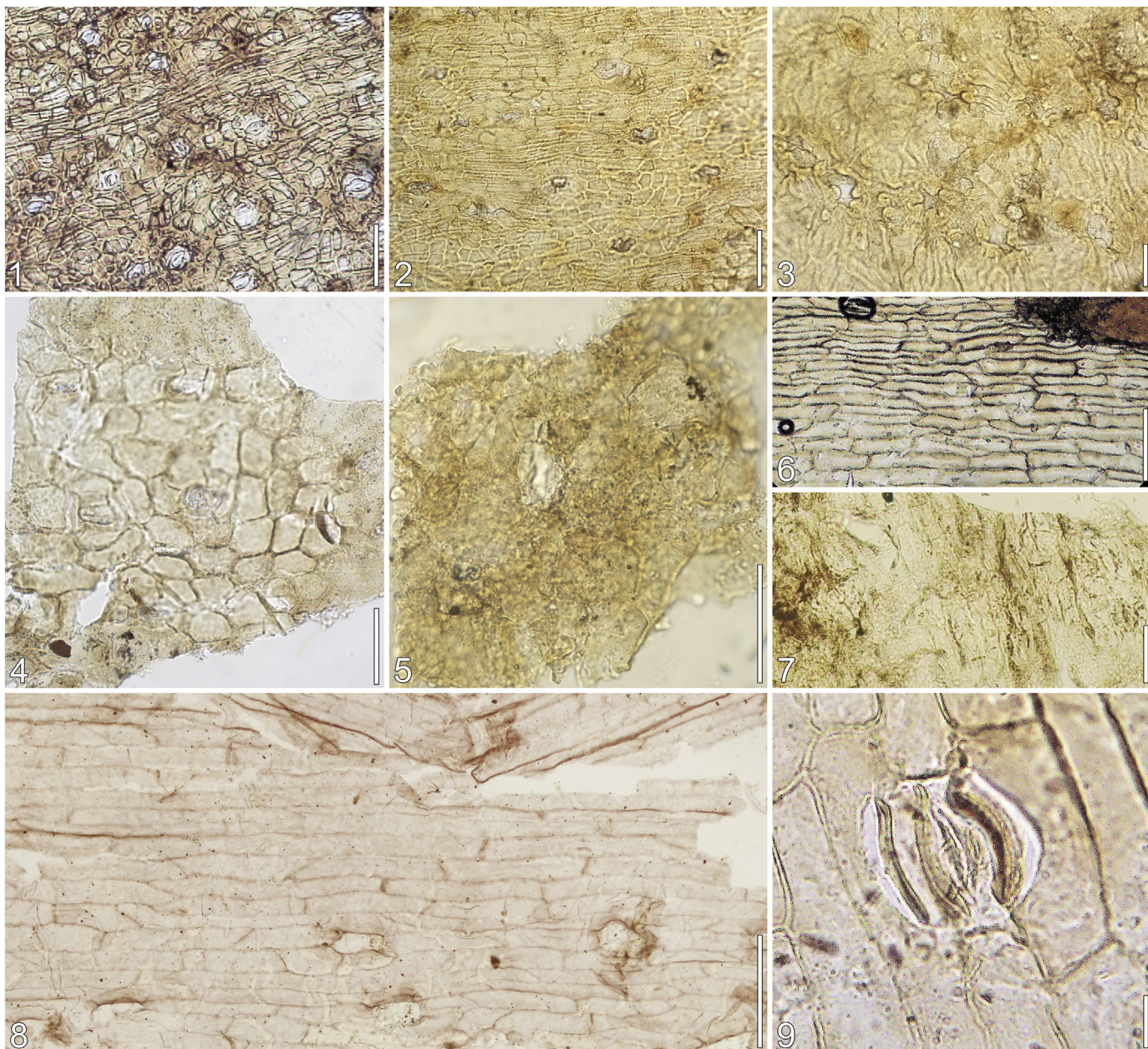**Plate V.** Cuticles of *Ginkgoites taeniatus* (Figs. 1–3), *Palissya sphenolepis* (Fig. 4), *Stachyotaxus septentrionalis* (Fig. 5) and *Schizolepis liasokeuperianus* (Figs. 6, 7, 9) from the Rhaetian of Wüstenwelsberg and *Pityophyllum angustifolium* (Fig. 8) from the Rhaetian of Skromberga (Scania, Sweden). 1. *Ginkgoites taeniatus,* abaxial cuticle fragment from the 'Blätterkohle" layer, showing rows of stomata, cuticle slide 479 (coll. S.S.). 2. *Ginkgoites taeniatus,* adaxial cuticle with less stomata, UU23330. 3. *Ginkgoites taeniatus,* a number of papillate stomata interconnected by epicuticular ridges, UU23330. 4. *Palissya sphenolepis,* cuticle fragment with several stomata, Q686/08. 5. *Stachyotaxus septentrionalis,* cuticle fragment with a stoma, Q758/09. 6. *Schizolepis liasokeuperianus,* adaxial cuticle, cuticle slide 434 from Q219/02. 7. *Schizolepis liasokeuperianus,* some longitudinally oriented stomata, cuticle slide 253 from 63wü03. 8. *Pityophyllum angustifolium,* abaxial cuticle with several stomata, Rhaetian of Skrombergia, S075823; courtesy of Stephen McLoughlin, NRM, Stockholm, Sweden. 9. *Schizolepis liasokeuperianus,* stoma from abaxial cuticle, cuticle slide 434 from Q219/02. Scale bars 1, 2, 6–8: 100 μm; 3–5: 50 μm; 9: 10 μm.

1864 *Voltzia schizolepis* — Braun, p. 1258; no illustration.

1847 *Schizolepis liaso keuperinus* — Braun, p. 86; no illustration.

1867 *Schizolepis liasokeuperina* Braun — Schenk, p. 179; no illustration.

1867 *Schizolepis braunii* — Schenk, p. 179; pl. 44, figs. 1–8.

1886 *Taxites angustifolius* Nathorst — p. 109; pl. 22, figs. 7, 8.

1903 *Pityophyllum angustifolium* (Nathorst) — Möller, p. 39; pl. 5, figs. 22, 23.

1914 ? *Schizolepis braunii* Schenk — Gothan, p. 160; pl. 26, fig. 4.

1959 *Schizolepis liasokeuperiana* — Kräusel, p. 109; pl. 5 figs. 22–25; text-figs. 5a, b.

1992 *Schizolepis liasokeuperiana* — Kirchner, p. 35; pls. 9, 10; text-figs. 6–9.

1995 *Schizolepis liasokeuperianus* — Kelber and Hansch, p. 128, fig. 275.

1997 *Schizolepis liasokeuperianus* — Kelber and Van Konijnenburg-van Cittert, p. 107; pl. 2, fig. 7.

Description: Many of the c. 45 specimens of *Schizolepis liasokeuperianus* comprise single needles or a small number of needles only. However, some slabs are completely covered by the same narrow needles (e.g., Q495/07, Q961/14a, b, Q962/14, Q963/14) (Plate IV, 1). The needles were never found attached to any axes forming shoots,

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although some seem to be arranged in bundles resembling caducous short shoots (Q495/07; Plate IV, 3). No needle or leaf is complete; the largest fragment is 47 mm long, and their width varies between 1.2 mm and 2.0 mm. In several needles, the lamina slowly tapers towards an obtuse apex (Plate IV, 2), while the proximal portions (bases) of the needles were not preserved in any specimen. In some specimens, a conspicuous midrib is visible (Q495/07; Plate IV, 3), while in others, the midrib is less conspicuous and only the lateral parallel fine bundles (striae or veinlets) are visible. Those latter specimens may have been preserved laying upside down.

Cuticles are very delicate and difficult to isolate. The leaves appear to be hypostomatic; so far, no stomata have been observed on the retrieved adaxial cuticle portions (Plate V, 6). Normal epidermal cells are irregularly elongate and rectangular (Plate V, 6). The midrib is indicated by slightly narrower elongate cells. Stomata on the abaxial epidermis are restricted to the two areas between the midrib and the margins, not arranged in distinct rows and longitudinally oriented (Plate V, 7). Stomata are monocyclic, elongate; guard cells commonly absent, surrounded by 4–6 unspecialized subsidiary cells (Plate V, 9).

Remarks: Detached needles of this morphology commonly are assigned to *Pityophyllum* (Nathorst) Möller, 1903; when they are attached to a short shoot, they are assigned to the fossil-genus *Pityocladus* (Nathorst) Seward, 1919. Such needles were found in Veitlahm in Bavaria as early as 1846, dispersed or attached to short shoots, and in close association with female cones and assigned the name *Voltzia schizolepis* (Braun, 1846). Later, Braun (1847) re-assigned the leaves to *Schizolepis* as *Schizolepis liasokeuperianus* with a brief diagnosis involving needle-like leaves, short shoots with attached leaves, ovulate cones and isolated ovuliferous scales. Based on the deeply cleft, two-lobed ovuliferous cone-scales, Braun (1847) distinguished it from the genus *Voltzia*, to which he had attributed the material initially. Schenk (1867) later described and figured the material in detail from various localities in Bavaria, including Veitlahm and Strullendorf as *Schizolepis braunii*, because he considered the epithet *liasokeuperianus* not well chosen due to the Rhaetian age of the Veitlahm and Strullendorf material. The latter is, however, now considered Hettangian in age (Van Konijnenburg-van Cittert et al., 2018b). Later records from the area include Gothan's detached needles from Hettangian localities near Bayreuth (Gothan, 1914), and ovuliferous cone-scales from Sassendorf near Bamberg (Kräusel, 1959). The most extensive study on *Schizolepis liasokeuperianus* was conducted by Kirchner (1992) describing and figuring leaves in detail from various Hettangian localities (as *Pityophyllum*-type), ovulate cones and ovuliferous cone-scales, including also descriptions of cuticles of the leaves and ovuliferous cone scales. For the first time, Kirchner (1992) also figured ovulate cones in organic connection to short shoots and leaves. Many more attached ovulate cones were found, mainly from the Hettangian locality of Pechgraben (between Kulmbach and Bayreuth), and numerous leaves of *Schizolepis liasokeuperianus* were recorded from the Rhaetian localities of Heilgersdorf near Coburg (Kelber and Van Konijnenburg-van Cittert, 1997) and Einberg, of which similar cuticles could be prepared (Plate VI, 7). The needles from Wüstenwelsberg closely match those of *S. liasokeuperianus* in all aspects and thus can be regarded identical with that taxon.

From the Rhaetian–Hettangian floras from Jameson Land, no fossils have been described assignable to *Schizolepis*, neither leaves of the *Pityophyllum* type (Harris, 1926, 1935, 1937). From the closely related Rhaetian–Hettangian floras from Scania, only one, poorly preserved cone fragment, described as *Schizolepis moelleri* Seward, 1907, was recorded (Antevs, 1919), the correct assignment of which has to be reviewed. In contrast to Jameson Land, *Pityophyllum* type leaves have been reported from severaly Rhaetian–Hettangian localities in Scania (Antevs, 1919; Johansson, 1922), of which *Pityophyllum angustifolium* most losely matches the leaves from Wüstenwelsberg macro-morphologically. The conspecificity of both taxa could be proven by

unpublished cuticle material of *P. angustifolium* from the Rhaetian of Skromberga and Stabbarp in Scania (Plate V, 8), kindly provided by the Swedish Museum of Natural History, Stockholm, that was identical with the cuticle of *S. liasokeuperianus*.

Pityophyllum angustifolium has also been recorded from the Sinemurian of the Holy Cross Mountains in Poland by Pacyna (2013), co-occurring with *Schizolepis braunii*. Stanislavski (1971) mentioned *Pityophyllum* sp. from the Donets Basin. Harris (1979) described isolated cone scales from a single locality in the Bathonian of Yorkshire as *S. liasokeuperianus*, but we doubt that the material is really conspecific and the cone scales are correctly assigned to *S. liasokeuperianus* by Harris (1979), since the cone scales were associated with *Pityocladus scarburgensis* Harris, 1979 – short shoots and detached leaves of the *Pityoyphyllum* type. These leaves are similar to the ones described here from Wüstenwelsberg, except that they are only half as wide (0.6–1.1 mm versus 1.2–2.0 mm) and amphistomatic. They stomata are scattered over both surfaces and never form files or bands. Moreover, the attachment area of the ovules/seeds is more towards the scale's centre than in *S. liasokeuperianus* from southern Germany.

Schweitzer and Kirchner (1996) recorded *Schizolepis pedicelata* Turutanova-Ketova, 1950, ovuliferous scales from the Liassic of Zirab, Iran and *Pityocladus* sp. from the Liassic of Zangerud (Iran). The latter is compared to *S. liasokeuperianus* short shoots and leaves, but the leaves are much wider (3–4 mm). The ovuliferous scales of *S. pedicelata* differ considerably from those of *S. liasokeuperianus* from Bavaria in being much larger and have the seed scars more proximal on the scales. In recent years, several more *Schizolepis* species have been described, mainly from the Jurassic and Lower Cretaceous of Russia and China [see Zhang et al., 2011 and Xu et al., 2013 for elaborate overviews].

Material examined: Q139/02, 179/02, 187/02, 217/02, 218/02, 219/02, 233/02, 240/02, 241/02, 267/03, 268/03, 304/03, 372/04, 410/05, 484/07, 495/07, 526/07, 697/08, 762/14, 763/14, 764/14, 788/09, 961/14a, b, 962/14, 963/14; C.662; 43wü02, 96wü02, 119wü02, 132 wü02, 14wü03, 63wü03, 139wü03, 70wü08, 100wü08, 130wü08, 81wü09, 40wü10, 02wü14, 04wü18, 07wü18; UU23248, UU23263, 23,269,? 23,275, 23,281, 23,339, 23,817.

Order: CYCADALES Persoon ex Berchtold et Presl, 1820
Family: INCERTAE SEDIS
Genus: **Becklesia** Seward, 1895
Diagnosis and discussion: See Seward (1895), Watson (1969), Watson and Cusack (2005).
Type species: Becklesia anomala Seward, 1895 from the Wealden (Berriasian/Valanginian) of Ecclesbourne near Hastings (UK).

Becklesia franconica spec.cvc nov.
Plate IV, 4–6, VI, 1–6.
Synonymy:
2018a *Rhaphidopteris* sp. — Van Konijnenburg-van Cittert et al., p. 197; pl. 2, fig. 6; pl. 3, fig. 7.
Holotype: UU27000, Plate IV, 4, here designated.
Repository: Laboratory of Palaeobotany and Palynology, University of Utrecht, The Netherlands.
Type locality: Main clay layer in the quarry near Wüstenwelsberg, N 50°08′ E 10°48′, a village in the vicinity of Coburg, Bavaria, Germany.
Type horizon and age: Contorta beds (Exter Formation), uppermost Rhaetian, Triassic.
Etymology: The epithet refers to the area Franconia in Bavaria (Germany) where the fossils were found.
Diagnosis: Leaf simply pinnate, straight; leathery leaflets inserted laterally to prominent rachis; leaflets or pinnae arising (sub)oppositely at an angle of c. 30°, attached with their whole base; leaflets showing a distinct, broad central depression (probably representing midvein) flanked by two flanges; leaves hypostomatic, cuticles thick; adaxial cuticle with slightly elongate epidermal cells, arranged in irregular rows; abaxial cuticle with two broad stomatal bands, with stomata-free
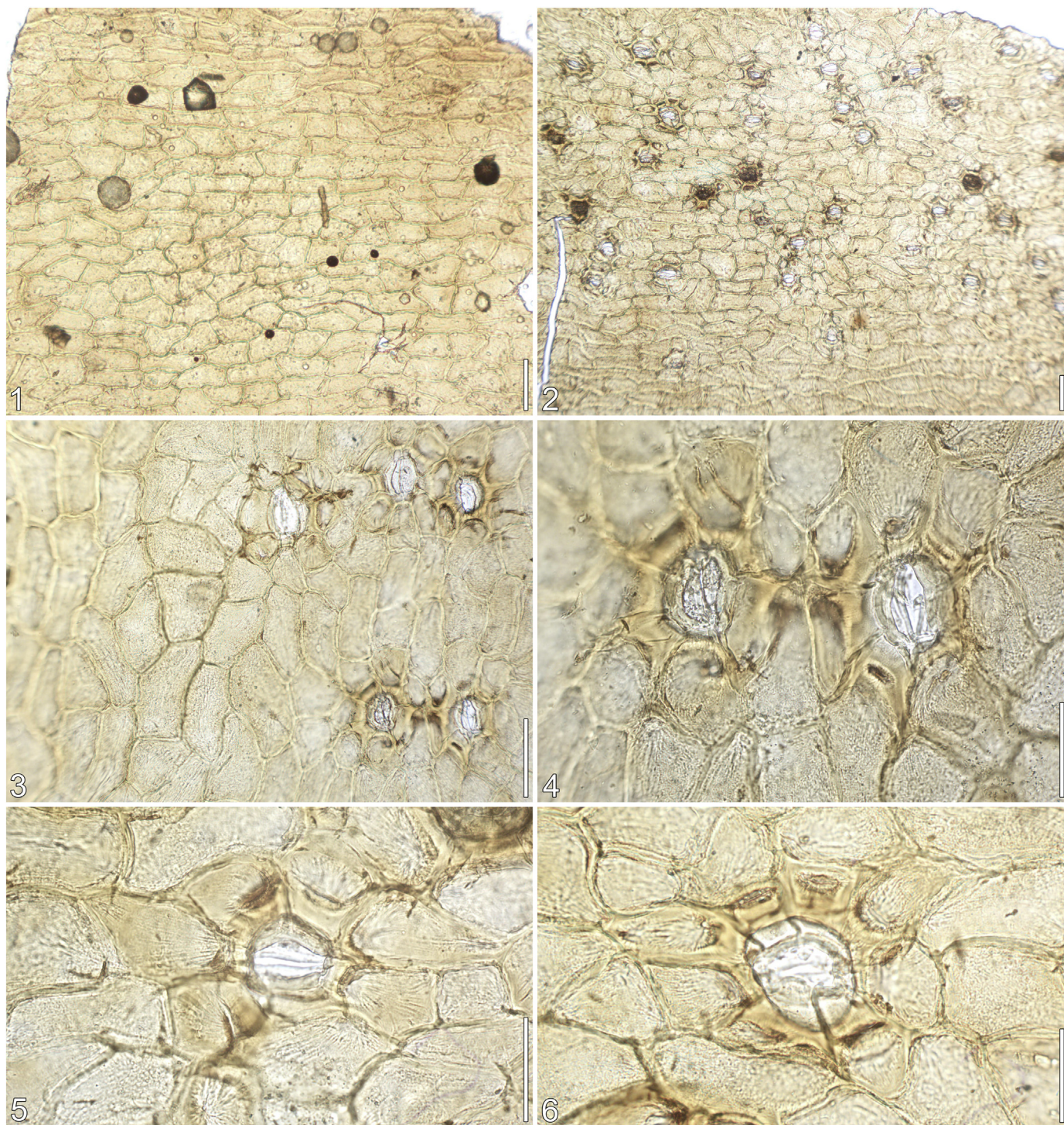
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Plate VI. Cuticles of *Becklesia franconica* from the Rhaetian of Wüstenwelsberg. 1. *Becklesia franconica*, adaxial cuticle, UU27000 (holotype). 2. *Becklesia franconica*, abaxial cuticle, showing a stomatal band, UU27000 (holotype). 3. *Becklesia franconica*, stomata in an abaxial cuticle, showing irregular distribution, UU27000 (holotype). 4. *Becklesia franconica*, detail of Fig. 3 showing two typical, adjacent stomata, UU27000 (holotype). 5, 6. *Becklesia franconica*, typical stomata with thickened subsidiary cells forming a ring around the stomatal pit and carrying hollow papillae, UU27000 (holotype). Scale bars 1–3: 100 μm; 4–6: 50 μm.

marginal zones and a stomata-free broad middle zone indicating midvein; stomata irregularly scattered within the bands, longitudinally oriented, guard cells sunken, surrounded by 6–8 subsidiary cells forming a ring around the stomatal pit.

Description: Some 15 specimens with segmented leaf fragments were encountered, of which one (UU27000; Plate IV, 4) yields a longitudinally striate, 2-mm-wide rachis with fragments of six pairs of leaflets attached. The leaflets arise (sub)oppositely at an angle of c. 30°; they are attached by their whole basal width. All leaflets are incomplete, the largest fragment is 29.0 mm long and 3.0 mm wide. The leaflets show a distinct, sunken or depressed central portion (1.5 mm wide, probably representing the midvein) with a bulging zone on each side, where the stomata are located in bands. No further venation is visible. Apart from two apical fragments that will be discussed below, there are a couple of detached leaflet fragments (Plate IV, 5, 6). All specimens demonstrate the typically sunken central portion

and bulging zones to each side (or a central portion flanked by sunken lateral zones if the specimen is preserved upside down). Specimen 09wü09 (Plate IV, 5) has two leaflet fragments, the longest of which is 53.0 mm long and 3.0 mm wide. All other specimens provide slightly shorter fragments that are rather uniform in width, varying from 2.7 to 3.0 mm. None of the specimens shows a distinct leaflet apex, although in Q138/02 and Q182/02, there is an indication in one of the two leaflet fragments in which margins converge towards an obtuse apex (Plate IV, 6).

Leaves are hypostomatic. The adaxial cuticle constitutes slightly elongate epidermal cells, more or less arranged in irregular rows. Cells are more elongate over the supposed midvein (Plate VI, 1). The abaxial cuticle shows a broad stomatal band to each side of the midvein, with stomata-free marginal zones and a stomata-free broad middle zone indicating the midvein. Stomata are irregularly scattered within the bands, sometimes relatively far apart and sometimes closely adjacent, but never sharing subsidiary cells (Plate VI, 2). Stomata are longitudinally oriented, guard cells sunken, surrounded by 6–8 subsidiary cells forming a ring around the stomatal pit (Plate VI, 3–6). Subsidiary cells sometimes carry papillae overhanging the stomatal pit.

Remarks: *Becklesia* was erected by Seward (1895) for a number of fossil leaves from the Wealden of Ecclesbourne near Hastings (UK). Its type species (*B. anomala*) consisted of an axis giving off "stout and stiff branches" (Seward, 1895, p. 179). The 'branches' show a number of parallel longitudinal striations on one surface, while on the other, a broad median rib with a small groove on either side is present.

Watson (1969) emended the description of Seward (1895) by adding epidermal features to the diagnosis and assigned the genus to the Cycadales. The Wüstenwelsberg material fits the characteristic features of *Becklesia*, especially the long, stiff pinnate leaves with their pinnae showing a broad midrib flanked by two narrow, shallow stomatal grooves, so we attribute it to the genus, although the known material of *Becklesia* was so far exclusively Wealden in age.

Becklesia is mainly differentiated from the very similar and also simply pinnate *Paracycas* Harris, 1964, by pinnae that arise at angles of almost 90° in the latter, and stomatal grooves sunken below the level of the broad midrib in the former versus even pinnae in *Paracycas* (Watson and Sincock, 1992). Cuticles of *Paracycas* are thin while those of *Becklesia* are thick reflecting leathery leaves.

While Le Couls et al. (2016) extended the stratigraphic range of Becklesia into the Jurassic with the description of *Becklesia maulnyi* Le Couls et al., 2016, from the Upper Jurassic of France, we can demonstrate an even longer stratigraphic range extending into the Rhaetian.

Specimens earlier assigned to the seedfern genus *Rhaphidopteris* Barale, 1972 by Van Konijnenburg-van Cittert et al. (2018a) based on grossmorphology, are now regarded as *Becklesia franconica* leaf fragments because the preserved leaf portions turned out to be hypostomatic, and thus, an attribution to *Rhaphidopteris* with its amphistomatic leaves is unwarranted (Zhou and Zhang, 2000). Based on epidermal morphology, those fragments are identical with the here recognized *Becklesia franconica* leaves. No fossils similar to *Becklesia franconica* have so far been found in the Rhaetian–Hettangian assemblages of Bavaria, neither have they been reported from the other Rhaetian–Hettangian under consideration here. The only, but only remotely, similar material is *Campylophyllum hoermannii* Gothan, 1914, from the Hettangian of the area around Nuremberg (Gothan, 1914; the exact locality is unknown, possibly Wolfshöher Tonwerke). However, *Campylophyllum hoermannii* is characterized by a very thick rachis and slightly falcate, long pinnae with a thick cuticle (and no stomata observed). Unfortunately, the illustrations of this very rare species do not make a close comparison possible, and an examination of the original material is warranted, but beyond the scope of this paper.

Nathorst (1876) described *Cycadites? longifolius* Nathorst, 1876 from the Rhaetian of Pålsjö in Scania (Sweden) for a number of dispersed leaf fragments that resemble the pinnae of *Becklesia franconica*. Later, Nathorst (1878b) transferred the material to the genus *Taxites*

(Nathorst, 1878) and Möller (1903) subsequently assigned it to *Pityophyllum* as *Pityophyllum longifolium* (Nathorst) Möller, 1903. It was also recorded from the Hettangian of Scania by Antevs (1919). *Pityophyllum longifolium* is similar to *Becklesia franconica* in its macromorphology including the presence of a strong midrib, but as no cuticle has ever been described, further comparison is impossible. Stanislavski (1971) briefly and incompletely described and figured *Pityophyllum* cf. *longifolium* from the Upper Triassic of the Donets Basin.

Material examined: Q138/02, 182/02, 278/02, 345/03, Q770/09; 20wü02 (cut), 30wü02, 09wü07,155wü08, 179wü08, 03wü09F, 09wü09, 04wü10, 01wü18; UU 23222, UU27000(Holotype).

4. Discussion

4.1. Composition of the flora

The Rhaetian flora from Wüstenwelsberg is been thoroughly studied by the authors in recent years (see Van Konijnenburg-van Cittert et al., 2020, and references therein). Here, we discuss the ginkgoalean and conifer taxa found in the assemblage, and describe a new species of the cycad genus *Becklesia*, which came to our attention when examining the remaining material initially assigned to ginkgoaleans and conifers.

Ginkgophytes include *Ginkgoites taeniatus* that has only been found as dispersed leaf fragments in the uppermost 'Blätterkohle' layer of Wüstenwelsberg (representing the boundary with the Hettangian). So far, all specimens of *G. taeniatus* had been found elsewhere in Hettangian sediments only, the record of this species in the layers under study here consequently slightly extended the species' stratigraphic distribution. Another ginkgoalean, tentatively assigned to *Ginkgoites* sp., is represented by a single small fragment from the layer just below that 'Blätterkohle' layer and hence is definitely Rhaetian in age (see e.g., Bonis et al., 2010).

The conifers are represented by two species of the Palissyaceae (*Palissya sphenolepis* and *Stachyotaxus septentrionalis*) that are equally common in Wüstenwelsberg. A third conifer, *Schizolepis liasokeuperianus*, is slightly less common.

4.2. Comparisons

4.2.1. Comparison with other Rhaetian floras from the Northern Hemisphere

Ginkgoites taeniatus is traditionally recorded from Hettangian strata only and was never found in Rhaetian sediments so far. The type area for the three conifer taxa recorded at Wüstenwelsberg is Bavaria and consequently, their occurrence is not unexpected, and all three can be regarded as common elements of the Rhaetian of Bavaria. Some of the species also occur in other Rhaetian floras; *Palissya sphenolepis* is reported from Scania (southern Sweden) and might have been thriving in Jameson Land (East Greenland) as well. *Stachyotaxus septentrionalis*, a characteristic species of Rhaetian conifers, has also been recorded from Scania and Jameson Land and, moreover, from Poland and other areas of Germany. *Schizolepis liasokeuperianus* was not described from any of the other floras so far, but detached needles of *Pityophyllum angustifolium* were found in Scania showing similar cuticular features to the leaves of *S. liasokeuperianus* rendering both taxa possibly conspecific.

Becklesia franconica or similar macrofossil remains assignable to the taxon were, as to our knowledge, never recorded from any Rhaetian locality. So far, it appears to be endemic to the Rhaetian of Wüstenwelsberg, but since it was here recognized for the very first time – rendering it a new species of the commonly Cretaceous genus *Becklesia*; re-evaluation of Rhaetian–Hettangian floras from elsewhere might uncover its presence in other regions, too. In most Rhaetian floras, representatives of the genus *Podozamites* occur, but have not been found in the Rhaetian of Wüstenwelsberg, although

Table 1
Comparison of the plant assemblage found at Wüstenwelsberg with those of the Rhaetian floras of Jameson Land, Scania, Poland, Donets Basin and Iran. For references, see paragraph 4.2.1. NB. The Polish record of *Desmiophyllum harrisii* is fro the lowermost Hettangian; its presence in the Rhaetian has not yet been proved (Barbacka et al., 2014).

		Jameson Land	Scania	S Poland	Wüstenwelsberg	Heilgersdorf	Donets	Alborz
Lycophytes	*Lepacyclotes* sp.				X			
	Selaginellites coburgensis				X			
Equisetophytes	*Equisetites laevis*	X	X		X	?X		X
Ferns	*Todites goeppertianus*	X	X		X			?*Todites williamsonii*
	Todites roessertii	?X	?X	X	X			
	Todites (Cladophlebis) scoresbyensis	X			X			
	Phlebopteris muensteri	X			X			X
	Phlebopteris angustiloba	X	X		X			
	Clathropteris meniscioides	X	X	X	X		X	X
	Dictyophyllum exile	X	X		X	X		X
	Thaumatopteris brauniana	X	X		X			X
Seed ferns	*Lepidopteris ottonis*	X	X	X	X	X	X	X
	Antevsia zeilleri	X	X		X	X		
	Peltaspermum rotula	X	X	X	X	X	?X	
	Peltaspermum sp.				X			
	Pachypteris sp. cf. *P. rhomboidalis*		?X	?X	X	?X		
	Ptilozamites nilssonii	X	X		X			
	Ptilozamites heeri		X		X			
	Hydropterangium roesleri				X			
	Carpolithes sp.				X			
Cycadales and allies	*Nilssonia pterophylloides*		X		X			
	Doratophyllum nathorstii		X		X			
	Ctenis latepinnata		X		X			
	Pseudoctenis florinii		X		X			
	Pseudoctenis cteniforme		X		X			
	Becklesia franconica				X			
Bennettitales	*Nilssoniopteris ajorpokensis*	X			X	?X		
	Nilssoniopteris jourdii	X			X			
	Pterophyllum astartense	X			X	X		
	Pterophyllum kochii	X			X			
	Pterophyllum pinnatifidum	X			X			
	Pterophyllum aequale	X	X		X		X	?X
	Welsbergia bursigera	X	X		X			
	Wielandiella angustifolia	X	X		X		X	X
	Anomozamites gracilis		X		X			
Ginkgophytes	*Ginkgoites taeniatus*				X			
	Ginkgoites sp.				X			
	Desmiophyllum harrisii			X	X		?X	
Conifers	*Palissya sphenolepis*	?X	X		X			
	Stachyotaxus septentrionalis	X	X	X	X	X		
	Schizolepis liasokeuperianus		?X		X	X		

they are common again in the Hettangian beds from Bavaria (see Section 4.2.2).

When comparing the entire flora from Wüstenwelsberg (Table 1) with other Rhaetian assemblages from the Northern Hemisphere. We can see that the similarity with the floras from Jameson Land and Scania is by far the largest, with resp. 21–23 taxa in common for Jameson Land and 22–25 for Scania, respectively. With the Rhaetian floras from Poland (6–7 taxa), Donets Basin (4–6) and Iran (7–9) the Wüstenwelsberg flora has much less taxa in common. This may be due to their higher (paleo)geographic distance (in the case of the latter two) from Wüstenwelsberg during the Rhaetian than Scania. Interestingly, the floras from Jameson Land and Wüstenwelsberg also share a high number of species, although Jameson Land was further away than, e.g., Poland. Reasons for the similarity of the floras may be found in the similarity of the environments, where the plants thrived in Jameson Land, Scania and Franconia, in contrast to a possibly different environment in the Polish Rhaetian (Raciborski, 1892; Pacyna, 2014). It may also be possible that an interconnection between Jameson Land and Wüstenwelsberg through the Viking and Koch straits played a role here (see Pott et al., 2018).

The specific composition reveals that only two taxa occur in all compared Rhaetian floras, viz., the fern *Clathropteris meniscioides* and the seed fern *Lepidopteris ottonis*. Especially ferns and seed ferns include a number of taxa that are also represented in a couple of other Rhaetian floras, except of course for those taxa that are so far only known

from Wüstenwelsberg. It is remarkable that almost all cycad taxa from Wüstenwelsberg also occur in Scania but have not been recorded from anywhere else (including Jameson Land). Vice versa, most (eight) bennettitalean taxa from Wüstenwelsberg occur in Jameson Land, but only four have also been encountered in Scania and two in the Donets Basin and possibly Iran probably revealing different dispersal strategies or habitat requirements.

With regard to the Ginkgoales, *Ginkgoites taeniatus* has not been found in any other Rhaetian flora, but up till now, this taxon was a Hettangian species, and our record from the uppermost layers at Wüstenwelsberg is the first Rhaetian occurrence. The Rhaetian conifer *Stachyotaxus septentrionalis* has a distribution strongly restricted to Central Europe (Scania, Greenland, Poland, Franconia; see Pott and McLoughlin, 2011); so far, it has not been found in the Donets Basin and Iran (the record of Boersma and Van Konijnenburg-van Cittert (1991) has been questioned by Schweitzer and Kirchner (1996) and Pott and McLoughlin (2011)), while the Rhaetian–Hettangian conifers *Palissya sphenolepis* and *Schizolepis liasokeuperianus* have been found in Jameson Land and/or Scania only. Finally, *Desmiophyllum harrisii* was also recorded from the Hettangian of Poland and putatively from the Donets Basin, but from nowhere else.

4.2.2. Comparison with the Hettangian flora of Franconia

The Rhaetian flora from Wüstenwelsberg shows some differences to the Hettangian flora from adjacent areas in Franconia (Table 2; see Van

Table 2
Comparison of the plant assemblage found at Wüstenwelsberg with that of the Hettangian localities in the area. For references, see paragraph 4.2.2.

Wüstenwelsberg	Hettangian floras Bavaria
Lycophyta	
Lepacyclotes sp.	
	Lepacyclotes kirchneri
Selaginellites coburgensis	
Equisetophyta	
Equisetites laevis	
	Equisetites muensteri
	Neocalamites lehmannianus
	Schizoneura carcinoides
Pteridophyta	
	Marattia intermedia
	Todites princeps
Todites goeppertianus	
Todites roessertii	*Todites roessertii*
Todites (Cladophlebis) scoresbyensis	
Cladophlebis sp.	
	Selenocarpus muensterianus
Phlebopteris muensteri	*Phlebopteris muensteri*
Phlebopteris angustiloba	*Phlebopteris angustiloba*
Clathropteris meniscioides	*Clathropteris meniscioides* very rare
Dictyophyllum exile	
	Dictyophyllum nilssonii
	Dictyophyllum muensteri
Thaumatopteris brauniana	*Thaumatopteris brauniana*
	Goeppertella microloba
	Phialopteris heterophylla
Spiropteris sp.	
Pteridospermae	
Lepidopteris ottonis	
Antevsia zeilleri	
Peltaspermum rotula	
Peltaspermum sp.	
Pachypteris sp. cf. *P. rhomboidalis*	*Pachypteris rhomboidalis*
	Pachypteris saligna
	Sagenopteris nilssoniana
	Ctenozamites (Ptilozamites) wolffiana
Ptilozamites nilssonii	
Ptilozamites heeri	
Hydropterangium roesleri	
Carpolithes sp.	
	Rhaphidopteris duetschii
Cycadales	
Nilssonia pterophylloides	
	Nilssonia acuminata
	Nilssonia polymorpha
	Nilssonia minima
	Cycadites sp.
Doratophyllum nathorstii	
Ctenis latepinnata	
Pseudoctenis florinii	
Pseudoctenis cteniforme	
	Pseudoctenis prossii
Becklesia franconica	
Bennettitales	
Nilssoniopteris ajorpokensis	
Nilssoniopteris jourdyi	
	Nilssoniopteris sp.
Pterophyllum astartense	
Pterophyllum kochii	
Pterophyllum pinnatifidum	
Pterophyllum aequale	
Welsbergia bursigera	
	Pterophyllum sp.
Wielandiella angustifolia	
Anomozamites gracilis	*Anomozamites gracilis*
	Anomozamites marginatus
	Zamites sp.
	Otozamites brevifolius
	Weltrichia mirabilis

Table 2 (*continued*)

Wüstenwelsberg	Hettangian floras Bavaria
Ginkgophyta	
Ginkgoites taeniatus	*Ginkgoites taeniatus*
Ginkgoites sp.	
	Schmeissneria microstachys
	Stachyopitys preslii
	Sphenobaiera spectabilis
	Karkenia hauptmannii
Coniferophyta	
Palissya sphenolepis	*Palissya sphenolepis*
Stachyotaxus septentrionalis	
Schizolepis liasokeuperianus	*Schizolepis liasokeuperianus*
	Hirmeriella muensteri
	Podozamites distans
	Podozamites schenkii
	Swedenborgia spp.
Incertae sedis	
Desmiophyllum harrisii	
	Desmiophyllum gothanii
	Piroconites kuespertii
	Bernettia inopinata
	Chlamydolepis lautneri
	Campylophyllum hoermannii

Konijnenburg-van Cittert et al., 2014, 2018b, 2020; Pott et al., 2016a, and references therein). Although the same genera may occur in both floras, the species composition is often different pointing to some floral turn-over in the composition of the vegetation at the T–J boundary. 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. (2016a) and Van Konijnenburg-van Cittert et al. (2018b, 2020). The formerly exclusively Hettangian *Ginkgoites taeniatus* was common in those floras of Bavaria; *Palissya sphenolepis* is more or less equally common in the Rhaetian and Hettangian floras, and the same is for *Schizolepis liasokeuperianus*. Both *Stachyotaxus septentrionalis* and *Becklesia franconica* have so far not been recorded in the Hettangian floras from Bavaria.

Lepacyclotes occurs in both floras, but in Wüstenwelsberg, we encountered only one specimen (Bauer et al., 2015). *Selaginellites coburgensis* Van Konijnenburg-van Cittert et al., 2016, is so far endemic to Wüstenwelsberg. The only equisetalean species in Wüstenwelsberg is *Equisetites laevis* Halle, 1908; it has not been found in the Hettangian flora, which comprises three other species [i.e., *Equisetites muensteri* Sternberg, 1833, *Neocalamites lehmannianus* (Göppert) Weber, 1968, *Schizoneura carcinoides* (Harris) Weber, 1968]. Few fern species occur in both assemblages, e.g., *Todites roessertii* (Presl in Sternberg) Kryshtofovich, 1912, *Phlebopteris muensteri* (Schenk) Hirmer and Hörhammer, 1936, and *P. angustiloba* (Presl in Sternberg) Hirmer and Hörhammer, 1936 (although rare in the Rhaetian flora), *Clathropteris meniscioides* (Brongniart) Brongniart, 1828 (common in the Rhaetian, very rare in the Hettangian), *Todites goeppertianus* (Münster) Krasser, 1922, and *Thaumatopteris brauniana* Popp, 1863. *Dictyophyllum exile* (Brauns) Nathorst, 1878, and *Cladophlebis scoresbyensis* Harris, 1926, were found in the Rhaetian only, whereas *Marattia intermedia* (Münster) Weber, 1968, and *Todites princeps* (Presl in Sternberg) Gothan, 1914, are common in the Hettangian floras just as both *Dictyophyllum* species [*D. nilssonii* (Brongniart) Göppert, 1846, and *D. muensteri* (Göppert) Nathorst, 1878]; *Selenocarpus muensterianus* (Presl) Schenk, 1867, *Goeppertella microloba* (Schenk) Ôishi and Yamasita, 1936, and *Phialopteris heterophylla* (Sternberg) Van Konijnenburg-van Cittert et al., 2018b, are rare taxa in the Hettangian floras.

Lepidopteris ottonis (Göppert) Schimper, 1869, with its reproductive organs *Antevsia zeilleri* (Nathorst) Harris, 1937, and *Peltaspermum rotula* Harris, 1937, is an index fossil for the Rhaetian and very common in Wüstenwelsberg; its last occurrence is at the top of the section and it

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has never been found in Hettangian floras. *Pachypteris rhomboidalis* (Ettingshausen) Doludenko, 1974, is very common in the Hettangian; in the Rhaetian of Wüstenwelsberg, only a few remains putatively assignable to this species have been recorded, extending the species' occurrence into the latest Rhaetian. *Pachypteris saligna* (Schenk) Doludenko, 1974, is locally common in the Hettangian of Bavaria just as *Sagenopteris nilssoniana* (Brongniart) Ward, 1900. *Ptilozamites nilssonii* Nathorst, 1878, and *P. heeri* Nathorst, 1878, are common in the Rhaetian, but were never found in the Hettangian, albeit another species is uncommonly occurring there, viz., *Ctenozamites* (*Ptilozamites*) *wolfiana* (Gothan) Harris, 1964. Finally, *Rhaphidopteris duetschii* Van Konijnenburg-van Cittert et al., 2001, is a rare element in the Hettangian floras.

None of the six cycadalean species from Wüstenwelsberg occur in the Hettangian floras although two genera extent into the Hettangian albeit with different species. *Nilssonia pterophylloides* Nathorst, 1879, is rare at Wüstenwelsberg, but two of the three Hettangian *Nilssonia* species (*N. acuminata* (Presl) Göppert, 1844, and *N. polymorpha* Schenk, 1867) are very common, whereas *N. minima* Gothan, 1914, is relatively rare. *Doratophyllum nathorstii* Florin, 1933, *Ctenis latepinnata* Florin, 1933, *Pseudoctenis florinii* Lundblad, 1950, and *P. cteniforme* (Nathorst) Harris, 1950, all occur in the Rhaetian flora but are absent from the Hettangian. Other species of *Doratophyllum, Pseudoctenis* and *Ctenis* have so far never been found in the Hettangian of Bavaria. *Becklesia franconica* is so far endemic to Wüstenwelsberg and material determined as *Cycadites* sp. (based on macromorphology and cuticular anatomy) from the Hettangian still has to be described.

The number of bennettitalean taxa in the Wüstenwelsberg assemblage is much higher than in the Hettangian. *Nilssoniopteris ajorpokensis* (Harris) Florin, 1933, and *N. jourdyi* (Zeiller) Florin, 1933, occur in the Rhaetian, while so far only a few specimens of *Nilssoniopteris* sp. were found in the Hettangian floras (generic assignment based on macromorphology and cuticle anatomy). The same applies to *Pterophyllum*, where four species are found in Wüstenwelsberg including the very common *P. astartense* Harris, 1932, and *P. aequale* (Brongniart) Nathorst, 1878, with its reproductive organ *Welsbergia bursigera* (Harris) Pott et al., 2016a, and *P. kochii* Harris, 1926, and *P. pinnatifidum* Harris, 1932), whereas the *Pterophyllum* specimens from the Hettangian so far only have been determined as *Pterophyllum* sp. *Wielandiella angustifolia* (Nathorst) Nathorst, 1913, only occurs at Wüstenwelsberg, in contrast to *Anomozamites gracilis* Nathorst, 1876, that is the only bennettitalean taxon that definitely occurs in both the Rhaetian and the Hettangian floras. *Anomozamites marginatus* (Unger) Nathorst, 1876, occurs solely and rarely in the Hettangian floras. *Otozamites brevifolius* Braun, 1843, is quite common in the Hettangian floras, together with a few specimens so far assigned to the genus *Zamites* Brongniart, 1828.

The only Ginkgoalean species in the Rhaetian of Wüstenwelsberg is *Ginkgoites taeniatus*, whereas it is a common species in the Hettangian of Bavaria. Two further ginkgoalean taxa including their reproductive organs are known from the Hettangian, viz., *Schmeissneria microstachys* (Presl) Kirchner and Van Konijnenburg-van Cittert, 1994, with its male reproductive organ *Stachyopitys preslii* Schenk, 1867, and *Sphenobaiera spectabilis* (Nathorst) Florin, 1936.

Two of the three conifer taxa found at Wüstenwelsberg are more or less equally common in the Hettangian of Bavaria (viz., *Palissya sphenolepis* and *Schizolepis liasokeuperianus*). *Stachyotaxus septentrionalis* is confined to Rhaetian sediments. In contrast to other European Rhaetian floras, no *Podozamites* species have been encountered in the Rhaetian of Bavaria (see e.g., Harris, 1937; Weber, 1968; Pott and McLoughlin, 2011; Pacyna, 2014; Barbacka et al., 2014). *Podozamites distans* (Presl) Braun, 1843, is very common in Hettangian assemblages in Bavaria, *P. schenkii* Heer, 1876, occurs as well, just as their female reproductive organs assigned to the genus *Swedenborgia* Nathorst, 1876. The same applies to *Brachyphyllum*-type of foliage and especially *Hirmeriella*

muensteri (Schenk) Jung, 1968. *Hirmeriella muensteri* (including its attached reproductive organs) occurs in almost every Hettangian locality and is locally very common.

Desmiophyllum harrisii Barbacka et Pacyna, 2014, is a rare fossil in the Rhaetian of Wüstenwelsberg (Van Konijnenburg-van Cittert et al., 2019), while the Hettangian *D. gothanii* Florin, 1936 (with its reproductive organs *Piroconites kuespertii* Gothan, 1914 ex Kustatscher et al., 2016, and *Bernettia inopinata* Gothan, 1914) is quite common (Kirchner, 1992; Kustatscher et al., 2016). The enigmatic *Campylophyllum hoermannii* Gothan, 1914, has only been found in one Hettangian locality near Nuremberg and is very rare.

4.3. Comparison with palynological data

Bonis et al. (2010) carried out a detailed palynological study on the Wüstenwelsberg section and gave a list of the macroplant remains (Bonis et al., 2010, table 1), which has, however, been revised since then. The plant remains discussed in the present paper and enlisted in Table 1 come mainly from three parts of the section (see Fig. 2). The light gry shale level in the 'Hauptsandstein' (Postera beds?) yielded mostly fragments of *Lepidopteris ottonis* plus a few fern specimens and *Stachyotaxus septentrionalis*. Most plant remains come from the 'Hauptton' (Contorta beds). Most plant remains were collected from the middle and upper part of the succession, mostly from the dark gry shales rich in coaly material including many remains of *Lepidopteris ottonis* and *Pterophyllum aequale* as well as rare fragments of *Phlebopteris, Dictyophyllum* and *Stachyotaxus*. The *Triletes* beds yielded in the uppermost part (light and medium gry shales; 'Blätterkohle'), almost exclusively fragments of *Ginkgoites taeniatus* and very few leaf fragments of *Lepidopteris ottonis*. From level *1 exist no pollen record since this part of the succession was covered with stones and mud during the year, when the palynological studies were undertaken.

Thus, the lowermost palynological sample of the section has not been used for comparisons (An overview of the comparison between the palynological and plant fossil data is given in Table 3).

The section yielded a large amount of sporomorphs (62 taxa, 50 genera) including a wide range of taxa that are not reflected in the macroplant assemblage, probably because they belong to plant remains that were not yet found in the outcrop and/or lived further away, in the hinterland area. For three fern taxa, however, i.e., *Phlebopteris muensteri, Phlebopteris angustiloba, Clathropteris meniscioides*, corresponding spore taxa have been recorded in the palynological samples (i.e., *Matonisporites, Dictyophyllidites* and *Converrucosisporites*, respectively; see Schenk, 1867; Lundblad, 1950; Tralau, 1965; Van Konijnenburg-van Cittert, 1993; Van Konijnenburg-van Cittert et al., 2020).

Bryophytes are rare but represented in the palynological assemblage by *Rogalskaisporites, Porcellispora* and *Stereisporites*, exclusively in level 3, a horizon rich in ginkgophyte fragments, but no other macrofossil remains were found so far.

Lycophytes are represented in the macroplant assemblage by the Isoetales (*Lepacyclotes*) and Selaginellales (*Selaginellites*), to which the spore genera *Aratrisporites* and *Uvaesporites* correspond, respectively, being a rare component of the flora, even if further nine spore taxa may be associated with lycophytes. The Isoetales are only represented by *Aratrisporites* in the palynoflora, but further three different spore taxa reflect a possible higher diversity of Selaginellales (see Bonis et al., 2010). Six further spore taxa with affinity to the lycophytes suggest a muc higher diversity of the group than reflcted in the macrofossil record.

The sphenophytes are represented in the macrofossil assemblage by *Equisetites laevis* and in the palynological record by *Calamospora*. Ferns are represented in the macrofossil assemblage by members of the Osmundales (3 species), Matoniaceae (2 species) and Dipteridaceae (3 species) facing at least 12 spore genera with a fern affinity, three of which have osmundaceous affinities (*Baculatisporites, Conbaculatisporites,*

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Table 3

Comparison between the palynological and plant fossil data from Wüstenwelsberg, based on Bonis et al. (2010), Bonis and Kürschner (2012). For the remainder of the references, see paragraph 4.3.

Dispersed palynomorphs from Bonis et al. (2010), Bonis and Kürschner (2012)		Basalmost samples	Level 2 (7–9 m, 'Hauptton')	Level 3 ('Blätterkohle')	Entire section	Corresponding plant fossils in WWB	General botanical affinity
Aquatic elements							
Bryophyta							
Stereisporites	Spores	x	x	Common	Rare	–	Sphagnales
Porcellispora	Spores	x	x	x	Rare	–	Bryophyta indet.
Retitriletes	Spores	x	x	x	Rare	–	Bryophyta indet
Rogalskaisporites	Spores	x	x	Rare	Rare	–	Bryophyta indet.
Lycophyta							
Aratrisporites	Spores	x	Rare	Rare	Rare	*Lepacyclotes* sp.	Isoetales
Lycopodiacidites	Spores	x	rare	x	Rare	–	Lycopodiales
Densosporites	Spores	x	x	Rare	Rare	–	Selaginellales
Heliosporites	Spores	x	Rare	x	Rare	–	Selaginellales
Uvaesporites	Spores	x	x	x	Rare	*Selaginellites coburgensis*	Selaginellales
Limbosporites	Spores	x	Rare	Rare	Rare	–	Selaginellales, Lycopodiales
Acanthotriletes	Spores	x	x	x	Rare	–	Lycophyta indet.
Carnisporites	Spores	x	Rare	Rare	Rare	–	Lycophyta indet.
Cingulizonates	Spores	x	Rare	x	Rare	–	Lycophyta indet.
Tigrisporites	Spores	x	Rare	Rare	Rare	–	Lycophyta indet.
Triancoraesporites	Spores	x	x	Rare	Rare	–	Lycophyta indet.
Retitriletes	Spores	x	x	x	Rare	–	Lycophyta indet.
Sphenophyta							
Calamospora	Spores	Rare	Common	Very abundant	Very abundant	*Equisetites laevis*	Equisetales
Pteridophyta							
Perinosporites	Spores	x	x	Rare	Rare	–	Filicales, Cyatheaceae
Zebrasporites	Spores	x	Rare	x	Rare	–	Filicales, Cyatheaceae
Deltoidospora	Spores	Common	Dominant	Dominant	Very abundant	*Thaumatopteris brauniana, Dictyophyllum exile, Phlebopteris* sp.	Filicales, Cyatheaceae, Dicksoniaceae, Dipteridaceae, Matoniaceae
Concavisporites	Spores	Rare	Very abundant	Very abundant	Very abundant	*Dictyophyllum exile, Phlebopteris* sp.	Filicales, Matoniaceae, Dipteridaceae
Polypodiisporites	Spores	x	Rare	Rare	Rare	–	Filicales, Schizaceae
Verrucosisporites	Spores	x	x	x	Rare	–	Marattiales, Osmundales
Baculatisporites	Spores	Rare	Rare	Rare	Rare	*Todites/Cladophlebis*	Osmundales
Conbaculatisporites	Spores	x	Rare	Common	Common	*Todites/Cladophlebis*	Osmundales
Todisporites	Spores	Common	Dominant	Common	Very abundant	*Todites/Cladophlebis*	Osmundales
Kyrtomisporis	Spores	x	x	x	Rare	–	Pteridophyta indet.
Lophotriletes	Spores	x	rare	rare	Rare	–	Pteridophyta indet.
Retitriletes	Spores	x	x	x	Rare	–	Pteridophyta indet.
Trachysporites	Spores	x	x	x	Rare	*?Clathropteris meniscioides*	Pteridophyta
Spore-producing plants of unknown affinity							
Asseretospora	Spores	x	x	Rare	Rare	–	unknown botanical affinity
Cosmosporites	Spores	x	x	x	Rare	–	unknown botanical affinity
Paraklukisporites	Spores	x	x	x	Rare	–	unknown botanical affinity
Semiretisporis	Spores	x	x	Common	Rare	–	unknown botanical affinity
Seed ferns							
Vitreisporites	Pollen	Dominant	Common	Common	Very abundant	*Hydropterangium roesleri*	Caytoniales, seed ferns such as *Ptilozamites*
Alisporites	Pollen	Common	Rare	Rare	Common	*Pachypteris* cf. *P. rhomboidalis*	Corystospermales
Lunatisporites	Pollen	x	x	Rare	Rare	–	Corystospermales, Peltaspermales
Cycadopites	Pollen	Common	Rare	Rare	Rare	*Antevsia zeilleri*	Peltaspermales
Vesicaspora	Pollen	x	x	Rare	Rare	–	Seed ferns indet.
Cycadophyta							
Chasmatosporites	Pollen	x	x	x	Rare	*Nilssonia pterophylloides*	Cycadales, Bennettitales
Cycadopites	Pollen	Common	Rare	Rare	Rare	All cycads and bennettitaleans; possibly Palissaceae	Cycadales, Bennettitales; possibly Palissaceae
Ginkgophyta							
Cycadopites	Pollen	Common	Rare	Rare	Rare	*Ginkgoites taeniatus, Ginkgoites* sp.	Ginkgophyta
Coniferophyta							
Araucariacites	Pollen	Common	Rare	Rare	Common		Araucariaceae

Table 3 (*continued*)

Dispersed palynomorphs from Bonis et al. (2010), Bonis and Kürschner (2012)		Basalmost samples	Level 2 (7–9 m, 'Hauptton')	Level 3 ('Blätterkohle')	Entire section	Corresponding plant fossils in WWB	General botanical affinity
Classopollis	Pollen	Common	Common	Common	Common		Cheirolepidiaceae
Granuloperculatipollis	Pollen	x	x	x	Rare		Cheirolepidiaceae
Pinuspollenites	Pollen	x	x	Rare	Rare	*Schizolepis liasokeuperianus*	Pinaceae
Quadraeculina	Pollen	Rare	x	x	Rare		Podocarpaceae
Perinopollenites	Pollen	Common	Very abundant	Abundant	Very abundant		Taxodiaceae
Tsugaepollenites	Pollen	x	x	Rare	Rare		Taxodiaceae
Lunatisporites	Pollen	x	x	Rare	Rare		Voltziaceae
Brachysaccus	Pollen	x	x	x	Rare		Coniferophyta indet.
Alisporites	Pollen	Common	Rare	Rare	Common		Coniferophyta indet.
Gymnospermae							
Ovalipollis	Pollen	Common	Common	Common	Very abundant		Gymnospermae indet.
Rhaetipollis	Pollen	Rare	Rare	Common	Rare		Gymnospermae indet.
Riccisporites	Spore	Dominant	Dominant	Dominant	Dominant –		Gymnospermae indet.
Eucommiidites	Pollen	x	x	x	Rare		Erdtmanithecales; Gnetales, Cycadales
Botryococcus	Algae	x	x	x	Rare		
Cymatiosphaera	Algae	x	x	Rare	Rare		
Dapcodinium	Dinoflagellates	x	x	x	Rare		
Leiospheridia?	Algae	x	Rare	Rare	Rare		
Rhaetogonyaulax	Dinoflagellates	x	x	Rare	Rare		
Tasmanites	Algae	x	x	x	Rare		
Tytthodiscus	Algae	x	x	x	Rare		

Todisporites). *Todisporites* is most abundant in the metres 7–9 of level 2, where also most of the fern macrofossil remains were found. *Verrucosisporites* might indicate the presence of Marattiales but the group has so far not been recorded in macrofossils. At least six spore genera have affinities of Filicales and can be connected to *Dictyophyllum exile*, *Thaumatopteris* or the matoniaceous *Phlebopteris* and *Clathropteris*. The fern families Cyatheaceae and Schizaeaceae are also represented in the palynological assemblage but did not preserve in the macrofossil record (Table 3). The fern spores thus also reflect a higher diversity than is recorded in the macrofossil record.

Whereas the spore-producing plants are generally underrepresented in the macrofossil record, the opposite is fact for most of the recorded gymnosperm plant groups (Table 3). In the seed ferns, Peltaspermales and Corystospermales are represented by respective taxa in the palynoflora, whereas *Vitreisporites* reflects the presence of Caytoniales and *Hydropterangium*. *Vesicaspora* has been assigned to the seed ferns but without any further affinity.

The cycadophytes include five cycad and eight bennettitalean foliage taxa and one *Nilssonia* as well as two bennettitalean reproductive organs (*Welsbergia*, *Wielandiella*). In comparison, only three pollen genera with cycadophyte affinity have been identified, one of which is *Cycadopites*, which has been found in situ in *Welsbergia*, but can originate also from other gymnosperm groups (Balme, 1995). Although cycadophyte macroplant remains are common to very abundant, only *Cycadopites* is common in the some of the palynological samples, and none is abundant in level 2, where most cycadophyte remains have been retrieved. The low abundance of *Cycadopites* pollen in such layers maybe explained by the fact that many cycadophytes including bennettitaleans are most likely insect-pollinated (see e.g., Peñalver et al., 2012; Pott et al., 2017, and references therein), and thus, a low pollen production per plant may be anticipated.

Ginkgophytes are even more underrepresented in the palynological samples despite suggested common wind-pollination in ginkgophyte taxa (but see Peñalver et al., 2012). Against two macroplant taxa, the only corresponding pollen is *Cycadopites*, a fossil-genus that has a wide

range of botanical affinities (see above) and the origin of the pollen grains can only be distinguished by their dimensions and ultrastructure (Van Konijnenburg-van Cittert, 1971; Zavialova and Van Konijnenburg-van Cittert, 2011). In level 3, *Cycadopites* is peculiarly rare und does not reflect the high abundance of ginkgophyte plants in this stratigraphic level.

The commonly wind-pollinated conifers are the only gymnosperm plant group with a distinct overrepresentation of pollen in Wüstenwelsberg, in comparison with the macrofossil record. The palynological record distinguishes at least 10 different pollen genera (Table 3). Although the genera *Alisporites* and *Lunatisporites* have both a conifer and a seed fern affinity, the other genera belong to either the Araucariaceae (*Araucariacites*), Cheirolepidiaceae (*Classopollis*, *Granuloperculatipollis*), Pinaceae (*Pinuspollenites*), Podocarpaceae (*Quadraeculina*), Taxodiaceae (*Perinopollenites*, *Tsugaepollenites*) and the Voltziaceae (*Lunatisporites*). In contrast, only three macrofossil taxa are recorded, two of which are assigned to the Palissyaceae, that have no equivalent in the recorded palynoflora. Consequently, the palynological record does not reflect the conifers found in the macroflora record. They have, so far, no correspondence in the palynological record and vice versa, although the Palissyaceae may also contain pollen of the *Cycadopites*-type in situ (Pattemore and Rozefelds, 2019). This, however, is explained by the easy transport of the bisaccate, wind-distributed and thus massively produced conifer pollen, which can happen over fairly long distances. This pollen flora in turn reflects consequently a rather diverse hinterland flora characterized by several conifer taxa constituting considerable woodlands. Some of the pollen taxa are common to very abundant in the palynological record suggesting that members of Cheirolepidiaceae and Taxodiaceae were the main components in the regional flora and of the further surroundings.

The most abundant taxon of the section, *Ricciisporites tuberculatus*, originally considered of bryophyte affinity (e.g., Bonis et al., 2010), was recently re-assigned to gymnosperms with unknown botanical affinity based on morphology and ultrastructure (Lundblad, 1959; Mander et al., 2012; Kürschner et al., 2014). If the latter hypothesis is confirmed by *in situ* findings, its palaeoenvironmental signal changes

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slightly: Kürschner et al. (2014) suggested an herbaceous, ruderal life habitat for this unknown gymnosperm indicating a disturbed/pioneer environment. *Eucommiidites* is possibly produced by cycads, Gnetales or Erdtmanithecales (e.g., Friis and Pedersen, 1996; Tekleva et al., 2006). A cycad origin of this pollen is the most likely given the Rhaetian–Hettangian age of the flora. *Ovalipollis* and *Rhaetipollis* have no clear botanical affinity, but are common to very abundant n the section; a *Circumpolles* affinity of the latter is suggested by some scholars (e.g., Zavialova et al., 2010).

The qualitative comparison between macrofossils and the palynological record permit to compare the results of both proxies and to integrate them. Marked differences between the results of both datasets were observed already in previous oeuvres (e.g. Kustatscher et al., 2010, 2012, 2014; Costamagna et al., 2018) and can be explained by the fact that the macrofossils reflect strictly local palaeoenvironments (very evident in level 3), whereas palynomorphs reflect more generally what type of plants were present and thus, may be used to assess the regional environmental conditions affecting the plants locally and, to some extent, a little further away.

The palynological study of Bonis et al. (2010) reflects the general palynological pattern observed at the Triassic-Jurassic boundary in Europe. Towards the end of the Triassic an increase and high abundance in *Ricciisporites* has been observed also by Lindström et al. (2017) and Mander et al. (2013), in combination with an increase in the abundance of ferns, and a relative increase in lycophytes and sphenophytes. Mander et al. (2013) observed also a particularly high abundance of *Deltoidospora*. The gymnosperm pollen, on the other hand, decrease towards the end of the Triassic but become more abundant in Lower Jurassic sediments, also well evidenced by the spore/pollen ratio (see Lindström et al., 2017). In the Danish Basin and in Greenland as well Cheirolepidiaceae, Cupressaceae, Taxodiaceae and Pinaceae are distinctively less represented in the palynological record across the boundary, with the Pinaceae becoming more important and abundant in the lower Jurassic of the Danish Basin (Lindström et al., 2017). The relatively low abundance of gymnosperm taxa (with the exception of *Ricciisporites*) in correspondence with a high abundance of spore-producing plants observed in Wüstenwelsberg is, thus, not a local or regional effect but reflects the existing climate and supra-regional conditions of the middle to middle-higher latitudes of the Northern Hemisphere during the latest Rhaetian.

4.4. Palaeoecological and palaeogeographical implications

The Rhaetian period in Europe is characterized by a warm climate with dry and humid episodes (see Preto et al., 2010; Kustatscher et al., 2018 for overview). Humid episodes are supported by the general abundance in hygrophytic spores and high diversity of different, moisture-loving plant groups in the palynological record. An abundance in lycophyte, fern and sphenophyte (viz. horsetails, ferns, lycophytes), spores is observed throughout the Wüstenwelsberg section, indicating the presence of stagnant water bodies and/or small river systems in the Wüstenwelsberg area during the latest Rhaetian (Van Konijnenburg-van Cittert et al., 2014, 2016, 2018b, 2020), and remains of freshwater and marine algae (e.g., representatives of the genera *Botryococcus*, *Cymatiosphaera* and *Tasmanites*) were found in some of the layers (Bonis et al., 2010). The diverse and abundant macrofloral assemblage, rich in hygrophytic elements (viz. horsetails, ferns, lycophytes), which in many cases are dependent on the presence of elemental water for their reproduction cycles, supports the interpretation of humid environments, such as riverbanks, lake shores or freshwater marshes. These elements were, however, also as colonizers of brackish environments in deltaic settings or highly disturbed environments as does also the prevailing presence of several bennettitalean elements that are commonly interpreted to represent mangrove-like vegetation in freshwater to brackish delta settings (e.g. Pott and McLoughlin, 2014; Pott et al., 2015, 2016a).

Seed fern leaves are in general rather coriaceous with small pinnules and are covered by thicker cuticles, adaptations to seasonal or periodical physiological droughts induced by more arid environments or climates or in deltaic or lowland settings with moisture-reducing effects such as marine influences (Rees et al., 2000; Hesselbo et al., 2003). In the case of Wüstenwelsberg the xeromorphic features were interpreted as being cause by a humid and coal-producing swampy environment low in nutrients rather than a dry environment (Bonis et al., 2010). For ginkgophytes, on the other hand, a more humid environment similar to extant *Ginkgo* is commonly suggested (Zhou, 2009) although many ginkgophytes yield rather robust cuticles pointing to leathery leaves suggesting the experience of physiological drought (e.g. Pott et al., 2007). Ginkgophytes were much more diverse in the Mesozoic, and amongst the known forms were certainly many that were adapted to a variety of environments, among which both wet and dry environments and upland forests (Van Konijnenburg-van Cittert and Van der Burg, 1996; Popa and van Konijnenburg-van Cittert, 2006).

Many cycadophytes grew during the Mesozoic in subtropical lowlands or co-occurred with ginkgophytes and conifers in open forests (Batten, 1974; Van Konijnenburg-van Cittert and Van der Burgh, 1989; Vakhrameev, 1991; Kustatscher et al., 2010). Commonly, *Nilssonia* was part of moderately disturbed, lowland areas and most likely adapted to more humid swamp/lake or fresh mangrove environments (e.g., Watson and Cusack, 2005; Pott and McLoughlin, 2014; Pott, 2019). Bennettitales are considered coal generators although they were not swamp dwellers (Vakhrameev, 1991). They thrived predominantly in deltaic and highly disturbed environments (including flood plains and silting-up lakes/marshes under warm and subtropical conditions, similar to modern mangroves (Harris, 1932, 1969; Popa, 2014; Pott, 2014a, 2014b; Pott et al., 2008; Pott et al., 2016a; Pott and McLoughlin, 2011, 2014); although some may be adapted to dry-savannah vegetation under arid conditions (Diéguez et al., 2009).

Mesozoic conifers in general are considered to have inhabited relatively drained and dry slopes of upland forests or hinterland vegetation (Batten, 1974; Vakhrameev, 1991; Wang et al., 2005; Falcon-Lang et al., 2009; Kustatscher et al., 2010). However, conifers must not necessarily have been restricted to the drier habitats (cf. modern *Taxodium* and *Glyptostrobus*), which might be the case for e.g., *Schizolepis liasokeuperianus* whose needles cover large slabs. These were probably shed by a deciduous conifer, which was growing on river banks or near ponds and swamps. Not much is known about the environment in which the Palissyaceae grew (Pattemore et al., 2014).

Considering these habitat and environment requirements of the different plant groups, the flora of Wüstenwelsberg may be reconstructed as a complex and multi-storeyed vegetation with plant groups strongly linked to standing or silently running water bodies with some plant groups colonizing the adjacent moderately moist or swamp-like environments of the understorey (some lycophytes, mosses and ferns, bennettites, conifers). Some of the ferns probably also formed large monotypic stands (e.g., Clathropteris; Choo et al., 2016; Pott et al., 2018) and/or colonized highly disturbed environments (*Phlebopteris*, *Thaumatopteris*; Van Konijnenburg-van Cittert, 2002). The mostly shrubby or arborescent gymnosperms were linked to moist environments (the ginkgophytes, cycads and bennettitaleans, some deciduous conifers) but might also have constituted smaller plants growing in areas of physiological drought and/or drier habitats (e.g. seed ferns). Several of the mentioned plants were able to grow in areas influenced by a coastal setting or near-coast conditions, which may be suggested for the middle and upper part of the succession of Wüstenwelsberg owing to the presence of marine elements in the palynological record (see Bonis et al., 2010; Pott et al., 2016a, fig. 3). A deltaic setting, similar to the one in the Rhaetian of Scania and Greenland, may also be inferred for the Wüstenwelsberg area, with a variety of different exposed and disturbed habitats or environments of wide floodplains within deltaic or coastal plain and mire settings or brackish to tidal mudflat areas, with ephemeral isles or sand bars that were regularly periodically

flooded such as in modern mangroves, and with moderately to rapidly changing conditions, which also might have yielded prevailing unfavorable environmental conditions.

5. Concluding remarks

In a series of papers, the authors conducted extensive collecting and subsequent study of Rhaetian–Hettangian compression plant fossils and palynological samples obtained from a quarry near Wüstenwelsberg in Bavaria. The flora is characterized by a wide range of taxa from this geographic area and stratigraphic unit, including a number of taxa new to science, in some cases notably extending the stratigraphic range of species and genera. Moreover, a comparison with the microflora evidences a relevant hidden diversity among the macroflora, especially on small herbaceous cryptogams (mosses, lycophytes, ferns) and elements growing in the hinterland flora such as gymnosperms. The present studies render it important to analyze Rhaetian floras of adjacent areas in detail in order to better reconstruct the complex Rhaetian vegetation to gain a better understanding of the floral turn-overs related to the end-Triassic mass extinction and the humid episodes present during the Late Triassic.

Declaration of Competing Interest

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

Acknowledgements

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