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DOI:

<https://doi.org/10.1127/njgpa/2023/1182>

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# Plant macrofossils from the Rhaetian of Einberg near Coburg (Bavaria, Germany). Part 3. Conifers, incertae sedis and general discussion

Johanna H.A. van Konijnenburg-van Cittert, Stefan Schmeißner, Günter Dütsch, Evelyn Kustatscher, and Christian Pott

With 12 figures and 5 tables

**Abstract:** The plant macrofossil assemblage from a Rhaetian succession of a quarry near Einberg (Franconia, Germany), of which ferns, cycadophytes and ginkgophytes had been published earlier, comprises two conifer species (*Schizolepidopsis liasokeuperianus* and *Stachyotaxus septentrionalis*) that are unambiguously identifiable. Though both occur in small numbers of specimens only, a large number of specimens of the enigmatic gymnospermous foliage type *Desmiophyllum harrisii* were encountered; the true nature of this taxon is yet unknown, but evidence points towards a coniferalean affinity. The three species are described by means of macromorphology and epidermal characters. Finally, a large number of conifer cones have been found in the assemblage, which are attributed to three different types, viz., one ovuliferous cone belonging to and attached on a twig of *Stachyotaxus septentrionalis*; the microsporangiate cone *Sphaerostrobos einbergensis* sp. nov. and the ovuliferous cone *Ourostrobos einbergensis* sp. nov. – the latter two might belong to *Desmiophyllum harrisii*. A comparison between the flora from Einberg with the Rhaetian floras of adjacent localities (viz. Wüstenwelsberg, Heilgersdorf and Kipfendorf) reveals distinct regional differences within the conifers between the respective floras; this is most likely induced by local ecological disparities of varying habitats. Moreover, brief comparisons with Rhaetian floras from adjacent European areas are made, and with the Hettangian floras from Bavaria as well. Lastly, an overview of the complete Einberg plant fossil assemblage is given, including palaeoecology and palaeogeography of the whole area around Coburg during the Rhaetian.

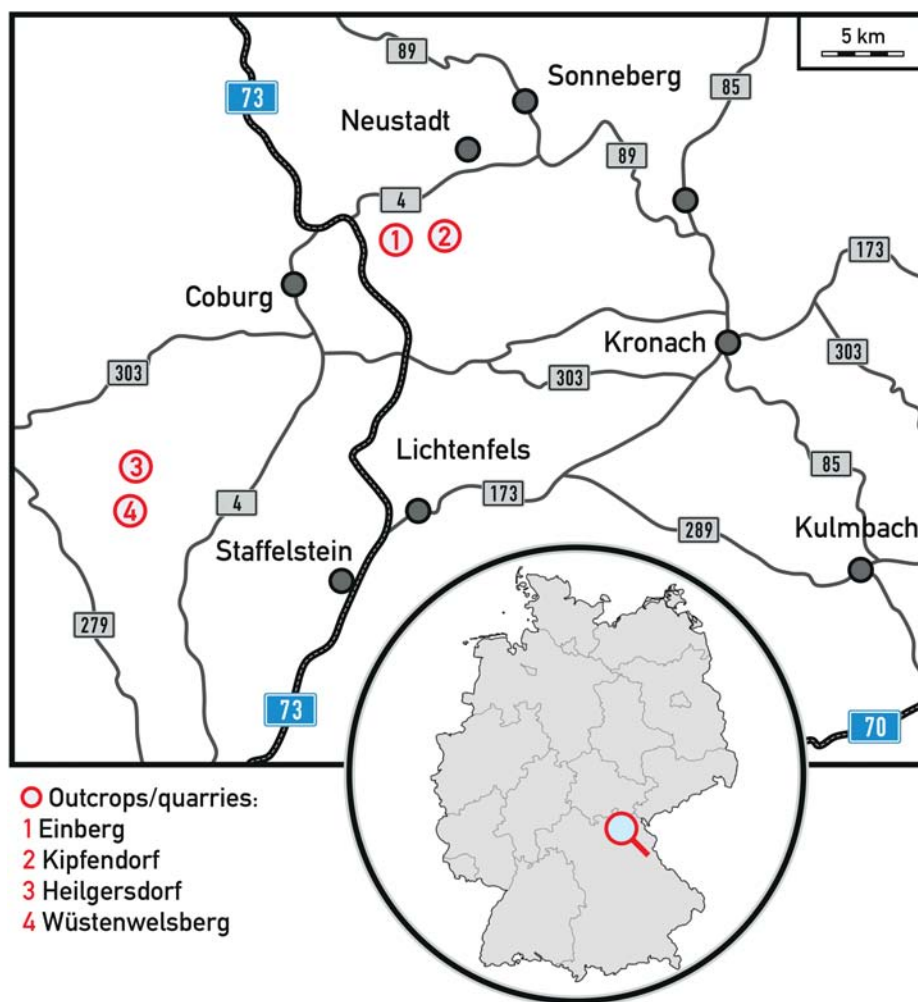
**Key words:** Late Triassic, Franconia, Palaeoecology, Palaeogeography, *Schizolepidopsis*, *Stachyotaxus*, *Desmiophyllum*.

## 1. Introduction

Late Triassic–Early Jurassic floral assemblages from Bavaria are commonly known as the “Rhaeto-Liassic flora” of Upper Franconia. Most of the assemblages, however, derive from purely Hettangian strata – widespread around Bayreuth and Nuremberg, whereas a few were obtained from entirely Rhaetian successions in the surroundings of Coburg (VAN KONIJENBURG-VAN CITTERT *et al.* 2021a, and references therein).

Recently, a diverse plant macrofossil assemblage obtained from a Rhaetian succession in a quarry near the village Wüstenwelsberg has been extensively studied (BONIS *et al.* 2010; VAN KONIJENBURG-VAN CITTERT *et al.* 2014, 2016, 2017, 2018, 2019, 2020, 2021a; POTT *et al.* 2016); this flora is currently the best-studied Rhaetian flora from the area.

The slightly less diverse flora from the Rhaetian sandstone of Einberg, also near Coburg, is the subject of this study. As the flora turned out to be more



**Fig. 1.** Map of Germany indicating the position of the locality Einberg near Coburg in Franconia (Bavaria), and the position of the other three Rhaetian localities in the same area: Wüstenwelsberg, Heilgersdorf and Kipfendorf.

diverse than it was originally thought to be, the flora is described in three parts. The remains of ferns, fern allies and seed ferns plus those of the cycadophytes and ginkgophytes have been published recently (VAN KONIJENBURG-VAN CITTERT et al. 2021b, 2022). The conifers and taxa *incertae sedis* are the subject of this third publication.

Additional small quarries around Coburg with Rhaetian–Hettangian strata yielding plant macrofossils are located near Heilgersdorf (KELBER & VAN KONIJENBURG-VAN CITTERT 1997) and Kipfendorf (Fig. 1). Kipfendorf represents a historical locality that is not accessible anymore (FISCHER 1907; KRUMBECK 1939; ACHILLES 1981; for details see VAN KONIJENBURG-VAN CITTERT et al. 2021b). From the

plant macrofossil assemblage of Heilgersdorf, 15 taxa have been reported (KELBER & VAN KONIJENBURG-VAN CITTERT 1997), whereas the Wüstenwelsberg plant fossil assemblage is much more diverse comprising at least 40 taxa. It can, however, not be excluded that the higher diversity recorded from the latter outcrop might, partly, be conditioned by extensive and systematic collecting and sampling over the course of several decades as well as its recent detailed study involving cuticle analyses. Based on the latter, the composition of the Rhaetian flora from the area had been revised reflecting an articulated landscape covered by a complex, multi-storeyed vegetation (VAN KONIJENBURG-VAN CITTERT et al. 2021a, 2021b, 2022).

	Local German denominations	Lithostratigraphy
Hett.	„Lias-Sohlbank/Einberg-Bank“	Bamberg Fm
Rhaetian	„Oberer Sandstein“	Oberer Keuper Exter Fm
	„Hauptton“	
	„Hauptsandstein“	
	[„Rathsberg-Schichten“]	
	„Feuerletten“	Trossingen Fm

Fig. 2. Simplified stratigraphical section and lithostratigraphic units of the Einberg locality.

## 2. Material and methods, geological information

The plant fossils were obtained from the open sand pit (“Sandgrube”) Langguth, located SE of the village of Einberg, not far from Rödentel, east of Coburg (Fig. 1). Sand extraction ceased in 2003 and subsequently, the sand pit was closed and refilled. Consequently, the fossil-bearing strata are not accessible anymore. The fossils studied here were collected by SS, GD and JHAvKvC during several field trips in 1993–2003. The fossils are stored in the palaeobotanical collection 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 O) and GÜNTER DÜTSCH (Untersteinach, Germany; numbers containing the acronym Ei). The +-symbol indicates that specimens belong together, commonly as part and counterpart.

Within the sand pit, the so-called “Rhätsandstein” (Rhaetian sandstone) of the Rhaetian Exter Formation is exposed (NITSCH *et al.* 2011). The plant fossils most likely derive from the so-called “Hauptton” (see KRUMBECK 1939: 55), which is, in the Einberg sand pit, exposed in the form of sandstones intercalated with small clay lenses. For details see Fig. 2 and VAN KONIJNENBURG-VAN CITTERT *et al.* (2021b, 2022).

Although a detailed lithological profile of the outcrop at Einberg was never logged, the general stratigraphic sequence indicates that the position of the fossiliferous bed is within the Rhaetian Contorta and/or Triletes beds – when compared with the succession at Wüstenwelsberg (BONIS *et al.* 2010). Recent palynological analyses of a rock sample with plant fossils from Einberg support an assignment of the fossiliferous strata to the Contorta beds of the Exter Formation (thanks to Guido Roghi, Padova, and pers. obs. JHAvKvC). Typical Rhaetian palynomorphs such as *Ovalipollis pseudoalatus* and *Rhaetipollis germanicus* confirm a Rhaetian age; a great abundance of *Ricciisporites tuberculatus* combined with some *Classopollis* sp. and *Duplicisporites granulatus* pollen, points towards the Contorta beds in the Exter Formation. The strata yielding the plant fossils at Kipfendorf have been assigned to the Contorta or the Triletes beds as well, based on general geological considerations and detailed palynological analyses (ACHILLES 1981).

The plant fossils studied here are commonly preserved as compressions (Figs. 3–11). Some of the better-preserved specimens yielded cuticles that have been extracted using the standard procedures, as outlined for example in KERP (1990). Cuticles were picked directly from the rock surface and were macerated using Schulze’s reagent (30% HNO<sub>3</sub> with a few crystals of KClO<sub>3</sub>) and subsequently treated with 5–10%

ammonia (NH<sub>4</sub>OH) 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, The Netherlands, and in the private collections of SS.

The macrofossil specimens were photographed with a Nikon D750/Nikkor AF-S Mikro 60-mm 1:2.8G ED system digital camera and a Panasonic DMC-FZ1000/Leica DC Vario-Elmarit 1:2.8–4.0/9.1–146 camera setting. Oblique lightning and polarising filters in front of the camera lenses and the lights were used to enhance contrast and fine details. The analysis of some of the hand specimens was performed with an Olympus SZX10 stereo-microscope, cuticles have been studied and photographed with a Keyence VHX 7000/VH-ZST RZ 20×–2000× digital microscope, and onscreen by using a high-resolution imaging software.

### 3. Systematic palaeobotany

Order Coniferales ENGLER & PRANTL 1899  
 Family Palissyaceae FLORIN 1958  
 Genus *Stachyotaxus* NATHORST 1886  
*Stachyotaxus septentrionalis* (AGARDH 1823)  
 NATHORST 1886  
 Figs. 3A–H, 7A–B

Selected synonymy:

- 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 septentrionalis* (AGARDH). – NATHORST, p. 11; pl. 2, fig. 28; pl. 3, figs. 1–9.  
 1908 *Stachyotaxus elegans* NATHORST. – NATHORST, p. 11; pl. 2, figs. 1–27; pl. 3, figs. 10–12.  
 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.

- 1997 *Stachyotaxus elegans* NATHORST. – KELBER & VAN KONIJNENBURG-VAN CITTERT, p. 107; pl. 2, fig. 2.  
 2011 *Stachyotaxus septentrionalis* (AGARDH) NATHORST. – POTT & MCLOUGHLIN, p. 1044; text-figs. 9 K–L, P–Q. (and references therein).  
 2021a *Stachyotaxus septentrionalis* (AGARDH) NATHORST. – VAN KONIJNENBURG-VAN CITTERT et al. p. 8; pl. 3, figs. 1–6, pl. 5, fig. 5 (and references therein).

**Description of the material:** About 30 specimens of small leafy shoot fragments of *Stachyotaxus septentrionalis* were recorded. The largest (O535/02) is 56 mm long and 8 mm wide (Fig. 3A). Leaves are 3–5 mm long and up to 1.1 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 and never overlapping. Leaves are single-veined, strongly decurrent basally and commonly with an obtuse apex although more acute ones are occasionally present (e.g., O424/01; Fig. 3B).

Cuticles are thin and difficult to prepare; thus, only small pieces were recovered. The adaxial cuticle is slightly thicker than the abaxial one. It reflects elongate polygonal cells that are slightly more elongate and thicker near the margins (Fig. 7A). The abaxial cuticle has similar but less elongate epidermal cells, especially in the two stomatal bands on both sides of the midvein. These epidermal cells are sometimes almost isodiametric. One small piece with three short rows of stomata was observed. Stomata were longitudinally oriented; guard cells were lacking and the 4–6 subsidiary cells are mainly unspecialised with occasional thickenings around the stomatal pit (Fig. 7B). No papillae, trichomes or hairs were found.

**Ovulate cones:** So far, 13 incomplete ovulate cones were found that most likely belong to *Stachyotaxus septentrionalis*. O251/99 confirms this assignment as the preserved cone on that slab was apically attached to a small leafy *Stachyotaxus septentrionalis* shoot (Fig. 3C).

**Description:** The shoot fragment is 15 mm long, the attached cone fragment is 42 mm long and 6.2 mm wide. The seeds are relatively small, 3 mm in diameter, and the scales are curved upwards, covering a large part of the seeds. This is probably due to immaturity of the cone. Other specimens (e.g., O461/01; Fig. 3D and UU25994I; Fig. 3F) represent more mature cone fragments; these are up to 11 mm wide, with ovulate falcate scales up to 6 mm long bearing seeds in their



**Fig. 3.** *Stachyotaxus septentrionalis* from the Rhaetian of Einberg. **A** – Largest specimen fragment; O535/02. **B** – Detail of a specimen showing single-veined leaves; O424/01. **C** – Ovulate cone attached to a small leafy shoot; O251/99. **D** – Ovulate cone fragment; O461/01. **E** – Microsporangiate cone fragment; O205/98. **F** – Ovulate cone fragment; UU25994I. **G** – Microsporangiate cone fragment showing pseudodistichous arrangement; O355/00. **H** – Ovulate cone fragment showing pseudodistichous arrangement; UU25994I. Scale bars: 10 mm.

axils that are between 3.5 and 5 mm in diameter. Just as with the leafy shoots, the ovulate scales appear to be arranged in two rows, but are in fact spirally arranged and only appear pseudodistichous; thus, they are twisted basally to be confined to one plane (Fig. 3H). No cuticles were recovered from any of the specimens.

*Microsporangiate cones*: Eleven microsporangiate cones were encountered, all fragmentary.

**Description:** The longest fragment is 61 mm long and up to 13 mm wide (O204/98 and its counterpart O205/98; Fig. 3E), showing two rows of falcate scales, and possibly some imprints of pollen sacs. A well-preserved fragment (O355/00) is 37 mm long and 9 mm wide (Fig. 3G). The two rows of up to 6 mm long falcate scales, are most likely representing a pseudodistichous arrangement only, and are in fact arranged in a spiral phyllotaxis. It is best represented in specimen O355/00 (Fig. 3G).

**Remarks:** Shoots of *Stachyotaxus septentrionalis* have been recorded from Heilgersdorf (KELBER & VAN KONIJNENBURG-VAN CITTERT 1997) and from Wüstenwelsberg in particular (VAN KONIJNENBURG-VAN CITTERT et al. 2021a). The latter paper also described ovulate cones. For nomenclatorial issues and further aspects, we refer to the extensive discussion in VAN KONIJNENBURG-VAN CITTERT et al. (2021a). NATHORST (1886) was the first to describe and figure an ovulate cone (NATHORST 1886, pl. 25, fig. 9) from the Rhaetian of Bjuv, although not attached to a leafy shoot. Later (NATHORST 1908), he described and figured ovulate cones in more detail, also attached to leafy shoots (e.g., NATHORST 1908, pl. 3, fig. 2). HARRIS (1926, 1935) described and figured microsporangiate and ovulate cones from the Rhaetian of Jameson Land (East Greenland). All these cones agree in all aspects with the material from Einberg.

**Occurrence in other Northern Hemisphere Rhaetian floras:** Canada: ASH & BASINGER (1991); Sweden: NATHORST (1878, 1886), ANTEVS (1919), JOHANSSON (1922); Greenland: HARRIS (1926, 1935); Denmark: MÖLLER (1903); Poland: PACYNA (2014); Iran: SCHWEITZER & KIRCHNER (1996); Russia: VOLYNETS & SHOROKOVA (2007).

**Material examined:** O138/98, 191/98, 249/99, 251/99 (with attached cone), 304/00, 313/00, 315/00, O320+321/00, O423+424/01, 503/01, 517/01, 535+540/02, 543/02, 568/02, 573/02, 581 +582/03;

18Ei99, 20Ei01, 39Ei01, 48Ei01, 55Ei01, 92Ei01, 1× without number; UU25966G, 25986, 25999B,C, 26001; Possible ovulate cones of *Stachyotaxus*: O69+70/98, O71/98, 77+78/98, 206/98, 251/99, 304/00, 407/01, 461/01; 17Ei99; UU25994I, 25999A, 26001, 26013A; Possible microsporangiate cones of *Stachyotaxus*: O163/98, 204+205/98, 281/99, 355/00, 405/01, 541/02, 559/02; 11Ei99b, 34Ei01; UU25994C.

#### Incertainae familiae

Genus *Schizolepidopsis* DOWELD 2001

*Schizolepidopsis liaso keuperianus* (BRAUN 1846)

DOWELD 2001

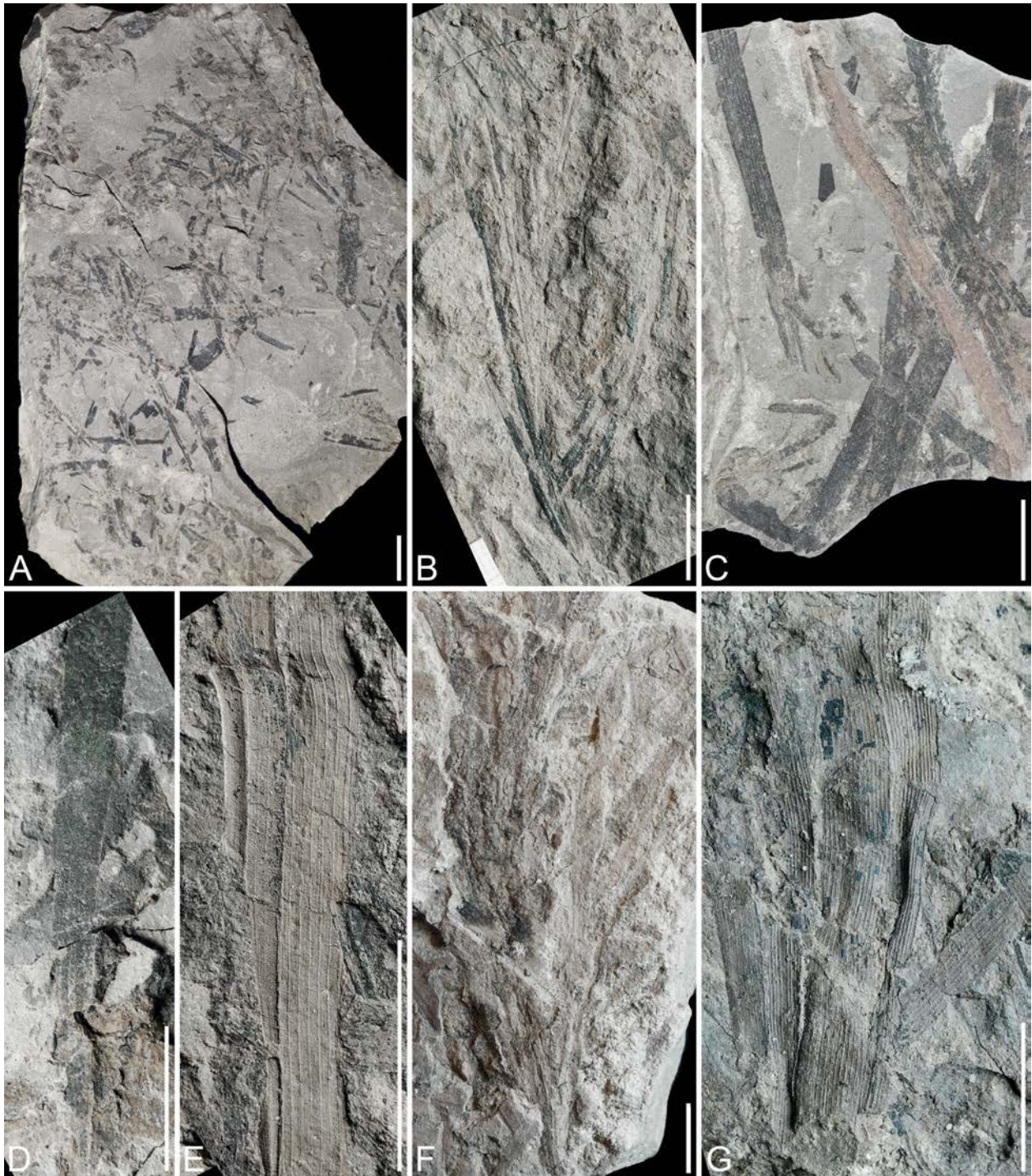
Figs. 4A–B, 7C–F

#### Selected synonymy:

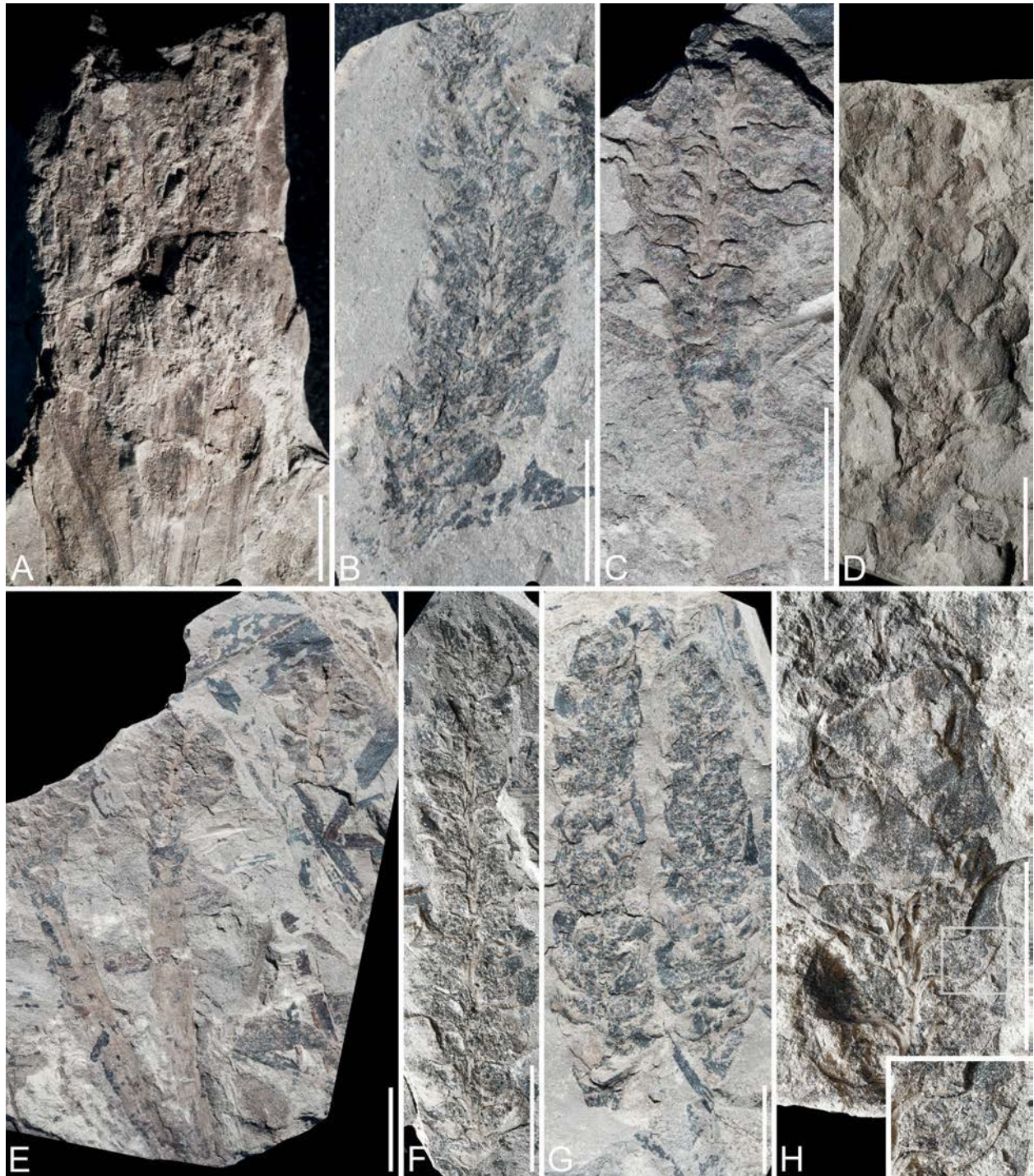
- 1846 *Voltzia schizolepis*. – BRAUN, p. 1258; no illustration.
- 1847 *Schizolepis liaso keuperinus*. – BRAUN, p. 86; no illustration.
- 1867 *Schizolepis liaso keuperina* BRAUN. – SCHENK, p. 179; no illustration.
- 1867 *Schizolepis braunii*. – SCHENK, p. 179; pl. 44, figs. 1–8.
- 1907 ?*Schizolepis braunii*. – FISCHER, p. 5 (probably *Desmiophyllum* leaves).
- 1914 ?*Schizolepis braunii* SCHENK. – GOTHAN, p. 160; pl. 26, fig. 4.
- 1997 *Schizolepis liaso keuperianus*. – KELBER & VAN KONIJNENBURG-VAN CITTERT, p. 107; pl. 2, fig. 7.
- 2001 *Schizolepidopsis liaso keuperianus* (BRAUN). – DOWELD, p. 86.
- 2021a *Schizolepis liaso keuperianus* (BRAUN) SCHENK. – VAN KONIJNENBURG-VAN CITTERT et al. p. 9; pl. 4, figs. 1–3, pl. 5, figs. 6–9; and references therein.

**Description of the material:** Most of the c. 25 specimens of *Schizolepidopsis liaso keuperianus* comprise single or very few needles only, except for some slabs that yield a fair number of the narrow needles (e.g., O186/98, O513/01; Fig. 4A). All dorsiventral needles are detached, no shoots or other organically connected material have been found, although some needles appear to be arranged in bundles (O513/01; Fig. 4B). All needles are incomplete; the largest fragment is 63 mm long; the width varies between 1.0 and 1.5 mm. In most specimens, a conspicuous midrib is visible (Fig. 4A).

Cuticles are delicate and difficult to isolate. The leaves are hypostomatic; no stomata have been observed on the adaxial cuticle (O341/99; Fig. 7C). The adaxial cuticle has elongate epidermal cells, on the abaxial cuticle they are irregularly elongate and



**Fig. 4.** *Schizolepidopsis liasoqueuperianus* and *Desmiophyllum harrisii* from the Rhaetian of Einberg. **A** – *Schizolepidopsis liasoqueuperianus*, slab with a number of needles; O186/98. **B** – *Schizolepidopsis liasoqueuperianus*, needles showing midrib; O513/01. **C** – *Desmiophyllum harrisii*, slab with several leaf fragments; UU26010. **D** – *Desmiophyllum harrisii*, basal part of a leaf fragment; O117/98. **E** – *Desmiophyllum harrisii*, leaf fragment showing venation; O206/98. **F** – *Desmiophyllum harrisii*, shoot with attached leaves and possibly also a microsporangiote cone (on the left); UU26000. **G** – *Desmiophyllum harrisii*, number of leaf fragments possibly originating from the same shoot; O520/01. Scale bars: 10 mm.



**Fig. 5.** *Desmiophyllum harrisii* and *Sphaerostrobus einbergensis* from the Rhaetian of Einberg. **A** – *Desmiophyllum harrisii*, bundle of leaves with attached cone fragment at the top; 16Ei99b. **B** – *Sphaerostrobus einbergensis*, specimen yielding pollen grains; it is associated on the same slab with *Desmiophyllum harrisii* leaves; O437/01. **C** – *Sphaerostrobus einbergensis*, detail of holotype showing shape of the microsporophylls; UU26998. **D** – *Sphaerostrobus einbergensis*, microsporangiate cone seen from the outside; O209/98. **E** – *Sphaerostrobus einbergensis* holotype, two cone fragments attached to axes; these are associated with *Desmiophyllum* leaves (on the right); UU26998. **F** – *Sphaerostrobus einbergensis* paratype, cone with *in situ* pollen; UU25994E. **G** – *Sphaerostrobus einbergensis*, two almost complete microsporangiate cones; O481/01. **H** – *Sphaerostrobus einbergensis*, small fragment of a microsporangiate cone showing external and internal structure. The

rectangular. The midrib is indicated by slightly more elongate epidermal cells. Stomata are restricted to the lateral areas, arranged in short, irregular rows and longitudinally oriented (Fig. 7D). Stomata are monocyclic, elongate; guard cells are commonly absent but visible from the cuticle's inner surface (Fig. 7E); they are surrounded by 4–6 unspecialized subsidiary cells (Fig. 7F).

**Remarks:** The generic name *Schizolepidopsis* is a substitute name for *Schizolepis* BRAUN 1847 because the latter generic name was preoccupied by an extant angiosperm genus (DOWELD 2001). VAN KONIJNENBURG-VAN CITTERT *et al.* (2021a) discussed this species extensively including a comparison with detached needles similar to the one recorded here but commonly assigned to *Pityophyllum* (NATHORST) MÖLLER 1903. The material from Einberg, although consisting only of detached needles, is attributed to *Schizolepidopsis liasokeuperianus* because of the agreement in macro-morphology and cuticle with needles of *S. liasokeuperianus* that have been found attached to shoots and together with the ovulate cones. The species has been recorded from all four Rhaetian localities around Coburg (see KELBER & VAN KONIJNENBURG-VAN CITTERT 1997; VAN KONIJNENBURG-VAN CITTERT *et al.* 2021a) but never in large numbers or as attached needles, except for Kipfendorf, where it is deemed to be the most common fossil in the assemblage covering complete slabs by FISCHER (1907), but it was not mentioned by ACHILLES (1981). One of us (SS) examined the Kipfendorf material in the Coburg Museum before it got lost and photographed two of these slabs (a short comparison between the flora from Kipfendorf as mentioned in ACHILLES (1981) and these data can be found in paragraph 4.1). The leaves FISCHER (1907) interpreted as needles of *Schizolepidopsis* are in fact leaves of *Desmiophyllum* (Fig. 11H). *Schizolepidopsis* is also known from most Lower Jurassic localities in Europe (see e.g., GOTHAN 1914; KRÄUSEL 1959; WEBER 1968; PACYNA 2013).

**Occurrence in other adjacent Rhaetian floras:** Germany: BRAUN 1847, KELBER & HANSCH 1995, KELBER & VAN KONIJNENBURG-VAN CITTERT 1997,

VAN KONIJNENBURG-VAN CITTERT *et al.* 2021a; Sweden: NATHORST 1878–1886, ANTEVS 1919, JOHANSSON 1922; Poland: PACYNA 2014; Donets Basin: STANISLAVSKY 1971, 1976; Russia: VOLYNETS & SHOROKOVA 2007.

**Material examined:** O78/98, 186/98, 221/98, 341/99, 407/01, 513/01. Dispersed cuticle, without parent specimen: C.107, 144, 302–308; 08Ei01, 62Ei01, 73Ei01, 85Ei0, 97Ei01; UU25961C, 25964A, C, 25965, 25973, 25975, 25978, 25981, 25983, 25997A, 26008B, 26012, 26013C, 26019I, 26019I, 26173.

Gymnospermae incertae sedis

Genus *Desmiophyllum* LESQUEREUX 1878

*Desmiophyllum harrisii* BARBACKA & PACYNA 2014

(in BARBACKA *et al.* 2014)

Figs. 4C–G, 8A–F

Selected synonymy:

- 2014 *Desmiophyllum harrisii*. – BARBACKA *et al.* p. 300; pl. 9, figs. 6–8, text-figs. 3, 4.  
2019 *Desmiophyllum harrisii* BARBACKA & PACYNA. – VAN KONIJNENBURG-VAN CITTERT *et al.* p. 532; figs. 2A–F, 3A–E.

**Description of the material:** *Desmiophyllum harrisii* appears almost as leaf litter in the assemblage from Einberg; slabs are sometimes covered by a number of leaf fragments (see e.g., UU26010; Fig. 4C) but no complete leaf has been found so far. Leaf fragments are generally short; none is exceeding 100 mm in length. The leaf width varies between 3 and 5.5 mm with an average width of 4 mm. One leaf fragment probably represents a basal part of a leaf, with a width of 1.8 mm increasing to 4.0 mm (O117/98; Fig. 4D). No apex has been found so far. The venation is distinct with veins running parallel at a concentration of 16–20/cm (O206/98; Fig. 4E). One rather poorly preserved specimen in the Einberg collection probably shows a shoot with attached leaves (UU26000; Fig. 4F). Specimen O520/01 also shows a number of leaves that seem to originate from a stem as the leaves diverge in direction, but there are no stem remains on the slab (Fig. 4G).

inset in the lower left hand corner, is a 1.5× magnification of the square box, in which the round microsporangia can be seen; UU26009A.

Scale bars: 10 mm.

Cuticles are thin and difficult to prepare; it is especially difficult to separate the upper and lower cuticle. When unseparated, the veins are clearly visible with long and narrow, longitudinally oriented epidermal cells. In between there are rows with shorter rectangular epidermal cells where stomata would be expected but none are discernible when the upper and lower cuticle have not been separated. The epidermal cells are irregularly rectangular and carry thickenings especially in transversal direction that seem to hold the upper and lower cuticle together in less well macerated specimens (O397/00, Fig. 8A; UU26020, Fig. 8B; UU26004, Fig. 8C). When fully macerated, the thickenings disappear gradually, and it is possible to separate small cuticle pieces of the hypostomatic leaves. The lower and upper cuticles are equally thick. Epidermal cells are similar on both the upper and lower epidermis and those probably representing the veins are long with parallel longitudinal walls (up to 150 µm long and 5–10 µm wide) The epidermal cells within the intercostal areas are shorter (up to 100 µm long and 20 µm wide, but commonly 20–30 µm long and 20 µm wide) (Fig. 8E). On the abaxial cuticle, longitudinally oriented stomata are sparsely distributed in irregular rows between the veins (Fig. 8D). They consist of 4–5 subsidiary cells surrounding the guard cells: two smaller polar cells and 2–3 long, slightly raised lateral cells (Figs. 8F).

**Remarks:** *Desmiophyllum harrisii* constitutes the most common plant fossil in the Einberg assemblage; almost every slab yields at least a leaf fragment, while there occur slabs that are covered by a number of leaf fragments (see e.g., UU26010; Fig. 4C). The one specimen with leaves that are possibly attached to a stem is much less well preserved than the specimen yielding a shoot fragment with a number of attached leaves described by VAN KONIJNENBURG-VAN CITTERT et al. (2019) from Wüstenwelsberg. We will not repeat the elaborate discussion of this species already carried out by BARBACKA et al. (2014) and VAN KONIJNENBURG-VAN CITTERT et al. (2019). Since the latter paper, no new occurrences from adjacent Rhaetian/Hettangian floras have been recorded. In the area around Coburg, the species has been found in Wüstenwelsberg (VAN KONIJNENBURG-VAN CITTERT et al. 2019), but it might also have been present in the historical flora from Kipfendorf. The specimens that FISCHER (1907) deemed to needles of *Schizolepidopsis* (see above) are in fact covered with leaves of *Desmiophyllum* (Fig. 11H). And it is also possible that the leaves cov-

ering a slab from Heilgersdorf do not only represent *Schizolepidopsis* needles but may contain also badly preserved *Desmiophyllum harrisii* leaf fragments, although these leaves are rather narrow (KELBER & VAN KONIJNENBURG-VAN CITTERT 1997, pl. 2, fig. 7).

**Occurrence in other adjacent Rhaetian/Hettangian floras:** Germany (Rhaetian): VAN KONIJNENBURG-VAN CITTERT et al. 2019; probably FISCHER 1907, and possibly KELBER & VAN KONIJNENBURG-VAN CITTERT 1997; Poland (Hettangian): PACYNA 2014, BARBACKA et al. 2014; Jameson Land (Hettangian): possibly HARRIS 1935.

**Material examined:** O15/93, 71/98, 75/98, 115/98, 223/99, 116/98, 117/98, 183/98, 187/98, 192/98, 206/98, 223/99, 241/99, 282/99, 307/00, 311/00, O334/99, 335/99, 336/98, 339/99, 343/00, 388/00, 396/00, 397/00, 398/00, 399/00, 401/01, 407/01, 414/01, 419/01, 420/01, 444/01, 520/01, 526/01; dispersed cuticle without parent specimen: C.75, 78, 206-208, 243, 247, 248, 294, 296, 301; 05Ei99a + b, 06Ei99, 07Ei99, 09Ei99b, 11Ei99b, 16Ei99b, 18Ei99, 01Ei00, 02Ei00b, 04Ei00, 05Ei00, 07Ei00, 09Ei00, 10Ei00, 11Ei00, 13Ei00, 15Ei00, 16Ei00, 18Ei00, 16Ei01, 24Ei01, 26Ei01, 34Ei01, 38Ei01, 48Ei01, 60Ei01, 62Ei01, 66Ei01, 67Ei01, 68Ei01, 69Ei01, 77Ei01, 82Ei01, 85Ei01, 91Ei01, 92Ei01, 93Ei01; UU25961, 25963L, 25964E, F, G, 25966C, 25968, 25973, 25975, 25976, 25979, 25980, 25981, 25982, 25983, 25984?, 25985, 25992, 25993F, 25998A, 25999A, 26000, 26004, 26009, 26010, 26013, 26019D,G,I, 26020, 26172, 26175, 26176.

Potentially articulate cones:

Specimen 16Ei99b (Fig. 5A) shows a portion of (one or) two bundles of *Desmiophyllum* leaves with two attached cones (16Ei99a, the counterpart of the leaf bundles, does not show cone remains). The leaf bundle remains are 40 mm long; the cone remains are, alas, not very well preserved, but it can be seen that they consist of scales, possibly of *Sphaerostrobis einbergensis* sp. nov. (Fig. 5A). The largest cone remain is 41 mm long and 12 mm wide. UU26000 (Fig. 4F) also shows a probably attached cone fragment, but this specimen is even less well preserved. The cone fragment is 46 mm long and 15 mm wide; in the more apical part scale remains are visible.

Much better-preserved similar cones are common in the assemblage; we can distinguish two types, likely representing microsporangiate and ovulate cones.

These are identified as new species and will be described as *Sphaerostrobis einbergensis* sp. nov. and *Ourostrobis einbergensis* sp. nov., respectively.

Genus *Sphaerostrobis* HARRIS 1935  
*Sphaerostrobis einbergensis* sp. nov.  
 Figs. 5C–H, 9A–E

**Etymology:** after the village of Einberg.

**Holotype:** UU26998 (Fig. 5E) here designated (cones attached to axis).

**Paratype:** UU25994E (Fig. 5F) here designated (cone with *in situ* pollen).

**Type locality:** former sand pit Langguth, located SE of the village of Einberg.

**Type horizon and age:** Exter Formation (Contorta Beds), Rhaetian.

**Diagnosis:** Simple, pollen bearing cones with helically arranged, S-shaped, acute and longitudinally striate microsporophylls; microsporophylls bearing groups of round microsporangia in the centre of the adaxial side, each c. 1 mm in diameter. *In situ* pollen smooth-walled, circular to oval in outline and probably monolucate.

**Description of the material:** Specimen UU26998 shows at least three microsporangiate cone fragments, two of which appear attached to 4-mm-wide axes (Fig. 5E). The basal portions of the cone axes are also 4 mm wide but increase rapidly to a final width of 12 mm. Microsporophylls are helically arranged, arise at c. 70° from a central axis with a narrow base, and rapidly bend outwards to almost 90°; the apical portion of each is bending upwards again (Fig. 5C). The total measurable length of the microsporophylls is 6–7 mm. As only basal cone fragments are preserved, more distal microsporophylls might have been even longer. Microsporophylls bear a large number (> 15) of microsporangia (pollen sacs) on their adaxial surface; these are round and up to 1 mm in diameter. In a number of cones only the outside of the microsporophylls is visible (e.g., 65Ei01, O208+209/98, O401/01). These are longitudinally striate, up to 7 mm wide and 9 mm long, with an acute apex (Fig. 5D; O209/98).

Specimen O481/01 yields two almost complete cones next to each other, suggesting that they arose

from the same axis (Fig. 5G). These cones are 54 and 57 mm long, respectively; their 3-mm-wide base rapidly increases to a final cone width of 11 mm. The microsporophylls are up to 9 mm long, arise at 70°–80°, bend almost immediately to 90° and later curve upwards. In some places, pollen sacs are discernible. Another almost complete cone (UU26009B) is 41 mm long and 12 mm wide.

UU26009A is only a small cone fragment but has been embedded in a skewed position in relation to the fracture plane so that external and internal structure become visible. In the apical part, microsporophylls are visible from the outside. More basally, the interior organisation of the microsporophylls can be observed (Fig. 5H, with the round pollen sacs visible on the adaxial side of the microsporophylls, see enlargement of the square square box in Fig. 5H). Specimen O528/01 (and its counterpart 529/01) yielded small cuticle fragments of the microsporophylls. The cuticle is relatively thick with isodiametric epidermal cells, but no stomata could be observed. Dispersed pollen sacs were also found but these did not yield any details apart from their circular outline and diameter of 1 mm.

Paratype UU25994E (Fig. 5F) yielded two large masses (Fig. 9A) of immature, small, smooth-walled pollen grains, 30–35 µm in diameter, probably each representing the unwrapped content of a pollen sac. These cones were apparently immature, and consequently the pollen masses could not be separated into single pollen grains, apart from one pollen grain that lies just outside the mass. It is oval in shape, monolucate and completely smooth (Fig. 9B, C). The two 11 mm wide cones on O437/01 (Fig. 5B) yielded masses of immature and smooth pollen grains as well as thin cuticular remains upon preparation of the coaly substance (Fig. 9D). UU25994M gave upon preparation also a small piece of pollen sac wall (Fig. 9E).

**Remarks:** The two attached cones on O210/98 are only attached to 4-mm-wide naked axes. Hence, we cannot prove that these microsporangiate cones belong to the same natural genus as the *Desmiophyllum* leaves but there is some evidence: on almost every specimen yielding a cones or cone fragments, there are also leaves of *Desmiophyllum*. The two attached cones on 16Ei99b are also attached to axes with some *Desmiophyllum* leaves preserved in a position suggesting that they probably originate from the same axes, but it is not entirely safe to identify whether these cones belong to a different cone type (see below).

The pollen cones are characterized, e.g., by the S-shape of the microsporophylls and the numerous small and round microsporangia attached to the upper side of the microsporophylls. These features occur only in the Rhaetian/Hettangian family Palissyaceae. And indeed, the pollen found *in situ* in UU25994E and O437/01 are similar to those known from the Palissyaceae (small, oval, almost smooth and monosulcate).

HARRIS (1935: 143, pl. 29, figs. 1–4, 6, 11) described *Sphaerostrobos clandestinus* from the Rhaetian of Jameson Land (East Greenland) as a male cone consisting of bracts with circular ‘cones’ (c. 3.5 mm in diameter) in their axil, of which details are not discernible. The recovered *in situ* pollen are small (c. 26 µm × 16 µm), oval and with a longitudinal fold or a sulcus. These cones resemble our material quite well, especially in the morphology of the bracts (see, e.g., HARRIS 1935, pl. 29 fig. 4 and our Figs. 5D, H) that are slightly smaller in *S. einbergensis* (up to 9 mm long) than in *S. clandestinus* (up to 15 mm long). However, HARRIS (1935) considered these as bracts whereas we interpret them as the microsporophylls. In our specimens, circular masses of pollen are gathered in a group in the middle part of the adaxial side of these sporophylls but there is no indication of a sporangial wall around each of them. The *in situ* pollen recovered both from our specimens and those from Jameson Land are similar in being small, oval and probably monosulcate.

Hence, we attribute our material to the same genus *Sphaerostrobos* but to a different species (viz. *S. einbergensis*), because of the size difference and of the interpretation of the bracts/microsporophylls. Therefore, the generic diagnosis of *Sphaerostrobos* has to be emended: Elongated, relatively slender axis, bearing lanceolate microsporophylls; microsporophylls bearing groups of round microsporangia in the centre of their adaxial side. *In situ* pollen smooth-walled, circular to oval in outline and probably monosulcate.

HARRIS (1935) regarded *S. clandestinus* to belong to the fossil genus *Podozamites* because of the resemblance between *Podozamites* leaves and the ‘bracts’ of *Sphaerostrobos*. However, *Podozamites* has not been recorded from any of the Rhaetian localities around Coburg. Thus, we consider this assignment doubtful, and believe *Desmiophyllum* a much more likely foliage genus belonging to the same plant (see discussion below).

**Occurrence in other adjacent Rhaetian/Hettangian floras:** We are not aware of similar cones in other

Rhaetian floras, other than *Sphaerostrobos clandestinus* in Jameson Land (East Greenland).

**Material examined:** 52/98, 64+65/98, O68/98, 80-83/98, 115/98, 208+209/98, 229/99, 296+297/00, 401/01, 405/01, 437/01, 481+482/01, 528+529/01, 542/02, 553/02, 556/02; 46Ei01, 60Ei01, 62Ei01, 65Ei01; UU25994E,H,M,P, 26003, 26007, 26009A,B,D,E,I, 26011, 26998.

Genus *Ourostrobos* HARRIS 1935  
*Ourostrobos einbergensis* sp. nov.  
 Figs. 6A–J, 10A–D

**Etymology:** after the village of Einberg.

**Holotype:** UU26008A (Fig. 6E) and B (Fig. 6A), here designated (cone with one seed per scale).

**Paratype:** UU26999 (Fig. 6B), here designated (cone seen from below).

**Type locality:** former sand pit Langguth, located SE of the village of Einberg.

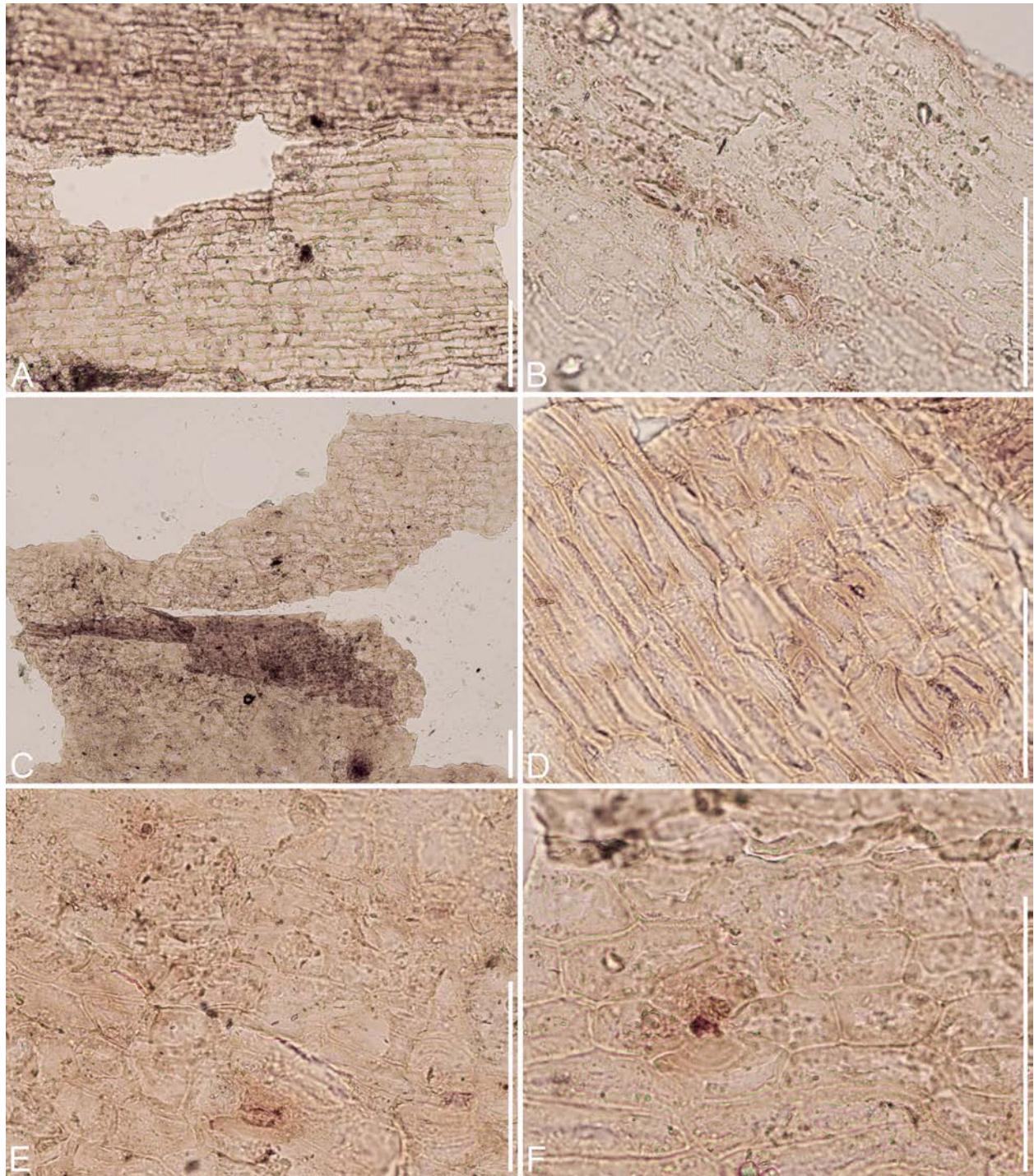
**Type horizon and age:** Exter Formation (Contorta Beds), Rhaetian, Triassic.

**Diagnosis:** Seed-bearing cone composed of a central axis, covered with pointing upwards scales. Scales up to 17 mm long and 7 mm wide, with their widest part at 1/3<sup>rd</sup> of their length, an acute apex and longitudinally striated. Each scale bearing one ovule/seed in its axil. Ovule/seed oval in shape.

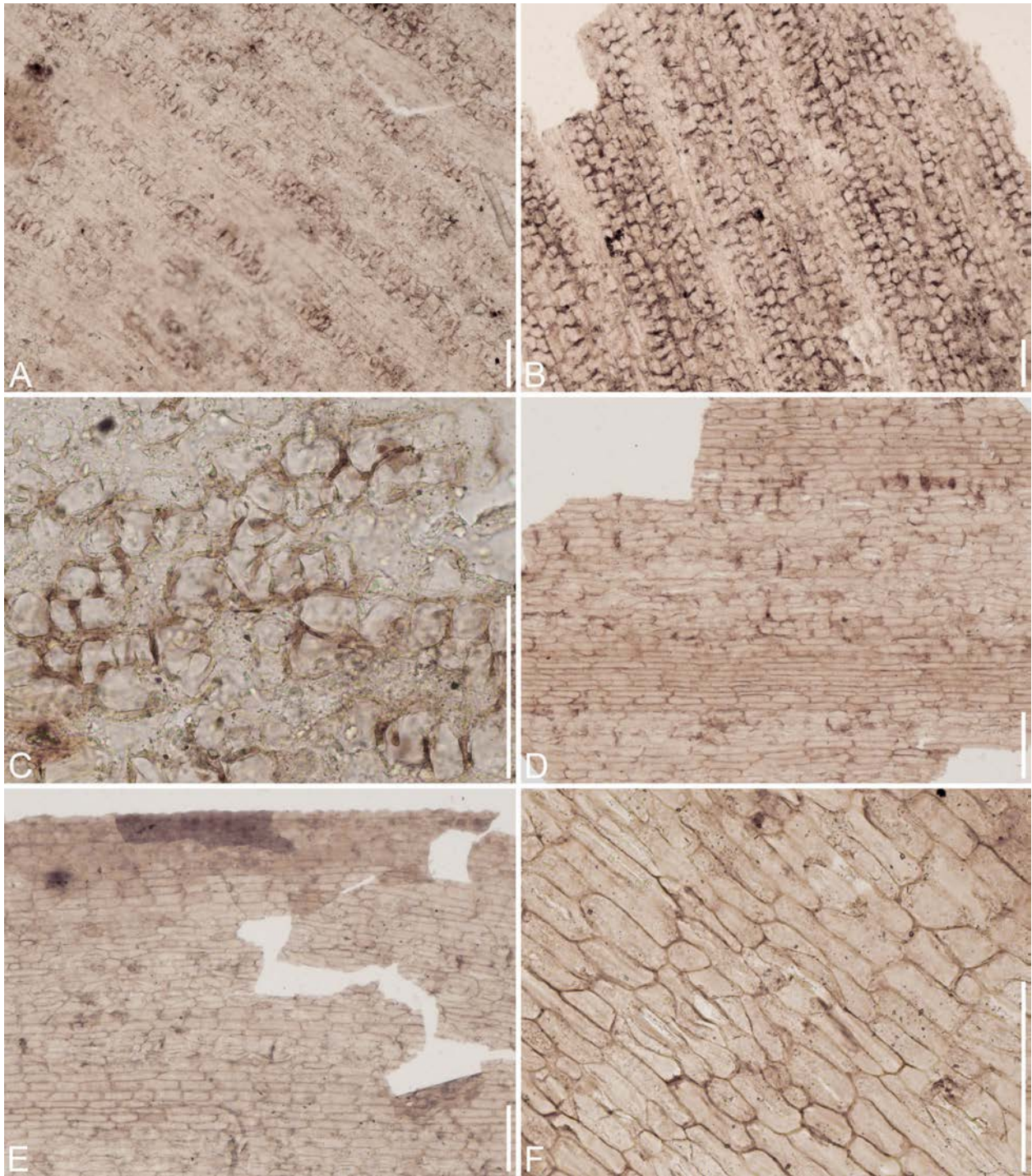
**Description of the material:** The type specimen UU26008A/B yields an incomplete cone fragment, 51 mm long and varying in width from 15 mm basally to 11 mm more apically (Fig. 6A). It consists of spirally arranged, longitudinally striate ovuliferous scales, c. 10 mm long; apices seem to be acute (see the lower scales in Fig. 6A). Some cuticular remains are preserved (Fig. 10A, B). Each scale bears one ovule/seed in its axil, c. 2 mm long, 1–1.2 mm wide and oval in shape (Fig. 6E). Although these seed-bearing cones occur less frequently than microsporangiate cones, they are still quite common, and are commonly embedded so that they can be seen from below, viz. O479/01 (Fig. 6B). The imprint is 10 mm in diameter; a central axis, 2.5 mm in diameter, and longitudinally striate portions of the most basal ovulate scales. O560/02



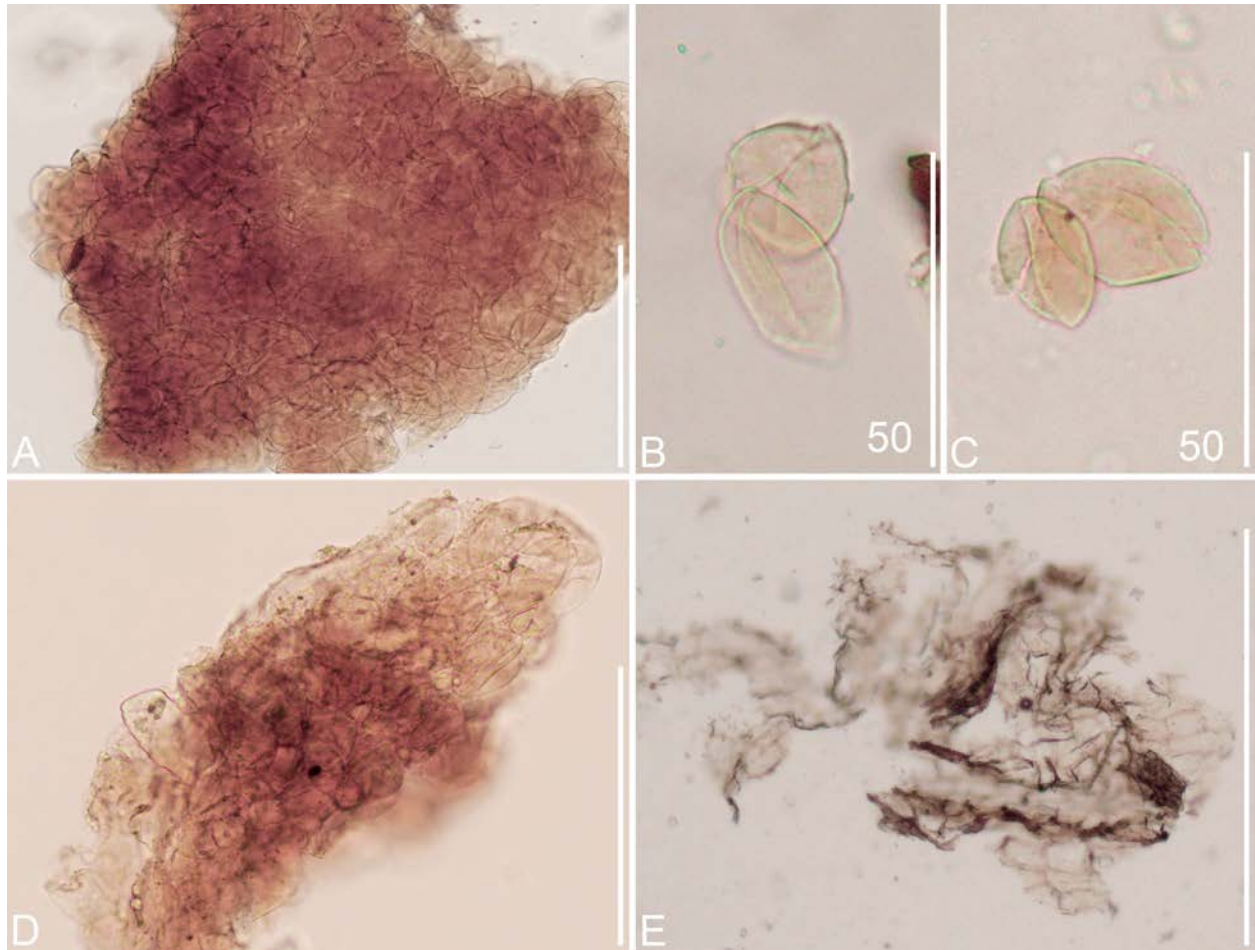
**Fig. 6.** *Ourostrobos einbergensis* from the Rhaetian of Einberg. **A** – Holotype (part), ovulate cone with one seed per scale (see arrow); UU26008B. **B** – Paratype, cone seen from below; UU26999. **C** – Detached, large scale; O188/98. **D** – Detached, bulging scale; O235/99. **E** – Holotype (counterpart), ovulate cone with one seed per scale (see arrow); UU26008A. **F** – Almost complete ovulate cone; O560/02. **G** – Almost complete ovulate cone seen from the outside; O50/98. **H** – Fragment of ovulate cone with well-preserved scales; O213/98. **J** – Ovulate cone associated with *Desmiophyllum harrisii* leaves; arrow indicates the possible presence of a seed on the internal side of the scale; O407/01. Scale bars: 10 mm.



**Fig. 7.** Cuticular remains of *Stachyotaxus septentrionalis* and *Schizolepidopsis liasoqueuperianus* from the Rhaetian of Einberg. **A** – *Stachyotaxus septentrionalis*, fragment of adaxial cuticle; from specimen O424/01. **B** – *Stachyotaxus septentrionalis*, fragment of abaxial cuticle; from specimen O424/01. **C** – *Schizolepidopsis liasoqueuperianus*, fragment of adaxial cuticle; from specimen O341/99. **D** – *Schizolepidopsis liasoqueuperianus*, fragment of abaxial cuticle; cuticle slide C.305. **E** – *Schizolepidopsis liasoqueuperianus*, cuticle fragment with stoma seen from the inside showing guard cells; from specimen O341/99. **F** – *Schizolepidopsis liasoqueuperianus*, cuticle fragment with stoma showing subsidiary cells; from specimen O341/99. Scale bars: 100  $\mu$ m.



**Fig. 8.** Cuticular remains of *Desmiophyllum harrisii* from the Rhaetian of Einberg. **A** – Unseparated cuticle fragment showing veins and rows with indiscernible stomata; from specimen O397/00. **B** – Undermacerated cuticle fragment showing epidermal cells with thickenings, holding upper and lower cuticle together; from specimen UU26020. **C** – Undermacerated cuticle fragment showing enlargement of epidermal cells with thickenings; from specimen UU26004. **D** – Abaxial, fully macerated cuticle showing irregular rows of stomata between the veins; Cuticle slide 301. **E** – Adaxial, fully macerated cuticle, showing veins and intercostal areas without stomata; Cuticle slide 301. **F** – Detail from Fig. 8D showing stomata. Scale bars: 100 µm.



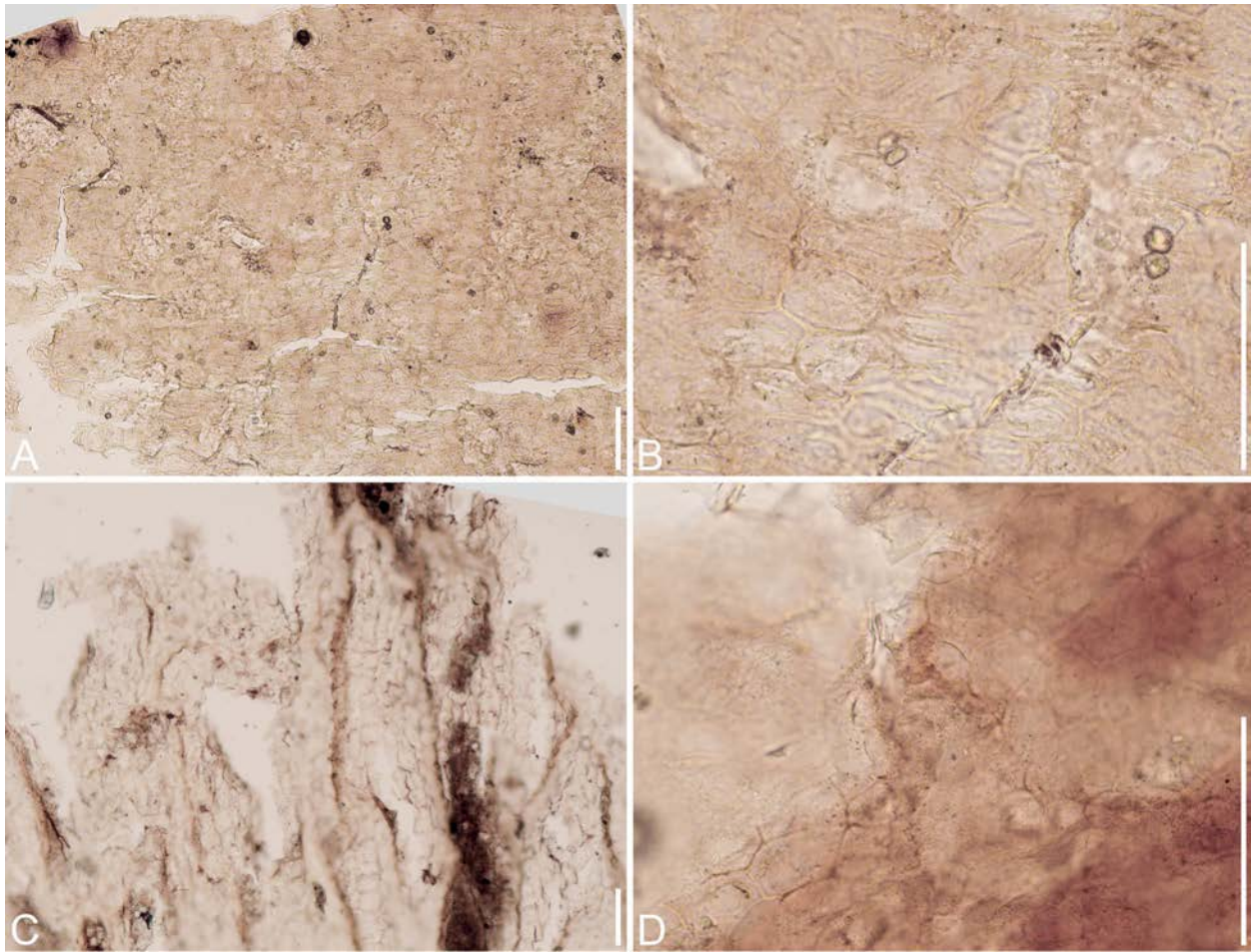
**Fig. 9.** *In situ* pollen sacs and pollen of *Sphaerostrobus einbergensis* from the Rhaetian of Einberg. **A** – *Sphaerostrobus einbergensis*, mass of immature pollen grains extracted from Paratype UU25994E. **B** – *Sphaerostrobus einbergensis*, two monosulcate, smooth pollen grains, extracted from Paratype UU25994E. **C** – *Sphaerostrobus einbergensis*, another pair of monosulcate, smooth pollen grains, extracted from Paratype UU25994E. **D** – *Sphaerostrobus einbergensis*, small mass of pollen grains with thin cuticular remains; from specimen O437/01. **E** – *Sphaerostrobus einbergensis*, small piece of pollen sac wall; from specimen S25994M. Scale bars: A, D, E 100  $\mu$ m; B, C 50  $\mu$ m.

(and its counterpart 561/02) yields an almost complete cone, 35 mm long and 10 mm wide, with longitudinally striate, spirally attached scales arising at an angle of c. 30°. The scales are up to 12 mm long (Fig. 6F). Specimen O49/98 and its counterpart O50/98 (Fig. 6G) provides an almost complete ovulate cone, 29 mm long, basally 5 mm wide, rapidly increasing to a width of 10 mm, with a number of up to 13 mm long scales; here interpreted as immature cone. The scales arise at angles of c. 30°, and are again longitudinally striate, with their widest part (5 mm) at probably 1/3<sup>rd</sup> of the scale length. In some places an acute apex can be detected. Better scales with apices are preserved in

the cone of specimen O213/98 (Fig. 6H), where the scales measure up to a length of 14 mm and a width of 4.5 mm at around 1/3<sup>rd</sup> of the scale length.

O337/99 yielded some larger cuticular remains (Figs. 10C, D) that resemble those of *Desmiophyllum harrisii* but are too badly preserved to make a definite statement.

Most cones are associated with *Desmiophyllum* leaves on the same rock specimen of e.g., O407/01 (Fig. 6J), where cones are partly overlying these leaves. One of these cones has a bulging appearance indicating the presence of seeds in the axils of the scales (see arrow).



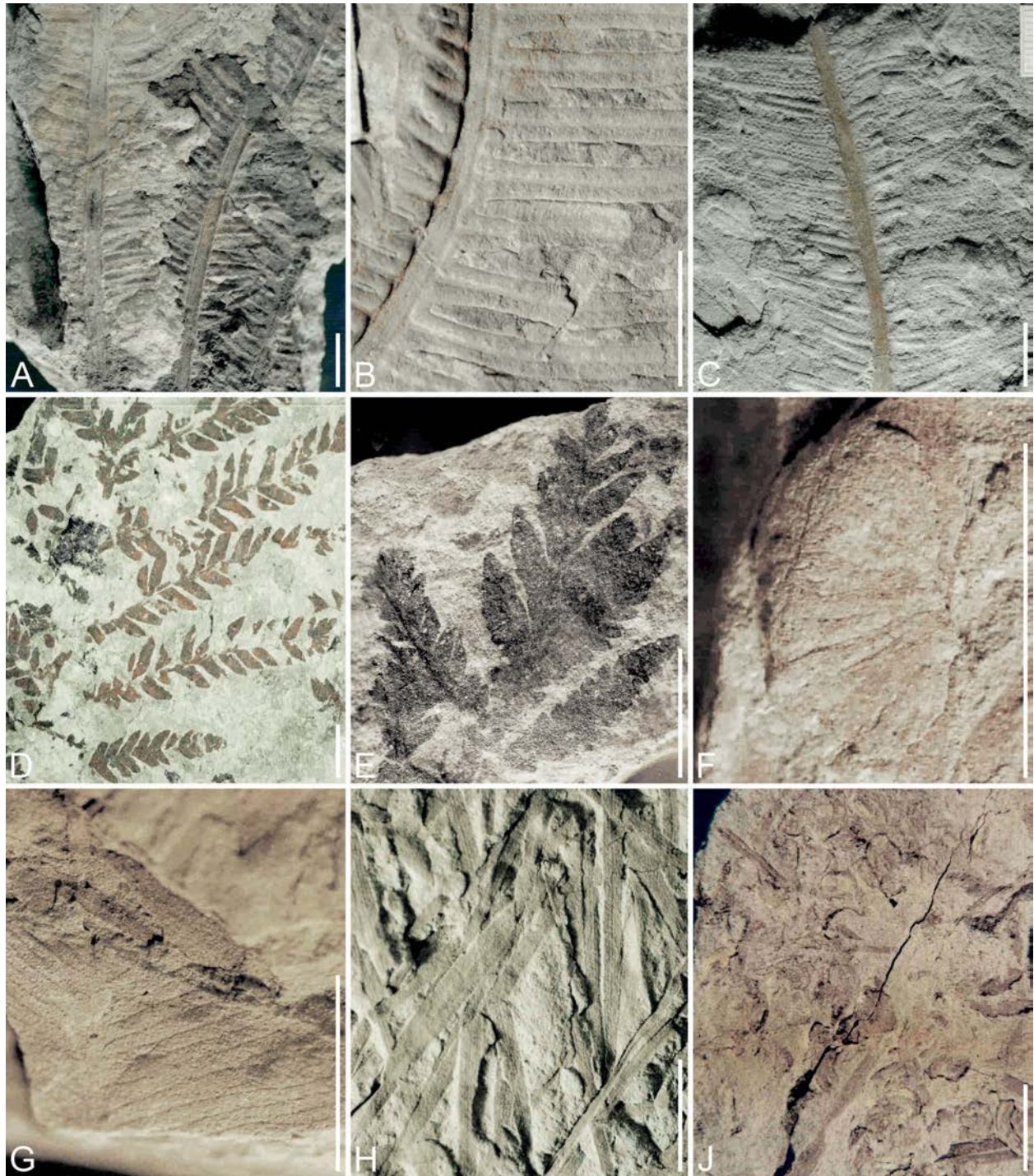
**Fig. 10.** Cuticular remains of *Ourostrobos einbergensis* from the Rhaetian of Einberg. **A** – Cuticle fragment from specimen UU26008B. **B** – Another cuticle fragment from specimen UU256008B. **C** – Cuticle fragment from specimen O337/99. **D** – Another cuticle fragment from specimen O337/99 showing a possible stoma. Scale bars: 100  $\mu$ m.

Detached scales occur commonly in the assemblage; the longest (O188/98; Fig. 6C) is 17 mm long and 6 mm wide at  $1/3^{\text{rd}}$  with a long, acute apex. O235/99 (Fig. 6D) is another example where the bulging of the scale is quite distinct, indicating that possibly the scales still carried their seed when they became detached and embedded.

**Remarks:** HARRIS (1935: 116, pl. 23, figs. 3, 6, 7, 11; pl. 27, fig. 11) described the monotypic genus *Ourostrobos* from the Rhaetian of Jameson Land (East Greenland) for a cone with upwards pointing, c. 15 mm long cone scales, each bearing one seed attached to its upper side near the place of attachment to the cone axis. Our ovuliferous cones also have scales of similar

size that bear only one seed in its axil. Hence our attribution to the genus *Ourostrobos*, as we are not aware of any other genus for this type of fossil ovulate cones that cannot be attributed to an extant family. However, the type species *Ourostrobos nathorstii* HARRIS 1935 differs clearly from our cones in having much more densely arranged ovuliferous scales. Therefore, we erected a new species for our material, viz. *O. einbergensis*.

**Occurrence in other adjacent Rhaetian floras:** We are not aware of similar cones in other Rhaetian floras, other than *Ourostrobos nathorstii* in Jameson Land (East Greenland).



**Fig. 11.** Historical specimens from Kipfendorf, photographed by one of us (SS) at the Museum of Coburg before the collection was lost. **A** – *Phlebopteris muensteri*, showing several adjacent pinnae. **B** – *Phlebopteris muensteri*, pinna fragment showing venation. **C** – *Phlebopteris muensteri*, fertile pinna fragment. **D** – *Lepidopteris ottonis*, frond fragment. **E** – *Lepidopteris ottonis*, apical frond fragment. **F** – *Hydropterangium* sp. **G** – *Pseudoctenis florinii*, small leaf fragment with typical venation. **H** – *Desmiophyllum harrisii*, slab crowded with leaves; formerly determined as *Schizolepis* (FISCHER 1907). **J** – *Peltaspermum* sp., seeds. Scale bars: 10 mm.

**Material examined:** Cones: O49+50/98, 181-182/98, 193+194/98, 195/98, 201/98, 213/98, 216/98, 254+255/99, 272/99, 337/99, 387/00, 407/01, 478+479/01, 530/02, 531/02, 533+534/02, 560+561/02; 04Ei00; UU25994N, 26008A, B, 26009H, 26011, 26999; detached scales: O179/98, 187/98+188/98, 201/98, 235/99, 272/99, 478+479/01, 562+563/02; 02Ei00a, 25Ei01.

**Comparison between *Sphaerostrobos einbergensis* and *Ourostrobos einbergensis*:** Both cones, *Sphaerostrobos einbergensis* and *Ourostrobos einbergensis*, are quite similar in appearance, especially in the morphology of the sporophylls. However, there are a few differences between the two types of cones. First of all, the size of the cones; in general, the microsporangiate cones (*S. einbergensis*) are slightly larger than the ovulate ones (*O. einbergensis*), but the number of sporophylls in the microsporangiate cones is larger than in the ovulate ones and also the sporophyll size in the microsporangiate ones is smaller than in the ovulate ones. The size difference of the sporophylls is partly due to the morphology of their apices; those of *Sphaerostrobos* have a short, acute apex (Fig. 5D), whereas those in *O. einbergensis* have a much more elongate acute apex (Figs. 6C, D). Moreover, there is a difference in angle of attachment of the sporophylls; those of *Sphaerostrobos einbergensis* arise at c. 70°, then curve almost immediately to 90° in the area where they carry the microsporangia, and their distal part is again bending upwards (Fig. 5C). Those of *Ourostrobos einbergensis* arise at c. 50–70° and normally do not curve. They carry the ovule in their axil and continue more or less straight upwards (Figs. 6A, E).

**Possible attribution of *Sphaerostrobos einbergensis*, *Ourostrobos einbergensis* and *Desmiophyllum harrisii* to the same natural species:** On almost every rock slab yielding a cone or cone fragments of *Sphaerostrobos einbergensis*, there are also leaves of *Desmiophyllum* preserved. Consequently, speculating about a conspecificity of the reproductive organs and foliage is warranted. Evidence is, however, only proven indirectly because the microsporangiate cones on O210/98 are only attached to 4-mm-wide naked axes, but those on 16Ei99b are attached to an axis with some *Desmiophyllum* leaves distributed in a position suggesting that they probably originated from the same axes. A drawback here is that these cones are unequivocally identified as *Sphaerostrobos einbergensis*. None of the *Ourostrobos einbergensis* ovulate cones found so far is attached to an

axis, but considering the high similarity of both cones in morphology and the fact that they bear the reproductive structures on the adaxial side of the sporophylls, we believe them to belong to the same natural genus.

**Possible affinity of the plants bearing *Desmiophyllum harrisii* leaves and *Sphaerostrobos einbergensis* and *Ourostrobos einbergensis* cones:** It is as yet undissolved where the affinities of these plants lie. The microsporangiate cone *Sphaerostrobos einbergensis* and the ovulate cone *Ourostrobos einbergensis* look like conifer cones in grossmorphology. The Palissyaceae is the only conifer family with a similar cone morphology with adaxial reproductive organs and similar pollen; but the leaf morphology of *Desmiophyllum harrisii* is completely different from those of *Palissya* and *Stachyotaxus*. These two genera have typical needle-like, single-veined leaves, while *Desmiophyllum* has long, strap-like leaves with a number of parallel veins. The *in situ* small, monosulcate, oval pollen found in *S. einbergensis* has also been found in the taxa from the Palissyaceae, but it occurs in the Ginkgophytes as well (see e.g., VAN KONIJNENBURG-VAN CITTERT 1971, 2010). However, Ginkgophyte fertile organs are so completely different from *Sphaerostrobos einbergensis* and *Ourostrobos einbergensis* that an affinity to the Ginkgophytes seems highly unlikely (see e.g., HARRIS 1935, 1937; HARRIS & MILLINGTON 1974; TAYLOR 1981). But as long as we cannot be absolutely sure about the natural affinity of *Desmiophyllum harrisii* and its fertile organs, we prefer to keep them in *Gymnospermae incertae sedis*.

## 4. Discussion

### 4.1. Composition of the flora and comparison to the other Rhaetian floras of the Coburg area

The plant macrofossil assemblage obtained from the Rhaetian strata of the Einberg sandpit constitutes a flora with a moderate species diversity, of which we here review the conifers and *Gymnospermae incertae sedis*. The conifer/*incertae sedis* portion of the flora is almost as diverse as the assemblage recorded from another Rhaetian locality around Coburg, viz. Wüstenwelsberg (see Table 1; POTTE et al. 2016; VAN KONIJNENBURG-VAN CITTERT et al. 2018, 2019, 2021a, 2021b, 2022), whereas it has two leafy species in common with the flora from Heilgersdorf (KEL-

**Table 1.** Occurrences of the various conifer and *incertae sedis* taxa at the four Rhaetian localities around Coburg. Based on Achilles 1981 (Kipfendorf), Kelber & Van Konijnenburg-van Cittert 1997 (Heilgersdorf), Van Konijnenburg-van Cittert et al. 2021a (Wüstenwelsberg), the present paper and personal observations (SS, GD and JHAvKvC).

	Taxon	Einberg	Wüstenwelsberg	Heilgersdorf	Kipfendorf
Conifers	<i>Palissya sphenolepis</i>		X		
	<i>Stachyotaxus septentrionalis</i>	X	X	X	
	<i>Schizolepidopsis liasokeyperianus</i>	X	X	X	
incertae sedis	<i>Desmiophyllum harrisii</i>	X	X		X
	<i>Sphaerostrobos einbergensis</i>	X			
	<i>Ourostrobos einbergensis</i>	X			

BER & VAN KONIJNENBURG-VAN CITTERT 1997), and none with that of Kipfendorf according to the literature data. But one of us (SS) saw the collection from Kipfendorf in the Coburg Museum before it was lost and made photos; those photos document the presence of *Desmiophyllum harrisii* leaves in the assemblage (Fig. 11H).

The most striking difference with the flora from Wüstenwelsberg is that *Palissya sphenolepis* is completely absent in Einberg (just as in the other two localities around Coburg). The second difference is the overwhelming presence of *Desmiophyllum harrisii* in the Einberg flora, which is rare in Wüstenwelsberg, absent in Heilgersdorf but probably present in the Kipfendorf assemblage (see Table 1). Moreover, the Einberg assemblage contains quite large numbers of the fertile cones *Sphaerostrobos einbergensis* and *Ourostrobos einbergensis* that are probably the fertile organs of *D. harrisii*. These have not been recorded from the other three localities so far.

Table 2 and Fig. 12 show all the taxa encountered in the four Rhaetian floras around Coburg, with their relative abundances. It is immediately clear that *Lepidopteris ottonis* – an index fossil of Rhaetian strata – is a very abundant fossil leaf in all assemblages, but no other taxon was recorded from all localities except for *Equisetites laevis*, which is present but commonly rare. The other equisetalean taxon, *Neocalamites lehmannianus*, is fairly common in Einberg and has been found in Kipfendorf but is absent from Heilgersdorf and the rich assemblage of Wüstenwelsberg. The two lycophyte taxa only occur in Wüstenwelsberg. Some of the fern taxa occur only in one locality, e.g., *Todites crenatus* is very common in Einberg but absent from any of the other localities. Others occur in two or three localities (see Table 2). The same applies to the ten seed fern taxa, which occur in one or maximal two assemblages (except for *Lepidopteris* and its

reproductive organs). The cycads are all endemic to Wüstenwelsberg, with the exception of *Pseudoclenis cteniforme*, which is common in Wüstenwelsberg and has been encountered in Einberg but not in the other two. Bennettites occur almost only, and in large numbers, in Wüstenwelsberg, although two taxa have been found at Einberg but are rare. *Ginkgoites taeniatus* occurs commonly in the topmost layer at Wüstenwelsberg but has not been encountered in any of the other three localities, probably due to the absence of uppermost Rhaetian layer there. The other four ginkgoalean/czekanowskialean taxa have only been encountered in the Einberg assemblage. Conifers are relatively rare, or even absent (Kipfendorf), in the four localities; two occur in the other three assemblages, *Palissya sphenolepis* has only been found at Wüstenwelsberg. Finally, *Desmiophyllum harrisii* (with its probable cones) is very common at Einberg, relatively common at Kipfendorf, rare at Wüstenwelsberg and absent at Heilgersdorf so far.

NB: The data in Table 2 have been based on the assemblage from Heilgersdorf (Kelber & Van Konijnenburg-van Cittert 1997), Wüstenwelsberg (Van Konijnenburg-van Cittert et al. 2014, 2016, 2017, 2018, 2019, 2020, 2021a; Pott et al. 2016), Einberg (Van Konijnenburg-van Cittert et al. 2021b, 2022, present study) and Kipfendorf. For the latter locality we used the data that SS collected from the actual specimens he saw in the Coburg Museum before these specimens could not be found anymore. The differences between the originally reported material (see Fischer 1907; Krumbeck 1939; Achilles 1981) and the observed material are as follows; the taxa mentioned in literature are *Equisetites muensteri*, *Neocalamites* sp., *Phlebopteris polypodioides* BRONGNIART, *Clathropteris meniscioides* (BRONGNIART) BRONGNIART, *Lepidopteris ottonis* (GOEPPERT) SCHIMPER, *Nilssonia minima* GOETHAN, *Pterophyllum angustum* BRAUN, *Schizolepidopsis*

**Table 2.** Comparison of all taxa found at the four Rhaetian localities around Coburg with their relative abundances – x = rare, xx = fairly common, xxx = very common. NB. *Ginkgoites taeniatus* occurs only in the topmost layer at Wüstenwelsberg. Based on [ACHILLES \(1981\)](#), [KELBER & VAN KONIJNENBURG-VAN CITTERT \(1997\)](#), [POTT et al. \(2016\)](#), [VAN KONIJNENBURG-VAN CITTERT et al. \(2014, 2016, 2017, 2018, 2019, 2020, 2021a, 2021b, 2022\)](#), the present paper and personal observations (SS, GD and JHAvKvC).

	Einberg	Kipfendorf	Wüstenwelsberg	Heilgersdorf
<i>Lepacyclotes</i> sp.			x	
<i>Selaginellites coburgensis</i>			x	
<i>Equisetites laevis</i>	x		xx	x
<i>Neocalamites lehmannianus</i>	xx			
<i>Todites roessertii</i>			xx	
<i>Todites (Cladophlebis) scoresbyensis</i>			x	
<i>Todites crenatus</i>	xxx			
<i>Todites</i> sp.	x			x
<i>Phlebopteris muensteri</i>	x	xx	xx	
<i>Phlebopteris angustiloba</i>			x	
<i>Clathropteris meniscioides</i>	x		xx	
<i>Dictyophyllum exile</i>			xx	x
<i>Thaumatopteris brauniana</i>			x	
<i>Spiropteris</i> sp.	x		x	
<i>Lepidopteris ottonis</i>	xxx	xxx	xxx	xxx
<i>Antevsia zeilleri</i>	x		x	x
<i>Peltaspermum rotula</i>	xx		x	x
<i>Peltaspermum</i> sp.		x	x	
<i>Scytophyllum</i> sp.	x			
<i>Pachypteris</i> cf. <i>rhomboidalis</i>			x	?x
<i>Pachypteris schwartzii</i>	x			
cf. <i>Kirchmuellia</i> sp.	x			
<i>Ptilozamites nilssonii</i>			xx	
<i>Ptilozamites heeri</i>			xx	
<i>Hydropterangium roesleri</i>			x	
<i>Hydropterangium</i> sp.		x		
<i>Carpolithes</i> sp.			x	
<i>Nilssonia pterophylloides</i>			xx	
<i>Nilssonia polymorpha</i>				?x
<i>Nilssonia</i> sp.	x			
<i>Doratophyllum nathorstii</i>			xx	
<i>Ctenis latepinnata</i>			x	
<i>Pseudoctenis florinii</i>		?x	xxx	
<i>Pseudoctenis cteniforme</i>	x		xxx	
<i>Becklesia franconica</i>			xx	
<i>Becklesia</i> sp.	x			
<i>Pterophyllum aequale</i>	x		xxx	?x
<i>Pterophyllum astartense</i>			xxx	
<i>Pterophyllum pinnatifidum</i>			x	
<i>Pterophyllum kochii</i>			x	
<i>Pterophyllum zygotacticum</i>	x			
<i>Anomozamites gracilis</i>			x	
<i>Nilssoniopteris jourdyi</i>			x	
<i>Nilssoniopteris ajorpokensis</i>			xx	
<i>Wielandiella angustifolia</i>			xxx	
<i>Welsbergia bursigera</i>			xx	

	Einberg	Kipfendorf	Wüstenwelsberg	Heilgersdorf
<i>Ginkgoites taeniatus</i>			XX	
<i>Ginkgoites</i> sp.			X	
<i>Sphenobaiera boeggildiana</i>	X			
<i>Arberophyllum</i> sp.	X			
<i>Czekanowskia nathorstii</i>	XX			
<i>Leptostrobus</i> sp.	X			
<i>Palissya sphenolepis</i>			XX	
<i>Stachyotaxus septentrionalis</i>	X		XXX	X
<i>Schizolepidopsis liasokeuperianus</i>	X		XX	X
<i>Desmiophyllum harrisii</i>	XXX	XX	X	
<i>Sphaerostrobos einbergensis</i>	XX			
<i>Ourostrobos einbergensis</i>	XX			

*liasokeuperianus* and *Podozamites schenkii* HEER. The taxa that SS actually observed and photographed in the Coburg Museum are *Phlebopteris muensteri* (SCHENK) HIRMER & HÖRHAMMER (Fig. 11A–C, G), *Lepidopteris ottonis* (Fig. 11D, E), *Peltaspermum* sp. (Fig. 11J), *Hydropterangium* sp. (Fig. 11F), probably *Pseudoctenis florinii* LUNDBLAD and *Desmiophyllum harrisii* (see Table 2 and Fig. 11H). So, both originally reported horsetails, the fern *C. meniscioides*, the cycadophytes *N. minima*, *P. angustum* and the conifer *P. schenkii* have not been found. *Phlebopteris polypodioides* specimens have now been determined as *Phlebopteris muensteri*, *Schizolepidopsis liasokeuperianus* as *Desmiophyllum harrisii*. The presence of *Peltaspermum* sp., *Hydropterangium* sp. and probably *P. florinii* are here newly reported (see also Fig. 11).

#### 4.2. Comparison of the conifers with other coeval floras in adjacent areas

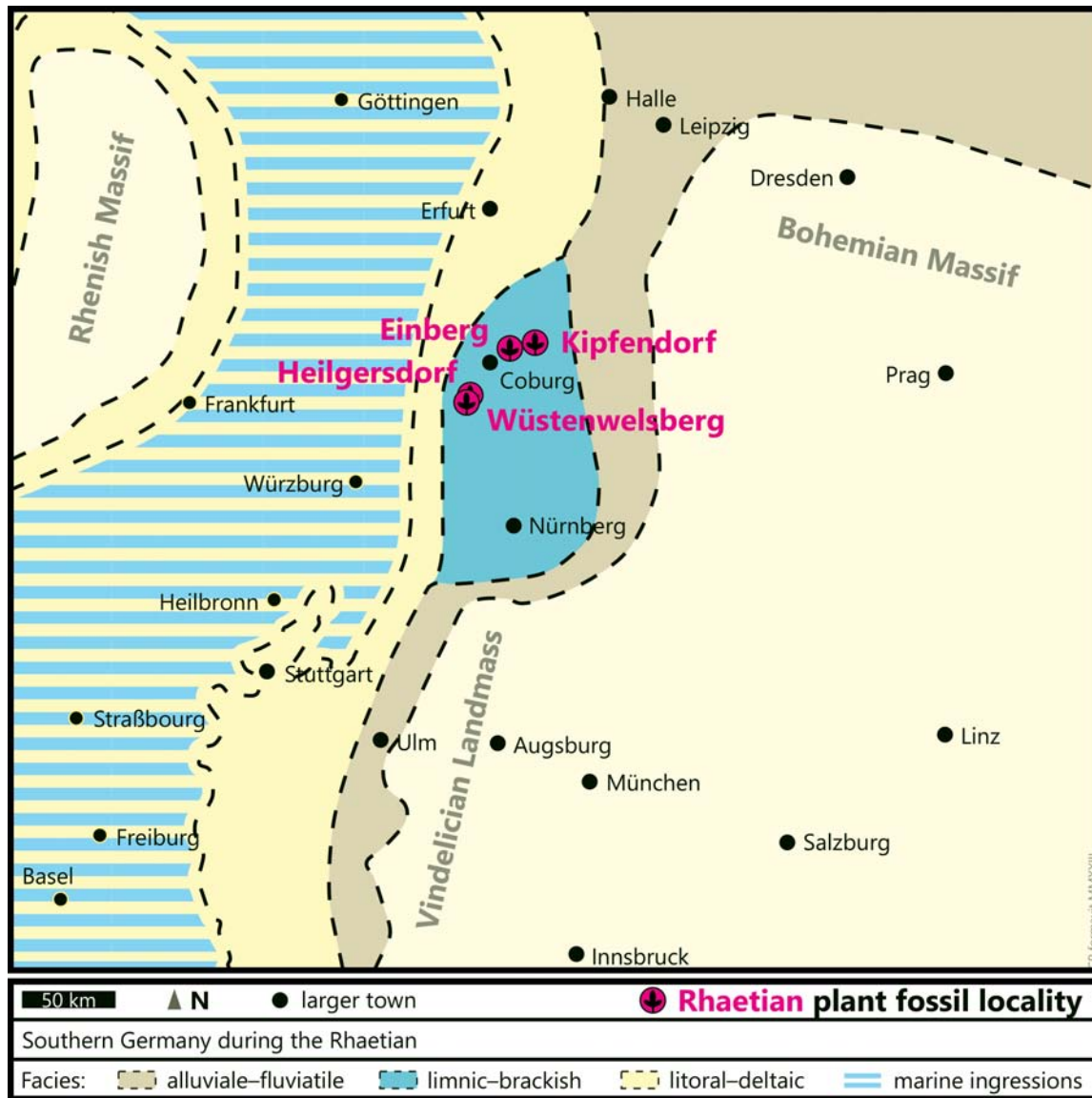
One of the striking differences between the four Rhaetian floras around Coburg and other Rhaetian floras in adjacent areas is that the genera *Podozamites* and *Hirmeriella* are represented in the assemblages. The genus *Podozamites* occurs in Rhaetian floras from Sweden (NATHORST 1878; ANTEVS 1919; JOHANSSON 1922), Canada (ASH & BASINGER 1991), Iran (BARNARD 1965, 1967; SCHWEITZER & KIRCHNER 1996), Jameson Land, Greenland (HARRIS 1926, 1935, 1946), Denmark (MÖLLER 1903), Poland (PACZYNA 2014), Donets Basin (STANISLAVSKY 1971, 1976), Russia (VOLYNETS & SHOROKOVA 2007; VOLYNETS et al. 2008) and China (ZHOU 1989). *Hirmeriella* is less common but

still occurs in a number of Rhaetian floras, e.g., Germany (FRENTZEN 1932; BARTH et al. 2014), Denmark (MÖLLER 1903), Sweden (NATHORST 1878) and Russia (VOLYNETS & SHOROKOVA 2007). *Hirmeriella* is very common in Hettangian floras (see e.g., Poland: BARBACKA et al. 2010; PACZYNA 2013; Germany: GOTHAN 1914; WEBER 1968).

Looking at the other conifer taxa (Table 3), *Palissya sphenolepis* has been reported from other parts of Germany, Poland, Scania and Denmark and possibly also from Greenland (NATHORST 1878; MÖLLER 1903; JOHANSSON 1922; FRENTZEN 1932; HARRIS 1935; PACZYNA 2014). *Stachyotaxus septentrionalis* has been recorded from all other Rhaetian floras with the exception of the Donets Basin and Russia (NATHORST 1878; JOHANSSON 1922; HARRIS 1926, 1935; ASH & BASINGER 1991; KELBER & VAN KONIJNENBURG-VAN CITTERT 1997; PACZYNA 2014), and *Schizolepidopsis liasokeuperianus* (or similar leaves) from almost all localities except Greenland and Iran (BRAUN 1847; NATHORST 1878; ANTEVS 1919; JOHANSSON 1922; STANISLAVSKY 1971, 1976; KELBER & VAN KONIJNENBURG-VAN CITTERT 1997; PACZYNA 2014).

#### 4.3. Comparison of the Rhaetian with the Hettangian floras from Franconia

Comparing the composition of all four Rhaetian assemblages around Coburg (see Table 2) with that of all the Hettangian assemblages known from Franconia (see e.g., GOTHAN 1914; WEBER 1968; KIRCHNER 1992), it is obvious that the differences are substantial (Table 4). The two lycophyte taxa found around Coburg,



**Fig. 12.** Palaeogeographical map of the area around Coburg during the Rhaetian, with the mainland areas (Rhenish Massif and Bohemian Massif) indicated in very pale yellow.

have so far not been recorded from the Hettangian (but there a different *Lepacyclotes* species was recorded) neither *Equisetites laevis*, in contrast to *Neocalamites lehmannianus* that is quite common in the Hettangian. Fern composition is different as well; Marattiales are completely missing in the Rhaetian flora. *Todites roesertii* occurs in both the Rhaetian and Hettangian, but other *Todites* species are either occurring in the Rhaetian (e.g., *T. crenatus*) or the Hettangian (e.g., *T. prin-*

*ceps*). Both *Phlebopteris* species occur in Rhaetian and Hettangian assemblages. *Clathropteris meniscioides* is common in all floras around Coburg but is very rare (if present at all) in the Hettangian (GOTHAN 1914); *Dictyophyllum exile* is present in the Rhaetian but absent in the Hettangian, where another *Dictyophyllum* species is quite common, viz., *D. nilssonii*. *Thaumatopteris brauniana* is quite rare in the Rhaetian but common in Hettangian assemblages. As to the seed

**Table 3.** Occurrences of the various conifer and incertae sedis taxa in other adjacent Rhaetian localities. Based on HARRIS (1926, 1935, 1937), NATHORST (1878, 1886), ANTEVS (1919), JOHANSSON (1922), MÖLLER (1903), PACYNA (2014), SCHWEITZER & KIRCHNER (1996), STANISLAVSKY (1971, 1976), VOLYNETS & SHOROKOVA (2007).

	Einberg	Jameson Land	Scania	Denmark	Germany outside Bavaria	S Poland	Donets	Russia	Alborz
<i>Palissya sphenolepis</i>		?X	X	X	X	?X			
<i>Stachyotaxus septentrionalis</i>	X	X	X	X	X	X			X
<i>Schizolepidopsis liasokeuperianus</i>	X		X	?X	X	X	X	?X	
<i>Podozamites</i> spp.		X	X	X			X	X	X
<i>Hirmeriella</i> spp.			X	X	X			X	
<i>Desmiophyllum harrisii</i>	X					X			
<i>Sphaerostrobos einbergensis</i>	X								
<i>Ourostrobos einbergensis</i>	X								

ferns, here the difference is even larger; no Rhaetian taxa are present in the Hettangian floras with the exception of *Pachypteris rhomboidalis* that might have occurred in two Rhaetian localities but is one of the most common fossils in Hettangian assemblages. Vice versa, *Sagenopteris nilssoniana* is common in the Hettangian but has so far not been found in the Rhaetian assemblages around Coburg.

None of the cycad taxa recorded from the Rhaetian has been found in the Hettangian with the possible exception of *Nilssonia polymorpha*, but the record of that species from the Rhaetian of Heilgersdorf is doubtful. The same applies to the Bennettitales (Table 4); this group was quite diverse in Rhaetian floras but not very common in Hettangian ones. *Anomozamites gracilis* is present in both stages and possibly *Pterophyllum angustum* as well, but all the other Rhaetian taxa are missing in the Hettangian strata; in contrast, the common Hettangian species *Otozamites brevifolius* has not been found in the Rhaetian.

Regarding Ginkgophytes, *Ginkgoites taeniatus* is common in the Hettangian and its range has been extended by the discovery of its presence in the topmost layer of Wüstenwelsberg. The other Rhaetian ginkgophytes have not been encountered in the Hettangian and vice versa. *Palissya sphenolepis* and *Schizolepidopsis liasokeuperianus* were present in both stages. *Stachyotaxus* is restricted to Rhaetian strata, and as already mentioned in Chapter 4.2., *Hirmeriella* and *Podozamites* spp. are absent in the Rhaetian floras around Coburg. Finally, *Desmiophyllum harrisii* is known from Einberg and to a lesser degree Wüstenwelsberg; there are no records from Hettangian assemblages so far.

#### 4.4. Palaeoecological implications

Climate conditions during the Rhaetian are commonly reconstructed as hot and arid (Preto et al. 2010), although more humid conditions likely prevailed locally and for short periods of time (HARRIS 1935; POTT & McLOUGHLIN 2009; BONIS et al. 2010) such as, e.g., in Jameson Land, Scania and Wüstenwelsberg (VAN KONIJENBURG-VAN CITTERT et al. 2021a).

A comparison between the four Rhaetian floras around Coburg in species occurrences and relative abundances (Table 2) shows significant differences in composition between them. This might reflect slightly different environmental conditions in which the plants grew, or different histories of transport selection and preservation potential of the plant remains in their respective sedimentary successions. Of course, a difference based on sampling biases cannot be completely excluded as well since the recovered plant fossil assemblages at Kipfendorf and Heilgersdorf are rather small.

Based on the composition of the flora, the Einberg assemblage mainly reflects a vegetation of a deltaic or marsh wetland with an array of different, partly restricted, habitats that change at a small scale since the four different localities under study represent differences in vegetation composition. The recovered assemblages at Kipfendorf and Heilgersdorf are rather small, and no definite conclusions can be made from their respective floral compositions. The ecology of the Wüstenwelsberg assemblage is somewhat better known; the abundance of lycophytes, sphenophytes and ferns throughout the section indicates the presence of moist environments with stagnant water bodies and/or small river systems in the Wüstenwelsberg

**Table 4.** Occurrences of genera found in the Rhaetian and Hettangian floras in Franconia; fructifications are included in the leafy taxa. Circle means genus is present but with different species. Based on the references mentioned for Table 2, and GOTHAN (1914), WEBER (1968), KIRCHNER (1992), VAN KONIJNENBURG-VAN CITTERT et al. (1998), BAUER et al. (2015).

<i>Neocalamites</i>	x	x
<i>Marattiopsis</i>		x
<i>Todites</i>	x○	x○
<i>Phialopteris</i>		x
<i>Selenocarpus</i>		x
<i>Phlebopteris</i>	x	x
<i>Clathropteris</i>	x	
<i>Dictyophyllum</i>	○	○
<i>Thaumatopteris</i>	x	x
<i>Goepfertella</i>		x
<i>Lepidopteris</i>	x	
<i>Scytophyllum</i>	x	
<i>Pachypteris</i>	○	○
<i>Ptilozamites</i>	○	○
<i>Sagenopteris</i>		x
<i>Nilssonia</i>	○	○
<i>Doratophyllum</i>	x	
<i>Ctenis</i>	x	
<i>Pseudoctenis</i>	○	○
<i>Becklesia</i>	x	
<i>Otozamites</i>		x
<i>Pterophyllum</i>	○	○
<i>Anomozamites</i>	x	x
<i>Wielandiella</i>	x	
<i>Ginkgoites</i>	x	x
<i>Baiera</i>		x
<i>Sphenobaiera</i>	○	○
<i>Schmeissneria</i>		x
<i>Arberophyllum</i>	x	
<i>Czekanowskia</i>	x	
<i>Palissya</i>	x	x
<i>Stachyotaxus</i>	x	
<i>Hirmeriella</i>		x
<i>Podozamites</i>		x
<i>Desmiophyllum</i>	○	○

area during the latest Rhaetian (VAN KONIJNENBURG-VAN CITTERT et al. 2020, 2021a), although in general some taxa of these groups might of course have grown in dryer places.

The differences in sphenophyte composition between the two assemblages might be caused by the fact that the species probably grew under different environmental circumstances, possibly in restricted habitats (VAN KONIJNENBURG-VAN CITTERT et al. 2021b). The extensive presence of the fern *Todites crenatus* only in Einberg also points towards differential hab-

itats between the Rhaetian localities around Coburg. The fact that no spores of that species have been found *in situ* in the very abundant material indicates that all sporangia matured probably at the same time and that most sporangia had fallen off prior to embedding of the fronds. This phenomenon may occur in coastal ferns (VAN KONIJNENBURG-VAN CITTERT et al. 2021b). The other fern and most seed fern species at Einberg are only represented by a few small fragments (except for the very common *Lepidopteris ottonis*) which might point to fairly long-distance transport from drier hinterland areas, contrary to those of Wüstenwelsberg, where remains of, e.g., *Ptilozamites* are common (VAN KONIJNENBURG-VAN CITTERT et al. 2020, 2021b). This might indicate a slight difference in habitats between the two localities, which is not uncommon in marsh or deltaic wetlands, and commonly subjected to water table height or tidal influence, if any.

Cycadophytes and ginkgophytes occur only in small numbers in the Einberg assemblage, and all specimens are only small remains; thus, it is possible that the material was washed in from further away areas. Cuticular remains are commonly thin and poorly preserved, which might be related to longer transport than e.g., the remains of the sphenophyte *Neocalamites lehmannianus* and the fern *Todites crenatus* (see VAN KONIJNENBURG-VAN CITTERT et al. 2021b). These thin cuticles on the other hand may indicate that those plants commonly grew under moister circumstances, especially Bennettitales (see Table 5). The ginkgophytes *Sphenobaiera boeggildiana* and *Czekanowskia nathorstii* have distinctly thicker cuticles than those of the cycadophytes in the assemblage. This might indicate that these species come from slightly drier lowland or hinterland communities and thus grew further away from the place of embedding (see Table 5). Another possibility is that these small trees grew in areas that were more exposed to sun radiation.

Many species of Mesozoic conifers are generally considered to have thrived in relatively drained and dry slopes of upland forests or as hinterland vegetation. 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., *Schizolepidopsis liasoqueuperianus* whose needles cover large slabs. These were probably shed periodically, such as by a deciduous conifer, which commonly occur on riverbanks or near ponds and swamps. Not much is known yet about the environment, in which the Palissyaaceae (here: *Stachyotaxus septentrionalis*) thrived (PATTEMORE et al. 2014).

**Table 5.** Palaeoecological considerations for the taxa found in the Einberg assemblage.**Palaeoecological considerations**

TAXON	PALEOECOLOGICAL CONSIDERATIONS
<b>Lycophyta</b>	
<i>Lepacyclotes</i> sp.	Growing in more open and disturbed habitats (VAN KONIJNENBURG-VAN CITTERT et al. 2020)
<i>Selaginellites coburgensis</i>	Small, delicate plant with prostrate primary axes growing in humid microenvironments near water bodies (VAN KONIJNENBURG-VAN CITTERT et al. 2020)
<b>Sphenophyta</b>	
<i>Equisetites laevis</i>	Growing in moist environments (WEBER 1968)
<i>Neocalamites lehmannianus</i>	Standing in moving water (WEBER 1968)
<b>Pteridophyta</b>	
<i>Clathropteris meniscioides</i>	Herbaceous plants with large fronds that grew in humid environments in the understory (BOMFLEUR & KERP 2010; VAN KONIJNENBURG-VAN CITTERT et al. 2020)
<i>Dictyophyllum exile</i>	Herbaceous plants with large fronds that grew in humid environments in the understory (e.g., BARBACKA et al. 2010; VAN KONIJNENBURG-VAN CITTERT et al. 2018).
<i>Phlebopteris muensteri</i>	Herbaceous plants with large fronds growing under humid conditions in the understory or as pioneer plants of disturbed, short-living, moderately wet areas formed by alluvial deposits (BARBACKA et al. 2010; POTT et al. 2018)
<i>Phlebopteris angustiloba</i>	Herbaceous plants with large fronds living as pioneer plants of disturbed, short-living, moderately wet areas formed by alluvial deposits (BARBACKA et al. 2015)
<i>Spiropteris</i> sp.	No data available
<i>Thamatopteris brauniana</i>	Pioneer plants of disturbed, short-living, moderately wet areas formed by alluvial or flood plain deposits (BARBACKA et al. 2015)
<i>Todites roessertii</i>	All <i>Todites</i> species were probably small arborescent plants with slender stems, growing in a close neighbourhood of water basins near fresh water (lake bank, riverbank) or possibly also in a brackish environment near the sea coast (BARBACKA & BODOR 2008)
<i>Todites (Cladophlebis) scoresbyensis</i>	
<i>Todites crenatus</i>	
<i>Todites</i> sp.	
<b>Pteridospermatophyta</b>	
<i>Antevsia zeilleri</i> / <i>Lepidopteris ottonis</i> / <i>Peltaspermum rotula</i> / <i>Peltaspermum</i> sp.	smaller plants growing in areas of physiological drought and/or drier habitats (VAN KONIJNENBURG-VAN CITTERT et al. 2021b)
<i>Pachypteris</i> cf. <i>rhomboidalis</i>	Growing in a humid and coal-producing swampy environment low in nutrients (BONIS et al. 2010; VAN KONIJNENBURG-VAN CITTERT et al. 2021b)
<i>Pachypteris schwartzii</i>	Growing in a humid and coal-producing swampy environment low in nutrients (BONIS et al. 2010; VAN KONIJNENBURG-VAN CITTERT et al. 2021b)
<i>Ptilozamites nilssonii</i>	Growing in the drier parts of the lowland or coastal ecosystems (VAN KONIJNENBURG-VAN CITTERT et al. 2018)
<i>Scytophyllum</i> sp.	Growing in the drier parts of the lowland ecosystems (VAN KONIJNENBURG-VAN CITTERT et al. 2021b)
cf. <i>Kirchmuellia</i> sp.	No data available
<i>Hydropterangium roesleri</i>	No data available
<i>Hydropterangium</i> sp.	No data available
<i>Carpolithes</i> sp.	No data available
<b>Cycadales</b>	
<i>Becklesia franconica</i>	No data available
<i>Becklesia</i> sp.	No data available
<i>Ctenis latepinnata</i>	Swampy environments
<i>Doratophyllum nathorstii</i>	Swampy environments
<i>Nilssonia polymorpha</i>	Weakly disturbed, moderately wet canopy (BARBACKA et al. 2015)
<i>Nilssonia pterophylloides</i>	lived in relatively undisturbed or weakly disturbed moister environments, in the shadowy understory close to water bodies (BARBACKA et al. 2014, 2015; VAN KONIJNENBURG-VAN CITTERT et al. 2018, 2020)

TAXON	PALEOECOLOGICAL CONSIDERATIONS
<i>Nilssonia</i> sp.	Lived in relatively undisturbed or weakly disturbed moister environments, in the shadowy understorey close to water bodies (BARBACKA et al. 2015; VAN KONIJNENBURG-VAN CITTERT et al. 2018, 2020)
<i>Pseudoctenis florinii</i>	Swampy environments (POTT et al. 2007)
<i>Pseudoctenis cteniforme</i>	Swampy environments (POTT et al. 2007)
<b>Bennettitales</b>	
<i>Anomozamites gracilis</i>	Inhabiting open vegetation communities in nutrient-deficient swampy settings (POTT 2014; POTT et al. 2016), no further details are known about Bennettitales.
<i>Nilssoniopteris jourdyi</i>	
<i>Nilssoniopteris ajorpokensis</i>	
<i>Pterophyllum aequale</i>	
<i>Pterophyllum astartense</i>	
<i>Pterophyllum pinnatifidum</i>	
<i>Pterophyllum kochii</i>	
<i>Pterophyllum zygoticum</i>	
<i>Wielandiella angustifolia</i>	
<i>Welsbergia bursigera</i>	
<b>Ginkgophyta</b>	
<i>Arberophyllum</i> sp.	No data available
<i>Ginkgoites taeniatus</i>	Lived in more humid environments (VAN KONIJNENBURG-VAN CITTERT et al. 2018)
<i>Ginkgoites</i> sp.	Weakly disturbed wetland (BARBACKA et al. 2015)
<i>Sphenobaiera boeggildiana</i>	Lived in less humid lowland environments (VAN KONIJNENBURG-VAN CITTERT et al. 2018)
<b>Czekanowskiales</b>	
<i>Czekanowskia nathorstii</i>	Growing in slightly drier lowland or hinterland communities (VAN KONIJNENBURG-VAN CITTERT et al. 2021b)
<i>Leptostrobus</i> sp.	Growing in slightly drier lowland or hinterland communities (VAN KONIJNENBURG-VAN CITTERT et al. 2021b)
<b>Coniferophyta</b>	
<i>Ourostrobus einbergensis</i>	No data available
<i>Palissya sphenolepis</i>	No data available
<i>Stachyotaxus septentrionalis</i>	Trees of the floodplain swamps (McELWAIN et al. 2007)
<i>Schizolepidopsis liasokeuperianus</i>	deciduous conifer, which was growing on riverbanks or near ponds and swamps
<i>Sphaerostrobus einbergensis</i>	No data available
<b>Incertae sedis</b>	
<i>Desmiophyllum harrisii</i>	Weakly disturbed, wet canopy or close to the fluvial system with presence of currents and stagnant water (BARBACKA et al. 2015; VAN KONIJNENBURG-VAN CITTERT et al. 2019)

*Desmiophyllum harrisii* is found in Bavaria in clay lenses in sandpits (e.g., in Einberg), which were deposited during periods of reduced sediment transport and/or in areas within the fluvial system with less strong currents or even stagnant waters. The thin cuticle of *D. harrisii* with completely unprotected stomata that are even with the epidermis surface can be interpreted as the plant thrived in a moist environment (VAN KONIJNENBURG-VAN CITTERT et al. 2019).

The Rhaetian floras from the four localities around Coburg can thus be reconstructed as a complex and multi-storeyed vegetation with plant groups strongly linked to standing or silently running water bodies

(sphenophytes, some of the lycophytes, mosses and ferns, shrubby bennettitaleans and conifers). Other plant groups have colonized the adjacent moderately moist or swamp-like environments of the understorey (some species of lycophytes, mosses and ferns, bennettites, conifers). The arborescent gymnosperms were mostly linked to moister environments (the ginkgophytes, cycads and bennettitaleans, some deciduous conifers), although some gymnosperms might have originated from drier upland floras. A deltaic setting, similar to the one in the Rhaetian of Scania and Greenland, may also be inferred for the Coburg 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 unfavourable environmental conditions.

#### 4.5. Palaeogeographic implications

From a strictly geographic point of view the sedimentary successions of Heilgersdorf and Wüstenwelsberg crop out close together (less than 3 km), at a distance of about 20 km from the quarries of Einberg and Kipfendorf, that again lay closely together (less than 3 km from each other, see Figs. 1, 12). This gives origin to two geographic groups, each of which is represented by one rich and recently well studied outcrop and a plant assemblage that is rather poorly known. This is nicely reflected in the assemblages of Einberg and Kipfendorf; the latter is represented by much less taxa, but the present taxa reflect well the species list and relative abundance found in Einberg, with the exception of the higher relative abundance of *Phlebopteris muensteri*, but the latter may represent a collection bias.

A similar picture is also visible for the couple Wüstenwelsberg and Heilgersdorf, where Heilgersdorf has only a limited number of taxa in comparison with Wüstenwelsberg. The discrepancies are limited to the putative presence of *Nilssonia polymorpha*, and the presence of *Todites* sp., where the latter could, however, represent a badly preserved specimen of *Todites roessertii* or *Todites (Cladophlebis) scoresbyensis*, both present in the plant fossil assemblage of Wüstenwelsberg. This permits us to restrict our palaeoecological considerations to the two main fossiliferous localities.

During the Rhaetian the area of study was situated about 35°–40° N (STAMPFLI & KOZUR 2006), in the south-eastern part of the Rhaetian Sea bordered to the east and south by the Vindelician–Bohemian High (e.g., FISCHER et al. 2012; BARTH et al. 2013; FRANZ & BARNASCH 2021). The transitional environment was characterised by marine, brackish or terrestrial conditions depending on the vicinity to marine inlets. The Rhaetian Sea served as a significant moisture source for rainfall that resulted in an increased fluvial discharge from the surrounding land areas (TUCKER & BENTON 1982; SUAN et al. 2011). The Vindelician–Bohemian

High gave origin to vast deltaic plains (GAUPP 1991; NIELSEN 2003; FRANZ & WOLFGRAMM 2008; BACHMANN et al. 2010) in which our study area was collocated. The Einberg/Kipfendorf area was probably positioned on the landward side of those vast deltaic plains whereas the Wüstenwelsberg/Heilgersdorf area, more to the south and west, could already be more influenced by the environmental conditions of the Rhaetian Sea.

These small differences in distance from the marine-influenced to more terrestrial environment could have given origin to the differences in composition of the four plant fossil assemblages. The area of Coburg reflects, thus, a vegetation of a deltaic to marsh wetland with an array of different, partly restricted, habitats that change at a small scale since the different localities under study represent differences in vegetation composition.

#### 5. Concluding remarks

The Rhaetian flora of southern Germany has been subject to detailed studies to better reconstruct the complex Rhaetian vegetation and gain a better understanding of the floral turn-over related to the end-Triassic mass extinction and the humid episodes present during the Late Triassic. Extensive collecting in the Rhaetian flora of the sandpit Einberg near Coburg in the 1990s to 2003 yielded a wide range of compression fossils. The plant assemblage is characterised by a diverse array of taxa; the composition of the assemblage differs from that of the nearby Rhaetian quarries of Wüstenwelsberg, Heilgersdorf and Kipfendorf. The composition of these four localities differs considerably from that of the Hettangian floras of Franconia indicating an extensive turn-over at the Triassic–Jurassic boundary, not so much in plant groups but in a change of taxa within the larger plant groups.

The Rhaetian vegetation around Coburg was probably deposited during a (regional?) humid episode present in the Late Triassic.

#### Acknowledgements

We want to thank the owners of the former sandpit Einberg, Father and Son Langguth, for their permission to collect in the sandpit. Thanks are also due to I.I. KUIPERS for photographing the Utrecht specimens. We are grateful to Dr. M. BARBACKA and Dr. G. PACYNA for their constructive

reviews. JHAvKvC is grateful for funding from the Laboratory of Palaeobotany and Palynology of the University of Utrecht, The Netherlands.

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Manuscript received: November 16th, 2023.  
Revised version accepted by the Stuttgart editor: January 8th, 2024.

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